Via Electronic Transmission

February 12, 2016

Wolf Plan Comments
California Department of Fish and Wildlife
wolfplan@wildlife.ca.gov

To the Department:

The following comments regarding the "*Draft* Conservation Plan for Gray Wolves in California" ("Draft Wolf Plan" or "Plan") are submitted on behalf of the following organizations and our combined total of more than 2.9 million California members and supporters:

Animal Legal Defense Fund
California Wolf Center
Cascadia Wildlands
Center for Biological Diversity
Defenders of Wildlife
Endangered Species Coalition
Environmental Protection Information Center (EPIC)
Friends of the Wisconsin Wolf and Wildlife
Howling for Wolves
Humane Society of the United States
Klamath Siskiyou Wildlands Center
Living with Wolves
National Wolfwatcher Coalition
Natural Resources Defense Council
Predator Defense
Project Coyote
Sierra Club California
WildEarth Guardians
Western Watersheds Project

INTRODUCTION

We recognize the extraordinary endeavor by many contributors that has resulted in the Draft Wolf Plan. We thank the California Department of Fish and Wildlife ("Department" or "CDFW") for assembling a Stakeholder Working Group ("SWG"), for the many SWG meetings held by the Department over a several-year process to discuss key issues with SWG members and obtain their input, for the writing of this Draft Wolf Plan for public review, and for providing public comment opportunity via written comments and public meetings. We especially appreciate the opportunity you made available for the public to provide input on the plan by hosting meetings throughout the state, from Yreka to Long Beach.

There are many parts of the Draft Wolf Plan with which we fully agree and support. Other parts are not based on science; we do not support them and believe it would be at best a terrible mistake and at worst a travesty should those provisions be adopted in a final version of the Plan.

We are pleased that the Draft Wolf Plan covers a wide range of topics which are both critical for wolf conservation and essential for public knowledge and understanding as we welcome wolves back to the Golden State. We agree with the Draft Wolf Plan's emphasis on nonlethal coexistence measures to deter or reduce livestock-wolf conflicts, which are more effective over the long term and far less costly than killing wolves or other predators.[1]

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[1] McManus et al., 2014; Imbert et al., 2016.

We also appreciate that the Draft Wolf Plan does not place a cap on the wolf population nor create wolf-and-no-wolf zones.

The Draft Wolf Plan's chapter on disease is extremely informative and will, we hope, bring a halt to the baseless claims that wolves will ravage our state with disease. Nothing could be farther from the truth and this chapter does an excellent, scientific and easy-to-understand job of dispelling such claims and presenting the facts.

However, we are concerned that some key topics have been entirely left out and that nearly all of the published literature provided to the Department a year ago by the environmental conservation caucus of the SWG is neither discussed nor cited to in the Draft Wolf Plan. Additionally, key concepts and documents that were drafted, shared and edited by all interested members of the SWG are missing. Additional significant concerns expressed during the SWG process remain among the environmental conservation caucus groups and among the additional groups who have participated in crafting this comment letter.

In the following pages, we address the topics in this bulleted list:

1. CDFW has a legal duty under the Public Trust Doctrine to manage wildlife on behalf of all citizens of California.

2. The Plan should seek to recover wolves, not simply conserve and manage them.

3. The Plan's tone should reflect that wolf recovery is a conservation opportunity, not a challenge to be overcome.

4. Promoting coexistence between wolves and livestock producers is of critical importance.

5. The Plan should prohibit the killing of wolves for depredations on public lands, require use of nonlethal measures before resorting to any lethal control of wolves, and must codify enforceable lethal take provisions.

6. The Plan should explain the correct use of livestock guarding dogs.

7. Depredation Investigations Protocols should be clearly articulated and included in the Plan.

8. Thresholds for population numbers and duration of time for phase transition are inconsistent, too low and not scientifically justified.

9. The threshold for seeking state-delisting is far too low and not scientifically defensible.

10. Seeking federal down-listing in protection levels and/or state legislative permission to obtain kill authority potentially creates confusing conflict between federal and state law, sets dangerous precedent and is unwarranted.

11. Outreach and education efforts should include compliance-enforcement information.

12. The Plan needs to prioritize recovery, conservation and management actions and prioritize securing funds from state and federal sources for implementation.

13. The Plan must include a comprehensive plan of action for public education aimed at recipients of wolf-location information.

14. The Draft Plan lacks key information referenced in the Draft Plan and/or which was discussed and intended by SWG members to be included in the Plan.

15. Wolves, coyotes and bears should not be killed to conserve wild ungulate populations.

16. Threats to wolves from illegal killing due to mistaken identification as coyotes have not been adequately addressed.

17. The Plan includes no discussion of potential economic benefit to local and regional economies from reestablishment of wolves, wolf-related ecotourism and consumer market for predator-friendly raised livestock products.

18. Comments regarding the Plan's assessment of wolf taxonomy, population size and genetics issues regarding hybridization.

19. Ungulate population and habitat management are important aspects of wolf conservation and recovery efforts.

20. CDFW should actively seek out all opportunities to weigh in on land management actions with federal agencies and participate in land management planning processes.

21. The Plan should describe priorities for protecting, restoring and enhancing habitat that would benefit wolves because the State Wildlife Action Plan identifies the gray wolf as a Focal Species of Conservation Strategies.

22. The Plan should identify habitat conservation and connectivity priorities that will benefit wolf recovery.

23. The Plan's trophic cascades discussion should include published research demonstrating wolves' positive impacts in the Western Great Lakes states.

24. The Plan's discussion on impacts of wolf mortality and wolf-killing on wolf packs should include the findings of a 2014 symposium on this very topic.

25. The Plan's discussion of human social tolerance for wolves should address and cite to additional sources.

26. The Plan's discussion of human perceptions and interactions with wolves should include discussion and citation to new paper establishing that the majority of attacks on humans by carnivores is due to inappropriate conduct by humans.

27. Evidence of historical wolf presence in California as indicated in languages, tales, practices and ceremonies of Native Peoples deserves a heading other than "Anecdotal Observations."

COMMENTS

CDFW Has a Legal Duty Under the Public Trust Doctrine to Manage Wildlife on Behalf of All Citizens of California

The State of California has a legal duty to manage its natural resources, including wildlife, in a manner that benefits all of its citizens. This duty is derived from California's statutes and a long common law tradition requiring each state to protect and preserve the natural resources shared by its citizens called the public trust doctrine.

Common law principles reaching back to antiquity place a duty on the state, as part of its sovereign nature as the representative of the people, to hold common natural resources in trust for its citizens.[2] This trust requires the state to preserve natural resources, and to protect its citizens' interests in those resources, by safeguarding against their exploitation for private gain at the expense of the public good.[3] Historically, the public trust doctrine arose to protect the public's right to access tidelands and navigable waters, specifically for their use in navigation, commerce, and fishing.[4] Over time however, the public trust duty has expanded beyond its traditional boundaries. In California, the public trust duty of the state includes the protection of wildlife resources.[5] California courts have reached this conclusion directly, citing the important shared resource provided by wildlife.[6] California Courts have also reached this conclusion implicitly through the recognition that the prudent allocation of other natural resources–namely State waters–requires the State to consider the effect of its decision making on wildlife.[7] In addition, California Fish & Game Code explicitly states that wildlife resources are held in trust by the State for the benefit of its citizens.[8] As such, it is clear that California law treats wildlife as an important natural resource that provides significant public benefits and therefore necessitates State protection through a public trust.

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[2] *National Audubon Society v. Superior Court of Alpine County*, 33 Cal.3d 419, 433 (1983).

[3] *Berkeley v. Superior Court*, 26 Cal. 3d 515, 521 (Cal. 1980); *See Illinois Central Railroad Company v. Illinois* 146 U.S. 387 (1892).

[4] *See Illinois Central Railroad Company v. Illinois* 146 U.S. 387 (1892) (In the past, the public trust doctrine limited the state's power to alienate submerged land and acted as a safeguard against the exploitation of those resources for private gain precluding public access).

[5] *See Center for Biological Diversity v. FPL Group, Inc.*, 166 Cal. App. 4th 1349 (2008).

[6] *Id.*

[7] *See National Audubon Society*, 33 Cal.3d 419, 433 (1983).

[8] California Fish & Game Code § 711.7(a); California Fish & Game Code § 1600.

Because the State represents its citizens in its sovereign capacity, CDFW must exercise its control over wildlife pursuant to the public trust for the benefit of the people as a whole, not only for the benefit of livestock owners, hunters, or individual landowners. The Draft Wolf Plan fails to consider the intrinsic value of wolves as a part of wildlife under the Public Trust Doctrine, thereby necessitating their protection and not simply their management. The Draft Wolf Plan examines the potential negative impacts of wolves on the environment without considering the potential benefits of wolves on the ecosystem. Under the Public Trust Doctrine California's citizens have the right to the aesthetic enjoyment of wildlife and ecological benefit that strong predator populations provide.

California Fish & Game Code § 1801 declares that it is the policy of the state to encourage the preservation, conservation, and maintenance of wildlife resources under the jurisdiction and influence of the State. This section states that fulfilling the objectives of this policy requires the perpetuation of wildlife for their intrinsic and ecological value as well as their more direct benefits to California residents. In contrast, the Draft Wolf Plan explicitly declines to preserve or conserve the impending wolf population, thereby violating CDFW's obligations under Section 1801.

California's Wolf Plan Should be a Recovery Plan, Not Simply a Conservation and Management Plan

The Plan provides for conserving, information-gathering and managing wolves in a 3-Phased approach but does not provide for active "recovery" efforts, despite the fact that in the midst of the SWG process the gray wolf was listed as endangered under the California Endangered Species Act (CESA). The environmental caucus repeatedly raised this issue during the SWG process, to no avail.

The Draft Wolf Plan asserts that CESA does not provide for preparation of recovery strategies except for one aquatic species. (Part I, p. 10.) However, CESA states as follows:

"[I]t is the policy of the state to conserve, protect, restore, and enhance any endangered species or any threatened species and its habitat . . . ." (F&G Code section 2052) The inclusion of the phrase "restore and enhance" is not mere surplusage but instead informs that it is state policy to take actions for listed species beyond conserving and protecting them. It is an implicit mandate for recovery of the species.

At the public meeting held in Long Beach on January 26, 2016, a Department representative told the public that there isn't enough information available about wolves in California to define "recovery" of wolves. If this is the case, it is all the more troubling that the Draft Wolf Plan provides for consideration of delisting the species when the wolf population reaches 50-75 animals. (Part I, p. 21.) Delisting implies that CESA's protections are no longer needed, *i.e.*, that the species is recovered. By no measure would a wolf population of 50-75 animals be considered biologically recovered and the Department cannot have it both ways. Either there is not yet sufficient scientific information about wolves in California to know what recovery would be and

therefore no population threshold for recovery can yet be set, or there is ample scientific information about wolves in California to propose a threshold number.[9]

All evidence points to the first option. Much of that evidence comes from the Department's own statements which appear repeatedly throughout the Draft Wolf Plan indicating that evidence of historical wolf distribution and abundance is speculative, and that California's landscapes, wild ungulate population numbers and human density are so vastly different from other states which have wolves that information from those states regarding wolves cannot be relied upon to be accurate predictors of how things will play out for and with wolves in California.

Actions and strategies proposed in the Draft Wolf Plan are aimed at conservation of an established wolf population and management of an establishing -- and then established -- wolf population. We recommend the Department revisit all of the action strategies set forth in the Plan and reassess what changes could be made that would aim instead for recovering the species.

The Return of Wolves to California is a Historic Conservation Milestone and Cause for Celebration and the Tone of the Plan Should Reflect This.

In California, as in almost every state of the coterminous United States, the gray wolf was driven to extinction by the early 1900's due to a concerted effort to eradicate the species on behalf of the livestock industry. The fact that the gray wolf is now returning to California is a remarkable event and a testament to the power of the federal Endangered Species Act to bring a species back from the brink when there is political willpower to do so. When wolf OR-7 from Oregon lifted a paw on the Oregon side of the border and set it back down on the California side of the border, he made history and international headlines. Media headlines throughout California laid a welcome mat for this wolf and for the wolves that would follow. After a nearly 90-year absence, the gray wolf is returning to California and the state has an opportunity to right a historic wrong. The tone of the state's wolf Plan should reflect that the return of wolves heralds a historic moment in conservation history in California and an incredible opportunity to restore a species whose presence and natural hunting practices lead to healthier, more biodiverse ecosystems.

Instead, the Draft Wolf Plan's tone regarding wolves is dry and filled with worry and reservations. Its pages contain words like "challenge," "challenging" and "concerned."[10] From all of our organizations' combined reading of the 311-page document, we noted only one sentence which expresses a view from the drafters of the Plan that wolves might be a positive

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[9] We agree with the Department's public statement that there is insufficient scientific information at this time specific to wolves in California to know what would constitute recovery of the species in California – and therefore no delisting threshold should be proposed at this time. We elaborate further on the Department's proposed delisting threshold in a subsequent section of this comment letter.

[10] The Draft Wolf Plan's tone regarding elk contrasts starkly with how wolves are portrayed. In one of the opening paragraphs of Chapter 6, elk are described in glowing terms as one of California's most important visible natural resources, a significant part of the food chain and a highly-valued species for viewing and hunting. Since elk became the majestic animals they are due to their coevolution with equally magnificent predators including their primary predator, the wolf, a few such similar sentences regarding wolves could be sprinkled throughout the Draft Wolf Plan.

addition to California. On page 17 of Part I, the Draft Wolf Plan posits: "Most interactions between wolves and the public will likely consist of memorable observations." This magnificent, charismatic and ecologically-important species, the gray wolf, deserves much greater acknowledgment of its significance, beauty and majesty than a one-sentence homage. The Draft Wolf Plan's perspective needs an attitude adjustment. We believe the vast majority of Californians who are aware that wolves are returning to our State agree with us.

The Plan should notify readers that scientists the world over are calling for the protection and recovery of apex predators like wolves and that the return of wolves is cause for celebration. Apex predators around the globe are in significant decline due to persecution by humans; their decline has serious detrimental effects on the planet's biodiversity, which in turn impacts human health and well-being.[11] The importance of top-level predators in their ability to help moderate impacts from climate change is even a subject of scientific agreement.[12] The Plan should discuss the published literature on this topic and should frame the protection and recovery of wolves in California as a welcome and essential action for wolves and humans alike.

Promoting Coexistence between Wolves and Livestock Producers is of Critical Importance.

Promoting coexistence between livestock producers and wolves is of critical importance for successful wolf recovery in California. We are especially grateful that that the Draft Plan has a strong emphasis on the use of proactive measures for protecting both livestock and wolves.

The use of nonlethal management tools to reduce wolf-livestock conflicts is the key to successful coexistence between ranchers, rural communities and wolves, and to the success of CDFW efforts to manage wolves effectively for all constituents.

In order to have an effective nonlethal management effort, more than a description of the tools is needed. The ranching community will need help to both learn how to use the tools effectively and to properly implement their use on the ground. Success is more than just knowing and having the tools. Success will come through understanding, education, training, local on-the-ground assistance, and local and state level support.

It is impossible to list all the individual actions, education tools and printed materials, as well as CDFW and outside support needed to make a nonlethal program successful. However, the nongovernmental organization ("NGO") community in consultation with the ranching community is working to produce a more complete program that CDFW should use as a foundation for developing a state sanctioned nonlethal management and conflict reduction program. Several NGOs have shared with CDFW the framework for this program, entitled the "California Wolf-Livestock Risk Management Plan Framework." This was shared with the Department in a meeting with Karen Kovacs and Eric Loft in November 2015.

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[11] Estes et al. 2014; Ripple et al. 2014.
[12] Urban and Deegan, 2016. http://mobile.nytimes.com/2016/02/06/opinion/t-shirt-weather-in-the-arctic.html?_r=0; Wilmers and Getz, 2005.

This document is a work in progress at this time. However, the NGO community is continuing to develop this program and make it very specific and useful for CDFW and ranchers. A subset of the signatories of this letter intend to have the program materials compiled by late spring of this year. We ask CDFW to work with interested NGOs to continue to develop and refine this program to help make it a something that will work for livestock producers and the Department, and meaningfully contribute to reduced conflicts between wolves and livestock. Once the program framework is more complete, we recommend the state review, edit, and develop it so it can be formally incorporated into the Wolf Conservation Plan.

The information in this conflict reduction program will need to be available, as well as a process to support livestock producers to implement the program. In the plan will be some suggestions on funding sources, from both government and private entities.

It is critically important that CDFW supports this process, and has plans to implement a thorough and well thought out conflict reduction plan. Everyone wins when wolf livestock conflicts are minimized.

California Must Not Kill Wolves for Depredations on Public Lands, Must Require and Rigorously Use Nonlethal Coexistence Measures Before Resorting to Lethal Control of Wolves, and Must Codify Enforceable Lethal Take Provisions.

If there is chronic depredation and correct use of nonlethal measures, and if that depredation is occurring while the livestock are on public land, it is not appropriate to kill those wolves whether the wolves, themselves, at the time of the Department's consideration of removal, are on public or private land. Those depredations, and the nonlethal measures taken to prevent them, should be costs of doing business on public land. As noted below, this is expressly one of the reasons that grazing fees are set so low. The key question is where the livestock were at the time of depredation.

Lethal control of wolves for chronic depredation of livestock should be a last resort and taken only after all reasonable efforts have been exhausted to correctly employ feasible nonlethal methods, strategies and tools, and only in the case of chronic depredations (*i.e.*, multiple depredations by the same pack or individuals). Further, lethal control of wolves in response to depredations on public lands is not acceptable. Public lands are owned by all members of the public, and public lands and wildlife are held in trust by state and federal agencies for all members of the public.[13] Public lands grazing rates have been set at a rate nearly 20 times lower than the cost to rent private lands for grazing, and American taxpayers subsidize the use of those lands at a cost of more than $120 million annually.[14] One basis for setting fees so low, as noted

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[13] As explained more thoroughly in the last section of this letter, the Public Trust Doctrine requires that the State manage its natural resources, including public lands and wildlife, to the benefit of all of the people of the State.

[14] Glaser, C., Romaniello, C. and K. Moskowitz. 2015. Costs and Consequences: The real price of livestock grazing on America's public lands. Special Report. Center for Biological Diversity. http://www.biologicaldiversity.org/programs/public_lands/grazing/pdfs/CostsAndConsequences_01-2015.pdf

in a 1977 report jointly issued by the Secretary of the Department of the Interior and the Secretary of Agriculture, is to account for the fact that on public lands there may be some losses of livestock due to predators.[15] Public lands are also frequently the very habitat where wolves can find their chief wild ungulate prey species, deer and elk. The killing of wolves and other native predators for livestock losses or for preying on elk or deer on public lands is unacceptable. Any actions or strategies the Department includes in the final Plan or implements on the ground must not include the killing of wolves (whether on private or public land) in response to depredations that occurred on public lands.

We understand from the Draft Wolf Plan that the Department intends to use lethal control of wolves in cases of chronic livestock depredation, after first employing nonlethal methods, tools and strategies, if the Department has lawful authority to do so. There are some very important lessons to be learned for California from wolf management examples set in neighboring Oregon and Washington. The most important of these is the codification of the wolf plan as an administrative rule, and for future provisions concerning lethal take of wolves, that such provisions also are codified.

In many respects, Oregon and Washington have similar wolf plans. However, Oregon has both statutes and agency rules governing wolf conservation, whereas Washington's plan is merely a non-enforceable guidance document.

The California Plan, when finalized, will reflect the agreements collectively arrived at by a diverse group of stakeholders. The Plan itself proclaims that it "covers key issues and potential actions CDFW believes important to the understanding and future conservation of wolves."

California could avoid the mishandling of wolf conservation, and learn from previous mishaps by codifying the Plan's provisions. Though both states have plans similar in substance, Oregon has seen substantial advances in wolf recovery with minimal conflicts, while Washington's wolf management has been plagued by controversy.

Oregon has been the model state for wolf recovery. The Oregon Department of Fish and Wildlife (ODFW) has developed and codified in rule predictable and reliable responses to conflicts and various situation that arise with wolves. While Oregon has permitted killing of wolves in response to livestock depredations, such actions are governed by enforceable rules that leave no party involved guessing as to the response. This predictable arrangement also minimizes the political push and shove that inevitably occurs when there are conflicts or difficult situations.

For example in Oregon, by statute, livestock depredation is only "chronic" if the appropriate authorities confirm at least four qualifying incidents within a consecutive six-month period during Phase I (0-4 breeding pairs).[16] Agency regulations require the livestock producer to prove that he or she removed "unnatural attractants of potential wolf-livestock conflict at least one

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[15]Study of Fees for Grazing Livestock on Federal Lands. A Report from the Secretary of the Interior and the Secretary of Agriculture. October 21, 1977.
[16] ORS § 498.014(a)(A)

week before the incident," and that prior to and on the day of the incident, he or she implemented at least one nonlethal measure deemed appropriate by ODFW.[17]

These rules governing lethal take of wolves in response to depredation has led to minimal political squabbling, an increasing wolf population (the state has not spent tax payer dollars killing wolves since 2011) and, due to the incentives for increasing preventative measures, depredations have decreased.

The Washington Department of Fish and Wildlife (WDFW) also spent considerable time developing a wolf plan, a document that incorporated the views of a 17-member stakeholder group, 65,000 written comments, and 23 scoping meetings. However, WDFW failed to codify the provisions in rule, and following the Washington Fish and Wildlife Commission's adoption of the Plan in 2011, the Commission decided to deny a petition for rulemaking to codify lethal control provisions of the Plan. The Commission reasoned that (1) determining the need to use lethal control to stop repeated depredations is a complicated issue, and (2) limiting the flexibility articulated in the Plan reduces the ability to address each case-specific conflict.

However, this flexibility has caused considerable problems for the state, and the discretion so desired by WDFW has led to massive conflict, state legislative investigations, numerous legislative battles, and public controversy. When problems arise with implementing the wolf plan, inevitably there are going to be forceful voices on all sides lobbying for a certain outcome. When there are dead animals involved, these voices tend to get very loud. Having provisions of the wolf plan codified in rule allow a state agency to stick to the Plan and gives state employees a defensible plan of action. Too much discretion can lead to bad outcomes.

As examples, two nearly identical lethal control mishaps in Washington illustrate the need for legally enforceable lethal take provisions. In 2012, WDFW exterminated the 7-member Wedge Pack, costing taxpayers $76,500. Despite the legislative mandate to "preserve, protect, [and] perpetuate" wolves as "[w]ildlife . . . property of the state,"[18] the commission elected instead to exercise its discretion to benefit the economic interests of a single individual. That individual was grazing his cattle on publicly-owned national forest land, without taking the appropriate nonlethal measures to protect his herd. The killing of the pack led to massive public outcry, administrative rule-making petitions, and a legislative investigation. A spokeswoman for Phil Anderson, then-director of WDFW, said he "never wants to do this again."[19] Clearly, WDFW's decision making would have benefitted greatly from clear standards governing agency response.

One month later, WDFW once again chose to subvert the Plan's standards for lethal take. The Huckleberry Pack situation was eerily similar to the circumstances surrounding the Wedge Pack. The rugged terrain leased by the rancher from a private timber company was ill-suited to sheep grazing. The rancher had experienced no depredations prior to late June 2014. A herder who had been managing the flock quit that summer at some point before the depredations occurred. This

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[17] OAR 635-110-0010(8)(b)(B)

[18] RCW § 77.04.012

[19] Cassandra Profita, *The Cost of Killing Washington's Wedge Wolves*, Oregon Public Broadcasting, Nov. 14, 2012, http://www.opb.org/news/blog/ecotrope/the-cost-of-killing-washingtons-wedge-wolves/

same rancher declined nonlethal conflict avoidance resources offered by WDFW and Washington State University earlier that spring. Eventually some depredations were discovered.

Although it was still unclear whether wolves were responsible and though it was likely the rancher's utter disregard for the plethora of resources offered to him that led to the depredation, WDFW agreed to kill four pups through aerial gunning based on the thought that less mouths to feed would result in less depredation. Unfortunately, the USDA/Wildlife Services sharpshooter hired by WDFW to carry out the kill order mistakenly killed the breeding female. The department embarked on its aerial gunning operation in the early morning hours of the weekend without notice to the public and, when contacted, officials at the department indicated they would not respond to comments or questions until the following week. The Huckleberry Pack fiasco occurred under Phil Anderson, the same director overseeing the department at the time of the Wedge Pack disaster. Again, legislative inquiries were launched, there was massive public outcry, and numerous bills lined up for the upcoming legislative session aimed at targeting the agency's funding.

These are clear examples of how discretion regarding wolf conservation and management can lead to horrible decisions and ongoing conflict with potentially devastating implications for a wildlife agency. The California Fish and Game Commission should learn from the examples set by Oregon and Washington. Codifying plan provisions sends a clear message that the will of the people of the state of California, embodied in the Plan, shall determine the department's course of action for wolves. Enforceable provisions provide the department with a shield to defend itself against various interests when attempting to develop plans of action in difficult situations that will inevitably occur. Establishing enforceable boundaries compels discourse and collaboration between parties holding opposite views with respect to wolves.

During the SWG process, the environmental caucus presented the Department and fellow SWG members with proposed regulatory language for codifying the lethal take provisions of the Wolf Plan. Tables in Appendix G refer to an "Operational framework for lethal control" and provide some descriptions of Options/Actions but nowhere does the Plan propose any specific, legally enforceable regulatory language on the use of lethal control of wolves for chronic depredation of livestock. We have included in Appendix A of this comment letter, the proposed regulatory framework prepared by the environmental caucus.

The Plan Should Explain the Correct Use Of Livestock Guarding Dogs.

Part II of the Draft Plan at p. 122 includes a section entitled Predicting the Potential Effects of Wolves on Livestock and Herding/Guard Dogs in California. We present a different perspective which we think is more accurate.

Livestock Guardian Dogs (LGDs) are most effective as sentinels for sheep and cattle when the livestock are bunched up or within fencing during the day or night. There are many existing breeds currently available in the U.S. that have proved effective at alerting humans about predator presence. Examples are Great Pyrenees, Spanish Mastiffs, Pyrenean Mastiffs, Maremma, Anatolian Shepherd, Akbash and others. It is not important, or desirable, to have

extremely aggressive fighting dogs as LGDs. No dogs should be expected or encouraged to fight wolves. Rather, the LGDs serve to alert humans, on site, about the presence of predators. For this reason it is important to have dogs that have instincts and training to stay with the flock or herd, in sufficiently large numbers on site to act as sentinels and deterrents.

It is thought that wolves moving through an area will avoid livestock surrounded by a sufficient size "pack" of LGDs. The LGDs should be trained to stay with the pack rather than roam across the open terrain. Single LGDs on the open range are not expected to serve a useful purpose. LGDs in combination with other tools serve to discourage wolves from seeing livestock as prey. LGDs should be thought of as deterrents rather than *"protection"* against wolves especially when used in combination with tools such as fencing, fladry, removal of boneyard attractants, animal husbandry techniques and lighting such as Foxlights. LGDs in combination with human presence are an effective tool to avoid negative interactions between wolves and livestock in the appropriate setting.

In summary, the Plan seems to regard LGDs as fighting protectors of livestock. We do not believe this is the appropriate way to view them.

Depredation Investigations Protocols should be Clearly Articulated and Included in the Plan.

As noted in the Draft Wolf Plan, wolf depredations on livestock in western states comprise a small fraction of all livestock losses. However, when a wolf-caused depredation is suspected and reported to officials, the ensuing investigation by agency staff is a matter of concern to all the public. The outcome of the investigation is important to livestock producers, conservationists and the general public and, because the outcome could end up designated as a strike against a particular wolf or wolves it is important to the lives of wolves, as well. Thus it is essential that investigations not be left to the whims of whoever is in charge in a particular circumstance.

It is essential that in the Plan the Department *enumerate* defensible procedures for training of investigators, the investigation itself, and criteria for determinations. The depredation investigation protocol should also set forth requirements and procedures for documentation and types of documentation, and for transparency to the public. It may also be necessary to enumerate procedures for review; if so, any third-party reviewer needs to be qualified and unbiased. The local vet, the local sheriff, the local USDA/Wildlife Services agent are not.

Some people want to see every dead animal blamed on wolves; others, none. What is most important is that California gets it right, that California's Wolf Plan includes a definitive protocol, and that the decisions be defensible and transparent so that conclusions can be verifiable.

<u>Thresholds for Population Numbers and Duration of Time for Phase Transition are Inconsistent, Too Low and Not Scientifically Justified.</u>

As a preliminary matter, we note that the number of breeding pairs ("BP") specified to mark phase shifts in the Draft Wolf Plan's adaptive management strategy are inconsistent throughout the document and thus confusing to the reader. Specifically we note the following inconsistencies which need to be rectified:

<u>Part I of the Draft Wolf Plan, at p. 21 states that:</u>
Phase 1 ends at 4 BP
Phase 2 starts at 5 BP
Phase 3 starts at 9 BP

<u>Part II of the Draft Wolf Plan describes these thresholds in a different fashion, in two different places. Part II at p. 272 states that:</u>
Phase 1 ends at 4 BP
Phase 2 starts at 4 BP
Phase 3 starts at 6 BP

<u>Part II at p. 283 states that:</u>
Phase 2 starts at 4 BP
Phase 3 starts at 8 BP

At a substantive level, the thresholds the Department is proposing for numbers of BPs and transitions between management phases is not scientifically-based, have not been adequately justified by the Department, and are unacceptably low. The transition also is proposed to occur after an insufficient period of time has passed to best ensure reliable predictions of the population trend and that breeding pair numbers won't immediately decline.

The Department asserts throughout the Draft Wolf Plan that California's landscape, prey base, and human population dynamics are different from other states where wolves are reestablishing. So let's wait for the science the Department and other researchers develop regarding wolf reestablishment in California over time, before setting numbers goals for Phase shifts (and for delisting).

Threshold numbers should not be set at this time, but instead the Phase I period will allow for information to be gleaned over time until a shift in strategies is warranted. If a Phase I goal is set now, a precautionary approach should be applied, and the Phase I goal should not be less than <u>12</u> breeding pairs for at least <u>three</u> consecutive years to allow the Department time to gather sufficient data to determine if that's even an adequate threshold. The shift from Phase II to Phase III should be left open until we know more about how wolves do in California as they populate the California landscape.

Additionally, time spans between shifts are of too short of duration to reliably indicate population trends and threats to wolf recovery and conservation. The Department should first conduct years of monitoring and data gathering to analyze trends in wolf and prey populations and distributions, among other factors. While Washington's and Oregon's state wolf plans set a

minimum duration of three consecutive years at a specified population level before shifting into a next phase of management strategies, the California Draft Wolf Plan inexplicably sets a time threshold of but two consecutive years. The Department provides no scientific justification for proposing a two-year period. Nor does it provide any scientific justification for lessening the time threshold from that employed by Oregon and Washington.

One thing we have learned from other states, as they have gone through or are now going through the early stages of wolf recovery, is that truly adopting proactive nonlethal coexistence methods, tools and strategies takes time. It especially takes time for livestock producers to embrace the concept of coexistence and accept it on a deeper, more cultural level, versus temporary willingness to accept the use of coexistence measures only because they aren't allowed to shoot wolves. Moving too quickly through the phases of an adaptive management approach to wolves can undo all the hard work to implement proactive methods and for nonlethal coexistence measures and philosophy to get a solid and accepted footing in the livestock community. It benefits no person and does not benefit wolves to rush through the phases because of political pressure or some preconceived notion that it is the best approach. Wolves and nonlethal coexistence measures must be given a real chance to succeed.

The Threshold of 50-75 Wolves to Consider State-Delisting is Far Too Low and Is Not Scientifically Defensible.

The Draft Wolf Plan's proposal to consider state delisting at 50-75 wolves (Part I, p. 21) is not based on science. Instead it appears that the Department has settled on these numbers by drawing upon the state Wolf Plans for Oregon and Washington and then setting the bar even lower. The population goals and delisting thresholds in Oregon's and Washington's Wolf Plans have been found to be inadequate by most scientists who have evaluated them. There is no scientific rationale to justify thresholds for delisting in California that are even more deficient.

Washington's wolf Plan divides the state into thirds, sets numerical breeding pair goals for each third of the state and a time duration for which those goals must be maintained before delisting can occur.[20] A decision by the Washington Fish and Wildlife Commission to delist wolves must be made "solely on the basis of the biological status of the species being considered, based on the preponderance of scientific data available."[21] And, " [a] species may be delisted only when populations are no longer in danger of failing, declining, are not longer vulnerable . . . or to meet recovery plan goals, and when it no longer meets the definition [of endangered]."[22]
Washington's Plan requires the existence for three consecutive years of 15 successful breeding pairs. Of those 15 successful breeding pairs, there must be 4 successful breeding pairs in each third of the state plus an additional 3 successful breeding pairs anywhere else in the state. Thus Washington's wolf Plan sets delisting numbers and time span durations which are significantly higher than what is proposed in the California Draft Wolf Plan and requires a distribution of the wolf population across the entire state. Washington's Plan also provides an option for gradually

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[20] Wolf Conservation and Management Plan. Wiles, GJ., Allen, H.L. and G.E. Hayes. Washington Department of Fish and Wildlife Wildlife Program. State of Washington. December 2011.
[21] WAC 232-12-297, §4.1
[22] WAC 232-12-297, § 4.2

reducing protections over time from endangered to threatened to state-sensitive to delisted, a safety net mechanism which is not proposed at all in California's Draft Wolf Plan.

Oregon's Wolf Plan includes a phased management approach, divides the state into halves, and sets numerical breeding pair goals for each half of the state and a time duration for which those goals must be maintained.[23] The "conservation population" objective in Phase I for each half of the state is defined as 4 successful breeding pairs for 3 consecutive years; the "management population" objective in Phase II for each half of the state is defined as 7 successful breeding pairs for 3 consecutive years; and in Phase III for each half of the state the Plan's objective is to ensure the wolf population does not decline below Phase II levels. Because Oregon's wolf population was reestablishing via dispersal westward from Idaho into eastern Oregon, when the state's Wolf Plan was drafted, it was presumed that Phase I objectives would be met in the eastern half of the state prior to meeting separate Phase I objectives in the western half of the state (which could occur only once dispersing wolves made their way into western Oregon).

Oregon state law does not allow for delisting of a species in only a portion of the state. Thus Oregon's Wolf Plan provides that consideration of delisting gray wolves can be undertaken when there are 4 successful breeding pairs for 3 consecutive years in the eastern half of the state, and that if state-delisting occurs at that point, the wolf population in the western half of the state will be managed by regulations as though the western half of the state were still fully state-endangered. Only upon reaching 4 successful breeding pairs for 3 consecutive years in the western half of the state may the wolf's west-side population be managed as though no longer state-listed.

The Oregon Endangered Species Act requires that before a species may be delisted, the state Fish and Wildlife Commission must evaluate five enumerated delisting criteria and determine that none of them any longer present a threat to the continued existence of the species. The Act also requires that the Commission's decision be based on documented and verifiable science. If the Commission is relying on data collected by and reports prepared by ODFW, for these to qualify as verifiable requires that the Commission engage an outside scientific peer review panel to evaluate those data and reports.[24]

In November 2015, ignoring the best available science and the law, the Oregon Fish and Wildlife Commission voted to state-delist wolves in Oregon.[25] Three conservation groups have filed a legal challenge and the case is currently pending.[26] At the time of the delisting vote by the Commission, ODFW estimated that Oregon's wolf population stood at 82 confirmed observed individuals (ODFW reported 85 confirmed wolves as of mid-July 2015, but in the following two

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[23] Oregon Wolf Conservation and Management Plan. Oregon Department of Fish and Wildlife. December 2005 and Updated 2010.

[24] ORS §§ 496.171 - 996

[25] ODFW news release: Fish and Wildlife Commission delists wolves statewide in split vote (4-2). http://www.dfw.state.or.us/news/2015/November/110915.asp

[26] Center for Biological Diversity press release: Legal Challenge Filed Over Removal of Protections From Oregon's Gray Wolves. http://www.biologicaldiversity.org/news/press_releases/2015/wolf-12-30-2015.html

months one of these animals was illegally killed and two others were found dead under suspicious circumstances, reducing the known population to 82 animals as of the November delisting decision). Ninety percent of these confirmed wolves reside in eastern Oregon. In western Oregon there exists only one known breeding pair, the Rogue pack (wolf OR-7's pack), and he and his mate have qualified as a successful breeding pair for only two years so far. It will be several more years before western Oregon has 4 successful breeding pairs, and several more years after that before achieving the duration benchmark of at least 4 successful breeding pairs for 3 consecutive years. By the time western Oregon's wolf population may be managed as though no longer state-listed, the overall state wolf population will likely be double the number of wolves which existed at the time the Commission made its delisting vote. Unless, of course, the statewide delisting and transition to Phase II and then Phase III management strategies results in more killing of wolves by agency actions and by legal and illegal killing of wolves by private citizens, which result in an overall state wolf population decline and/or an inability of dispersing wolves to safely make it to the western half of the state.

Thus Oregon's Wolf Plan sets delisting numbers and time span durations which are significantly higher than what is proposed in the California Draft Wolf Plan and requires a distribution of the wolf population across the entire state. It also includes regulatory mechanisms for continuing to protect and manage wolves as though still state-listed in the entire western one-half of the state to which wolves are just starting to make their way. California's Draft Wolf Plan has no similar protective regulatory mechanism to keep dispersing wolves safely protected after an initial population of 50-75 wolves establishes. Since California's wolves are arriving as dispersers from Oregon, an initial population of 50-75 wolves most likely will first reestablish in California's northernmost counties. If delisting were to take place at that population level, the Draft Wolf Plan contains no regulatory mechanism like Oregon's to protect and best ensure the safe establishment of wolves which disperse further south in the identified suitable wolf habitat in the central Sierra Nevada.

The pending Oregon wolf-delisting lawsuit was filed because the Commission violated the Oregon endangered species act when it voted to delist the gray wolf. The Act's delisting criteria were not met, and the Commission did not seek an outside unbiased peer review of ODFW's own status review of gray wolves, as is required by the Act. As part of the public comment period leading up to the Commission's November meeting, 26 highly-credentialed scientists submitted comments on their own. The scientists who wrote comments are among the most experienced professionals in the U.S. and abroad in the field of wolf biology and ecology, mammalogy, population viability analysis and human-carnivore conflict social science. The scientists resoundingly denounced ODFW's status review, population viability analysis and recommendation to delist as being fundamentally flawed, not justified by science, counter to science, ignoring the chief threat to wolf recovery and failing to demonstrate that delisting criteria had been met. A key criticism was that a population of only around 80-85 wolves, inhabiting only 12 ½ percent of identified current suitable wolf habitat in the state could by no measure be considered recovered and in fact this status of population and range distribution demonstrated that wolves are still very much endangered in Oregon. The Commission unfortunately chose to ignore the comment letters sent to them by outside expert scientists, and instead relied on ODFW's status review and some short remarks prepared by four scientists who

were handpicked by ODFW shortly prior to the hearing and whose remarks were not made known nor available to the public until the delisting hearing was already underway.

The comprehensive comments submitted by the 26 outside expert scientists are relevant to California's Draft Plan. The Department proposes to consider removing state protections for the gray wolf throughout California when the species' population reaches a population threshold even lower than that set by Oregon and without consideration for how much of its suitable range gray wolves may or may not be occupying at that point in time. We have compiled these comment letters and provided them to you in Appendix B.

Seeking Federal Down-listing in Protection Levels and/or State Legislative Permission to Obtain Kill Authority Potentially Creates Confusing Conflict Between Federal and State Law, Sets Dangerous Precedent and is Unwarranted

Beginning on page 6, the Draft Wolf Plan details the legal status of wolves in California, highlighting the fact that wolves are currently protected under federal and state law. The Draft Wolf Plan clearly considers this protected status as a burden, as it "affects the state's ability to manage the species with respect to any possible use of lethal take for management." It is highly concerning that the Draft Wolf Plan provides that the CDFW will consider petitioning US Fish and Wildlife Services (USFWS) to down-list wolves to "threatened" in California when two breeding pairs are documented for two successive years, *if wolves in California are still federally listed as endangered*. The Draft Wolf Plan does not state any scientific or legal basis upon which such a request to the USFWS would be made, other than that a down-list would make the task of wolf management in the state of California easier for CDFW, whom, presumably, would seek special status for wolves in the state under ESA Section 4(d), granting the State kill authority.

CDFW offers no explanation for a down-listing request nor does the Draft Wolf Plan state how or why CDFW can show that the wolf population in California is significant and discrete from the Oregon and Washington populations, thus justifying any 4(d) special status. Moreover, considering the Plan's own detailed discussion of how wolves have crossed borders between these states, it is not foreseeable how CDFW could even make such an argument. The Draft Wolf Plan should not be considering taking steps to override federal determination of the protected status of wolves at this point in time merely to allow CDFW more discretionary authority as to how to best manage wolf population. Such an approach degrades the importance of the ESA and listing decisions and creates dangerous precedent for any state to put its individual interests above the best interests of preserving wildlife on a national level.

Even if wolves are federally down-listed and CDFW successfully obtains kill authority, under Section 4(d) of the ESA, if wolves remain listed under CESA, CDFW will still lack kill authority. Thus it is clear that in such a situation, CDFW intends to seek state legislative authority to kill wolves once "Phase 2" population levels are reached, even if the CESA legal status of wolves remains listed as endangered.[27] At numerous points in the Plan, CDFW discusses potentially working through the State's legislative process in order to obtain kill authority for wolves, despite the existence of protections under CESA. Again, it is misguided for

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[27] *See* Plan, Part I, pp. 21-22, Part II, p. 272 and Appendix G.

CDFW to consider circumventing decisions made about listing status under CESA in order to make its job of wolf management easier. If and when the population of wolves in California reaches a level at which CESA listing may no longer be necessary, proper procedures should be implemented under Section 670.1, Title 14 of the California Code of Regulations to change the legal status of wolves in the State. To do otherwise disregards the significance of species being listed under CESA and thus meriting State protection.

Outreach and Education Efforts Should Include Compliance-Enforcement Information

Compliance-Enforcement Information. The "Outreach Goals" section to "Inform the public" is beneficial. Disseminating facts to dispel rumors and myths and correcting falsehoods are important to all aspects of "Interactions" listed in the "KEY ISSUES for WOLF CONSERVATION" section (Part I). Due to the palpable hostility to wolf recovery programs by a misguided or mis-informed minority, along with a number of reported and well-documented illegal killings of wolves in other states, it is incumbent upon the Department to take extra precautionary measures for wolf conservation.[28] Two outreach focus areas that might reduce potential illegal activities should be considered for inclusion in the Plan—compliance and penalties for violation. This may be accomplished by expanding the "Inform the public" section.

Code and Regulation Compliance. Expanding Outreach Goals to cover compliance information related to Fish and Game codes, as well as Federal Endangered Species Act (ESA)[29] and California ESA (CESA)[30] regulations would be prudent and helpful to the public. The Draft Wolf Plan emphasizes that implementation of any of the strategies must always reflect the legal status of wolves, but the public, as well as livestock owners and sport/trophy hunters, may not be fully aware of more restrictive regulations with listed species protection. The Plan should inform all citizens of ESA's and CESA's legal obligations in the event of wolf (or any listed species) interaction. This type of educational outreach information is slightly different from implementation Strategy 7, which seems to focus on the public's knowledge of wolves and attitudes—also important and worthwhile.

Enforcement—Potential Fines and Penalties. When enforcement reaches citation levels, the public should be apprised of the penalties for violations of ESA and CESA. This information should be included in the Plan:

ESA: Violations may be punished with fines up to $50,000 and/or one year imprisonment for crimes involving endangered species, and $25,000 and/or six months

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[28] In a "Mexican Wolf Conservation Assessment" of 2010, the FWS reported that the "illegal shooting of wolves is the single greatest source of wolf mortality in the reintroduced population." US District Court, Arizona, Tucson Division, Wildearth Guardians and NMWA v US Dept of Justice, Case 4:13-cv-00392-DCB, 5/30/13, p4, item 11.

[29] Federal ESA: To "take" means "to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or to attempt to engage in any such conduct." 16 U.S.C. §1532(19).

[30] CESA: Prohibits the take, possession, purchase, or sale of endangered, threatened or candidate species. CA Fish and Game Code defines "take" as to, or attempt to, "hunt, pursue, catch, capture, or kill."

imprisonment for crimes involving threatened species. Misdemeanors or civil penalties are punishable by fines up to $25,000 for crimes involving endangered species and $12,000 for crimes involving threatened species. A maximum of $1,000 can be assessed for unintentional violations. Rewards of up to $2,500 are paid for information leading to convictions.[31]

CESA: Penalties may be imposed for violations of CESA. For taking or possession of a fully protected mammal, the base fine is $5,000; additional fees to the state, county, courts and surcharge can bring the total bail to $20,000.[32] CalTIP is a confidential secret witness program that provides a number of options (toll free number, 24/7; a website; cell phone texting; or smartphone APP) for the public to report poachers, polluters, or any wildlife violation. If the information leads to an arrest, the caller becomes eligible for a reward. CalTIP rewards are funded by donations; no state funds are used.

By having legal obligations described more thoroughly as well as some semblance of the range of penalties and bail upon conviction, the implementation of the Plan, and especially "Strategy 2—Assess and address threats to wolf conservation," are more likely to be successful. Strategy 2, c, "Minimize wolf mortality from accidental killing, and 2, d, "Minimize disturbance at active wolf den and rendezvous sites," are examples of strategies that would benefit from expanded or more in-depth consequential information. Such material does not have to be either threatening or oppressive, but rather educational, which may be helpful to the public. It may also serve as an indicator of how serious the ESA/CESA listings are and how invested CDFW is in wolf conservation.

"Law enforcement" is mildly referenced throughout the Draft Wolf Plan in different roles (communication, presence to reduce poaching, enforcement of game laws, etc.). However, in order for the Plan to reach its goals, the law enforcement component should and will play a much greater role than may be implied. In fact, it may be the linchpin with regard to successful wolf conservation outcomes in light of the aforementioned wolf hostility. In addition to the need to increase wildlife officer staff for law enforcement, the Plan should confirm both the authority and **obligation** of wildlife officers to cite offenders.

The Draft Wolf Plan Should Prioritize Recovery, Conservation and Management Actions and Prioritize Securing Funds from State and Federal Sources for Implementation.

The Draft Wolf Plan has many laudable goals and strategies for conserving and managing wolves here in California. However, the Draft Wolf Plan does not detail specific priorities. It's imperative that the Department clearly delineate priority actions for implementing the actions detailed in the Draft Wolf Plan.

Priority number one: Secure funding specifically to create and implement a Department wolf program with adequate staffing levels, appropriate training on livestock depredation investigations, and resources to run such program. This program should be equipped to provide

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[31] http://www.endangeredspecieshandbook.org/legislation_endangered.php
[32] Uniform Bail and Penalty Schedules, Judicial Council of California, July 2011, page 121.

information and on-going support on the use of proactive tools and strategies available to ranchers for reducing conflicts between livestock and wolves. This should include having nonlethal tools available to lend to ranchers in need on a temporary basis.

Once funding is secured for a Department wolf program and personnel has been hired and trained for such program, the next highest priority for the Department is to ensure that at least one member of each known wolf pack should be captured and outfitted with a GPS-enabled collar so that location data can be used to inform outreach efforts, especially within the ranching community. The Department should expedite establishing Depredation Prevention Agreements with interested and willing livestock producers, which will include nondisclosure agreements to ensure that wolf location data is not inappropriately shared. (See subsequent section for additional details on this subject.)

The Department should work with the Department of Finance and other necessary entities to establish a fund to provide compensation for livestock depredations; this will go a long way to promoting goodwill among the livestock community critical to ensuring long-term wolf recovery.

The Plan Must Include a Comprehensive Plan of Action for Public Education Aimed at Recipients of Wolf-Location Information.

In addition to including a copy of the written nondisclosure agreement that wolf-location information recipients will be required to sign and adhere to, we note a specific, essential need for educational efforts by the Department to recipients of radio-collar information. Recipients must receive educational information about wolf behavior, biology and ecology, appropriate conduct around wolves and legal requirements in advance of their receipt of such sensitive information, and on an ongoing basis.

At the January 21, 2016 public meeting the Department held in Yreka, nearly 300 individuals attended, 37 of which provided oral testimony at the meeting. Much of the testimony from local residents expressed anger, resentment and fear – a desire to not have wolves in California, a disregard for state and federal law protecting wolves, and utter misinformation on what degree of threat wolves could pose to livestock or to human safety. At the same time, several spoke of the need to get radio-collars on wolves and to provide wolf location information to area ranchers.

We agree radio-collar information is important, to help the Department monitor wolves, detect if wolves have been illegally killed, and to help ranchers know when to implement or ramp up use of nonlethal conflict deterrents. Stakeholders in the planning process agreed this was important -- and conservation group stakeholders expressed strongly the need for that disclosure to remain confidential to recipients, to simultaneously be as protective of wolves as possible. Yet the wolf plan refers only vaguely to a confidentiality requirement and does nothing to address how to best ensure those in receipt of the information will not themselves become a source of harm to wolves.

Conservation groups and the public aren't likely to support giving wolf location information to people who hate federal and state government, hate and fear wolves based on inaccurate information and cultural-based beliefs, and are unwilling to follow the law. And the Department has a responsibility to take all steps necessary to ensure that those in receipt of wolf-location information will adhere to the confidentiality requirement, follow the law and have as accurate as possible an understanding regarding wolf biology, behavior and ecology. For the Department to have public support for limited disclosure of wolf location information, it must develop a comprehensive plan of action, described in the Plan, for public education in areas where wolves are likely to return and specifically aimed at those individuals who will be recipients of wolf-location information.

The Draft Plan Lacks Key Information Referenced in the Draft Plan and/or which was Discussed and Intended by SWG Members to be Included in the Plan.

While the Draft Plan has a wide variety of critical provisions that will guide the state's conservation and management of wolves into the future, it also lacks some key information that was discussed and intended by SWG members to be included in the Plan. This includes the following:

- As indicated in a separate section of our comments, Depredation Investigations Protocols should be clearly articulated and included in the Wolf Plan.
- Both Wolf-Livestock and Wolf-Ungulate Conflict Management Strategies, as referenced in Table G.2c on Phase 2 Conservation Actions/Options in Appendix G are missing from the Draft Wolf Plan and should be written up and included. (Chapter 6 of the Draft Wolf Plan also states in its opening paragraph that the chapter will conclude with a discussion of the tools and strategies available for managing wolf-ungulate interactions in California, but no such discussion is included.)
- The Livestock Depredation Protocol that is available on the Department's wolf web page should also be contained within the Plan, with the understanding that it may evolve over time as we learn more about how best to address wolf-livestock conflicts in California.
- List of "Priority Counties" for payment for presence and any other components relevant to these counties should be defined. We suggest Siskiyou, Modoc, Shasta and Lassen be included as Priority Counties at minimum.
- More information is needed on the charge and structure of the Local/County Advisory Groups and the Plan should specify that a Statewide Advisory Group will also be established, with its charge and structure also described within the Plan.
- A specific budget for the Department's Wolf Program, including start-up and annual operating costs associated with the program.
- A collaring plan and confidentiality agreement for wolf location data that will be shared by the Department with any outside interests.
- An outline for how the Department will gather and use information in an adaptive management framework to undertake any future updates to the Wolf Conservation Plan and the required 5-year status review under CESA.

<u>Wolves, Coyotes and Bears Should Not Be Killed To Conserve Wild Ungulate Populations</u>

Proposed triggers for strategies for addressing any future impacts wolves – or coyotes or bears – might have on CA's wild ungulate population allude to unspecified authority, are counter to science and do not comport with modern understandings of the ecological importance of predators. CDFW offers no peer reviewed science to buttress this approach. If anything recent research has demonstrated that killing coyotes and other predators to boost ungulate populations is questionable at best and may even be counterproductive. Therefore these unsupported and scientifically questionable triggers should be removed from the Plan.

In late 2014, the Department sent an internal draft version of the Plan for peer review by outside scientists. Reviewer Dr. Cristina Eisenberg expressly stated in her comments that while wolf recolonization and recovery in California will undeniably have impacts on ungulates, "the strengths of these impacts are impossible to fully predict" and she does "not expect that wolf predation on elk will be as much of an issue as predicted in the Plan." Dr. Eisenberg continued, "Relocation of wolves subsequent to a reduction of allocated big game tags is not based on science, it is based on natural resources management economics. It is inappropriate to apply such an economic approach to a wolf population that is in the early stages of becoming established. It risks scapegoating wolves further, and this could have negative impacts on human perception of wolves." Finally, she noted that, "[l]ethal control of wolves to promote elk and other prey species population growth . . . is unacceptable. Other strategies need to be implemented, such as ungulate or wolf translocation. This opens the door for lethal take without sideboards and scapegoats the wolf in a system in which predator-prey relationships will be highly complex ecologically."[33]

Recent decline in elk in Montana's Bitterroot Valley was at first attributed to wolf predation. What the Montana Department of Fish, Wildlife and Parks (MFWP) discovered, however, is that the primary predator was mountain lion, not wolves. But the action that precipitated the original decline was too generous an issuance of hunting cow tags and thus human hunting was a major factor in the original decline.[34]

A report issued by MFWP this year surveying elk in Management Unit 313 demonstrates the effect that hunting is having on elk near Yellowstone National Park.[35] The final chart in the report (Fig. 3) shows six-point bulls declining in numbers, which represents the impact of hunting outside of the Park. Decline in bulls is likely affecting the overall productivity of the elk herds. While elk herds within Yellowstone have declined over the years since the reintroduction of wolves (Fig. 2), most observers think the 19,000 elk that existed in the park prior to wolves was far too many and that the elk numbers there today are far more sustainable.

The Draft Wolf Plan acknowledges elsewhere how a decline in ungulate populations sometimes had a beneficial effect on vegetation, yet the Department and the Plan clearly consider a decline

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[33] Eisenberg, Dr. Cristina. California Wolf Plan Peer Review comment letter to CDFW, January 2015.
[34] Perry Backus. Solving the Bitterroot Elk Mystery. How biologists and local volunteers finally figured out what was reducing the popular Ravalli County elk population. Montana Outdoors, Nov-Dec 2014. http://fwp.mt.gov/mtoutdoors/HTML/articles/2014/BitterrootElkResults.htm#.VruPem_2aM9
[35] Montana Fish, Wildlife and Parks. 2016. Winter 2016 Hunting District 313 Elk Survey (Gardiner to 6-mile Creek). Prepared by MFWP biologist Karen Loveless.

in elk to be a "negative", as expressed in Chapter 6 and in the coyote/bear/wolf management strategies enumerated in that chapter (and in the tables in Appendix G) that would be triggered by specified declines in ungulate population numbers and/or ratios. In reality, a decline in elk herbivory pressure could be beneficial to many other species--assuming that elk numbers are high enough to be having an impact--which one can't tell from the Department's own documentation. Studies cited elsewhere in the Plan documented higher song bird nesting populations where elk herbivory on willows declined. More willows can also result in greater beaver colonization -- which in California would be a real advantage as beaver impoundments would aid in keeping water flows during drought periods. It would also help endangered species of salmon and trout. The Plan does acknowledge that wolves might affect coyote numbers and cause other changes such as an increase in jackrabbit or higher fox survival. Yet the Plan acts as though these changes are not important if elk numbers decline.

Regarding the Plan's reliance on specific cow/calf ratios as triggers, it is essential for the Plan to note that declines in elk cow/calf ratios usually self-correct to some degree if given time. In both the Bitterroot Valley example mentioned above, as well as in Yellowstone National Park, elk numbers declined due to predators including wolves as well as human hunting (hunting outside of Yellowstone), but after a period of time -- five to seven years -- their numbers began to recover. So the time frame is important. What may seem like a one-way decline may be more of an oscillation. The resulting elk herd is healthier with a higher proportion of reproductive age cows.

The Plan at pp. 104-105 of Chapter 6 contains some discussion of how weather/climate would affect elk and deer. The discussion is focused largely on how climate change could affect the abundance, distribution and structure of natural plant communities on which deer and elk depend for browse, and how that might affect deer and elk. However, the Plan fails to discuss the impacts of drought. This is a remarkable omission given the state of extreme drought that currently exists across much of the western United States and quite notably in California. Productivity declines significantly in drought. In Yellowstone for instance, in 1989, severe drought caused 1/3 of the elk herd to die off due to starvation (this was before wolves were present). Drought will also make elk and deer vulnerable to wolf predation, and though mortality would then in a sense be compensatory, we see a dangerous trend in this Plan which would instead blame wolves for the decline.

The Plan's proposed action strategies for how to address an elk decline are extremely troubling and based on a pro-hunting philosophy, as opposed to being approached as a science issue. The first step should be to eliminate all human mortality, i.e. hunting pressure, and to let elk populations find their own balance. Wolves should not be killed merely to increase elk for hunters to kill. Killing wolves to increase elk for human hunters is a strategy based in philosophy, not a science-based ecosystem approach.

Threats To Wolves From Illegal Killing Due To Mistaken Identification As Coyotes Have Not Been Addressed.

In her peer review comment letter regarding the Draft Plan, Dr. Cristina Eisenberg emphasized the conservation threat to wolves of killings due to mistaken identity as coyotes, and urged that "coyote hunting be eliminated in California, in order to enable wolf conservation to proceed."[36]

Dr. Eisenberg's call to action is well justified and the Draft Plan's failure to discuss this conservation threat to wolves is incomprehensible. Chapter 9 addresses Wolf Conservation and contains a discussion of threats to wolves including human-caused mortality, yet lacks any discussion whatsoever of human-caused mortality of wolves due to mistaken identification nor proposes any strategies to address this conservation threat. The environmental caucus of the SWG submitted to the Department extensive comments, proposed text and literature citations on this topic more than a year ago, yet none appear in the Draft Plan. The sole statement in the Draft Wolf Plan regarding such killings appears on p. 137, footnote 44, as a token mention of the radio-collared wolf from Wyoming which dispersed to Arizona, was named 'Echo" by schoolchildren in a nationwide naming contest, but was then killed two months later by a hunter claiming to have mistaken the animal for a coyote.

The fact is, state and federal officials have reported wolves being shot mistakenly as coyotes in all parts of the country where wolves are returning. Environmental caucus comments sent to the Department more than a year ago included the following:

"It is essential for the safety of this state- and -federally-protected species that members of the public in California know how to distinguish a wolf from other canids. In many states where wolves are starting to return, lone dispersing wolves have been shot by hunters or landowners who stated they thought the animal they were shooting was a coyote. Between 1980-2014, 56 instances of wolves dispersing to areas outside of core recovery areas have been documented; 36 of the animals were shot and killed, another 12 found dead or killed in another manner and the fate of 8 are unknown (Weiss et al. 2014).[37] Of the 36 that were shot and killed, in 11 instances the shooter expressly indicated thinking it was a coyote (Weiss et al. 2014). In late December 2014, a radio-collared wolf that had dispersed nearly 500 miles from Wyoming into Utah was killed by a hunter who said he thought it was a coyote.[38] In California, as in all states, it is imperative that hunters be certain of the identity of their target before pulling the trigger; in the case of wolves, it is illegal to kill an endangered species and there are penalties, including the potential of jail-time and fines, for violating the law."

In the 15 months since the release of the report by Weiss et al. until now, at least an additional four instances have been reported of wolves shot by hunters claiming they thought the animals were coyotes. These include the killing of the wolf known as Echo, who weighed 110 pounds; a wolf killed in Oregon in the fall of 2015, and two wolves killed in Iowa in December 2015,

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[36] *Id.*
[37] Weiss et al. 2014.
[38] http://www.sltrib.com/news/1999741-155/utah-hunter-kills-wolf-near-beaver

which weighed, respectively, 103 and 98 pounds.[39] In addition, in North Carolina, at least five red wolves were killed by hunters in 2012 engaged in night-spotlight-hunting of coyotes. The instances we describe here are only the ones that agencies know about. It is highly likely far more dispersing wolves have been mistaken for coyotes and killed than have been reported or discovered.[40]

The Department is on notice of this threat to wolves not just because conservation group SWG members included this topic in our comment letter to the Department a year ago. In early 2013, conservation groups called the Department's attention to a California coyote-killing contest conservation groups had just learned of, which takes place annually since its inception in 2006. That contest, sponsored by Adin Supply and the Pitt River Rod and Gun Club, based in the town of Adin in Modoc County, is held on public and private lands in the northern California counties. This region is the very pathway for dispersing wolves from Oregon to enter into and reestablish in California. Starting in 2013 and continuing over the next several years, conservation groups and the public urged state and federal officials to halt this contest and others like it in California, because contest-hunts are scientifically indefensible, unethical and inhumane to coyotes, and because they create significant risk of harm or death to legally-protected wolves that may be traversing the landscape where the contests are taking place. In the two years that the administrative petition filed by conservation groups in 2012 to list the gray wolf under CESA was pending, the Department admitted it was concerned for the safety of wolves during these contests and had sent law enforcement to the area to advise participants how to distinguish between wolves and coyotes and that it was illegal to kill a federally-protected species.[41] Wolves subsequently in 2014 were listed under CESA by the California Fish and Game Commission, who also in 2015 banned giving out inducements or prizes in contest hunts of nongame mammals and furbearers, however the Adin coyote contest hunt continues to take place each year in the direct path of any wolves migrating into California from Oregon.

In light of the extensive amount of documented death-by-mistaken-identification of wolves which has occurred in states across the nation, and in light of strong concerns expressed by conservation groups and members of the general public to the Department and to the Commission since at least 2013 that coyote-killing contests in northern California are not only counter to science but a conservation threat to wolves entering the state, it is stunning that the Draft Wolf Plan includes no discussion of this threat to wolf recovery and conservation nor any discussion of strategic actions the Department will take to halt or lessen this threat. It is

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[39] Despite being 2-3 times larger and weighing 3-4 times more than the average coyote, wolves are being shot by hunters claiming mistaken identification.

[40] Illegal killing of wolves occurs for a number of reasons. One of the chief reasons is accidental killings, either through mistaken identity or when caught in traps set for other species. 76 Fed. Reg. at 26117. It is likely that most illegal killings intentional or not, are never reported to government authorities. *Id*. Because the killings generally occur in remote locations and the evidence is easily concealed, there are no reliable estimates of illegal killings of gray wolves. *Id*.

[41] In its notice of findings for the gray wolf CESA listing, the Commission confirmed that "dispersing wolves and small wolf populations are inherently at risk due to . . . being killed by hunters that mistake them for coyotes" and "[Department staff] have been fearful that . . . unknown wolves that could be in California would be mistaken for a coyote and shot or harmed." California Fish and Game Commission, Notice of Finding and Notice of Proposed Rulemaking Gray Wolf (2014).

imperative this omission is remedied, complete with a strategic plan of action described by the Department.

Comments Regarding The Plan's Assessment of Wolf Taxonomy, Population Size And Genetics Issues Regarding Hybridization.

Taxonomy.
Part II of the Draft Plan, at p. 16 discusses wolf taxonomy. It is good to see that CDFW considers *Canis lupus* at the full species level with respect to the Wolf Plan, as we feel that this view is appropriate. The Plan is also correct that the proliferation of subspecies was a historical error and the only potential subspecies relevant to California is the Mexican gray wolf, *C.l.baileyi*. All of the wolves that may migrate into California, from the north, are of the same species *Canis lupus*.

However, we would like to comment on the inclusion in the Plan of the reference to Chambers *et al*., 2012. The Plan is correct to point out that scientific peer reviewers have disputed the approach and conclusions of Chambers *et al*. 2012. The lead author on the paper was on the USFWS staff which may have led to bias. In addition, this paper was not subject to independent peer review as is expected for legitimate scientific research. Nor is it at all clear why the conclusions of Chambers *et al*. 2012 would be relevant to this Plan even if its conclusions were thought to be valid by the research community.

We feel that the Chambers *et al*. 2012 paper should not be cited in the text or listed in Table 1.1. Disputed findings that are suspected of being biased and appeared in a non-peer reviewed journal really have no place in the CDFW wolf plan. We believe the inclusion of this material only unnecessarily confuses the reader.

Population Size.
Part II of the Draft Plan, at p. 148 discusses population size. We agree that "California's wolf population will likely be connected through migration with the larger wolf metapopulation in the Pacific Northwest, which will provide important infusions of genetic variation toward population health" and that genetic bottlenecks are unlikely. However, for this to remain true it is important that Washington, Idaho and Oregon maintain a healthy and sufficient size wolf population. California should work with those states to insure healthy populations in all.

Hybridization.
Part II of the Draft Plan, at p. 150, discusses concerns regarding wolf hybridization with other canid species. We disagree with Coppinger *et al*. 2010 that wolves' genomes should be considered as "fixed entities". Nothing in nature is fixed and that is particularly true about the genomes of living animal. Variation at the level of DNA occurs continually, albeit slowly, through mutation, genetic drift and hybridization. Although hybridization with domestic dogs should not be encouraged it is nothing to excessively fear. Wolves and dogs have continued to interbreed for the past 40,000 years ever since the first wolves began to spend time near Pleistocene humans on the hunting trail. And they will in the future. In fact, one of the reasons that it is proving so difficult to establish the timeline of dog domestication is that wolves and

dogs have continued to interbreed over the millennia. As noted in the example of Anderson *et al*. 2009 dogs introduced the black coat color to the wild wolf population. We do not see hybridization as a significant threat to wolves.

The Plan Should Discuss Potential Economic Benefit to Local and Regional Economies from Wolf-Related Ecotourism and Consumer Market for Predator-Friendly Livestock Products.

The Plan does not – but should -- discuss the potential economic benefit that could accrue to entire communities or regions due to wolf-related ecotourism and those visitors' expenditures in local economies. Conservation groups submitted published literature to the Department on this topic previously, and it should be included. The Plan also should discuss the potential financial benefit to individual ranchers who adopt predator-friendly, nonlethal coexistence measures and are able to market their product as such. Many West Coast residents would be willing to pay a premium price for beef or lamb produced without wolves being killed. A complete list of all published literature we submitted to the Department one year ago can be found in Appendix C. Articles pertaining to economic benefit from recolonizing wolves are contained in that list.

Ungulate Population and Habitat Management are Important for Wolf Conservation and Recovery Efforts.

It is important that elk populations are adequately assessed before hunting tags are increased, as was proposed in the recently rescinded Elk Environmental Assessment. The Department states that most elk populations are increasing, however, Rocky Mountain elk populations may be static and systematic surveys for elk have not been implemented in northern California.

We expect CDFW to conduct comprehensive Elk and Deer Management Plans that incorporate the needs of wolves and their effects on native elk populations. Because wolves may rely on healthy populations of ungulates it is imperative that the management plans incorporate clear goals and strategies from the California Wolf Conservation Plan, specifically relating to habitat connectivity and restoration, as well accounting for increasing wolf populations when determining ungulate population thresholds that would initiate management strategies of either species.

Throughout Chapter 6, Wolf Interactions with Ungulates, the Department stresses the difficulty of determining cause-specific mortality of ungulate populations. The cause of specific mortality for elk has not been studied in California and the overall impact from black bear, coyote and mountain lion predation on elk in California is not fully known. Deer mortality is influenced by a long list of factors that are constantly changing. The wolf plan must rely on fact rather than assumptions, when contemplating the initiation of management considerations, particularly in relation to increasing hunting of other predators such as bear and coyote.

The Department should consider the negative effects of livestock grazing on public and private lands. Cattle compete with native ungulates for habitat and forage. Based on six years of field

monitoring by the Project to Reform Public Land Grazing in Northern California, EPIC volunteers have found the impacts of poorly managed grazing on water quality and prime ungulate habitat has resulted in degradation, fragmentation, and overgrazing of native vegetation, such western bunchgrasses, which wild ungulate populations depend on.[42]

The Department Should Actively Seek Out All Opportunities to Weigh in on Land Management Actions with Federal Agencies and Participate in Land Management Planning Processes.

As outlined in Chapter 8, Coordination with Other States and Federal Agencies, we agree that working with federal land management agencies is extremely important. A strong recommendation from the Department to the U.S. Forest Service and BLM to properly manage current grazing allotments on public lands would go a long way. Current management needs to change in order to improve habitat quality, accommodate for ungulate populations and to minimize overutilization. We strongly urge the Department to participate in forthcoming national forest and BLM plan revisions in the interest of all native California wildlife, including the gray wolf.

We are encouraged to see that strategies defined in Part I of the plan include increased collaboration. We urge the Department to embrace their responsibilities in wildlife management by actively participating and collaborating with the US Forest Service, BLM, US Fish and Wildlife Service and NOAA Fisheries, as all of these agencies, including the Department, are directed to work together. Working together can include participation in upcoming national forest land management plan revisions, as is suggested on page 138, and on a project level through the National Environmental Policy Act planning processes, collaborative and partnership endeavors, such as the Western Klamath Restoration Partnership, Trinity County Collaborative and Firescape Mendocino. These large-landscape collaboratives, which include the US Forest Service as a key partner, cover a vast expanse of Northern California that includes important wolf habitat. These working partnerships are addressing issues such as wildfire, cultural and prescribed burning, wildlife habitat needs and planning treatments that will greatly affect long-term management of our public lands and habitat for both wolves and their native prey species. Please also work with the Department's Landscape Conservation Cooperative Network.

The Plan Should Describe Priorities for Protecting, Restoring and Enhancing Habitat That Would Benefit Wolves Because the State Wildlife Action Plan Identifies the Gray Wolf as a Focal Species of Conservation Strategies

We request that CDFW develop priorities to protect, restore, and enhance habitat that would benefit gray wolves. We would like to remind CDFW of the goals, targets and strategies that are outlined in the State Wildlife Management Plan (SWAP). Table 5.2-3 in the SWAP, identifies the gray wolf as a Focal Species of Conservation Strategies Developed for Conservation Targets

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[42] Pace, F. 2015. Project to Reform Public Land Grazing in Northern California. http://www.wildcalifornia.org/wp-content/uploads/2016/01/Annual-Report_2015_final-final.pdf

in the Cascades and Modoc Plateau Province, dwelling within the North Coastal mixed evergreen and montane forests. The table below contains conservation strategy categories for the two bioregions that are associated with the gray wolf in the SWAP.

Gray wolf conservation units and targets

North Coastal Mixed Evergreen and Montane Forests	Western Upland Grasslands
Data Collection and Analysis	Data Collection and Analysis
Management Planning	Direct Management
Land Acquisition/ easement/ lease	Economic Incentives
Law and Policy	Land Acquisition/ Easement/ Lease
Outreach and Education	Land Use Planning
	Law and Policy

The Plan Should Identify Habitat Conservation and Connectivity Priorities that will Benefit Wolf Recovery

The Draft Wolf Plan acknowledges the significance to wolves of habitat conservation and connectivity with this statement: "First and foremost, large landscapes of suitable and non-fragmented habitat capable of supporting wolves and their primary prey are needed. This priority is not dissimilar from the habitat needs of hundreds of California wildlife species and is a basic tenet in any species conservation plan." Part I page 13. We agree.

All of the potential concerns for wolf conservation detailed in the Habitat Alteration section of Chapter 9 point to a dire need for habitat connectivity, however the Connectivity section on page 158 of this chapter is extremely limited and is verbatim of what was in the initial Draft plan presented to the SWG a year ago. None of Environmental Caucus comments were included in this version of Draft Wolf Plan which is now out for public comment.

We are perplexed as to why the Department does not recognize its own work done on connectivity. The maps below are from the 2010 Essential Habitat Connectivity Project: A Strategy for Conserving a Connected California. For ease this document can be found online at http://www.dfg.ca.gov/habcon/connectivity/

We ask that the Department begin developing tangible tasks and deadlines to begin establishing these essential habitat corridors, and incorporate the maps below into the wolf Plan.

California Essential Habitat Connectivity Project   43
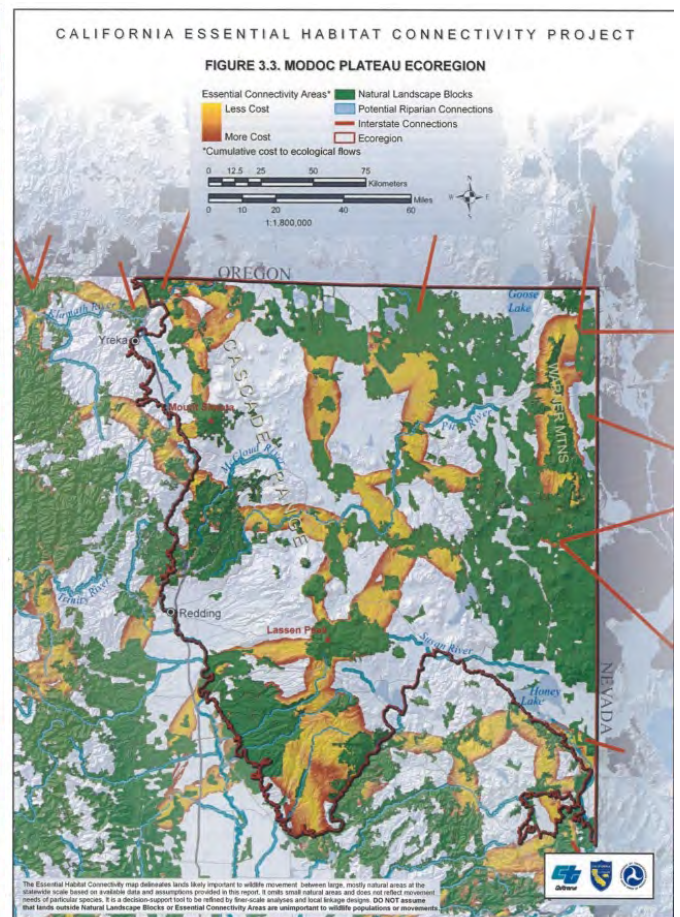
California Essential Habitat Connectivity Project   46

The Plan's Trophic Cascades Discussion Should Include Published Research Demonstrating Wolves' Positive Impacts in the Western Great Lakes States.

Chapter 1 of the Draft Wolf Plan introduces the reader to essential information about wolf biology and ecology. In general, it's well-written but the section on trophic cascades seems to do its best to downplay potential effects generated by reestablishment of wolves. In discussing what effects wolves may or may not have on their wild ungulate prey and other parts of the ecosystem, the Draft chapter gives limited examples. It should give readers a broader, more informed perspective on this topic.

For instance, research results are discussed from a study conducted in Banff National Park showing an elk population decline after wolf recolonization. A more inclusive discussion would also contain information from the Wyoming, Montana and Idaho state agencies on elk populations, which are at or above management unit objectives nearly everywhere, and hunter harvest success rates which have for several years been at all-time highs despite the presence of

approximately 1600 wolves across those states. A year ago, conservation group SWG members submitted information, text and citations to the Department on this very topic. None were included in the Draft Wolf Plan but the final version of the Plan should include this information. Citations for this literature are again provided to the Department in the comprehensive list found in Appendix C.

The Draft Wolf Plan's discussion of trophic cascades cautions against assuming that any wolf-related effects on vegetation in Yellowstone National Park could occur outside of parks. A more expansive discussion would include the research from Wisconsin examining vegetative understory in non-wolf-occupied, low-wolf-occupied and high-wolf-occupied areas. Several studies showed positive vegetative responses, especially when comparing low-wolf to high-wolf occupied areas and when sufficient time elapsed, but indicated that research design was important and design factors may have negatively impacted research results. Research results suggested that trophic cascade effects exist, are subtle, require about a decade before they are apparent, do not resemble deer-free conditions, and might become more apparent over time.[43]

This chapter should also include a discussion of the research from Wisconsin in which researchers concluded that as distribution of Chronic Wasting Disease in deer and wolf range overlap in the future, wolf predation may suppress disease emergence or limit prevalence.[44]

Chapter 1 is where most readers will obtain essential information about wolves. It is imperative that information provided regarding trophic cascades effects of wolves be more broadly representative of the current science and facts on the ground.

The Plan's Discussion on Impacts of Wolf Mortality and Wolf-Killing on Wolf Packs Should Include the Findings of a 2014 Symposium on This Very Topic.

Part II, Chapter 9, on "Wolf Conservation" includes a short discussion on pp. 144-145 regarding responses of wolves to different levels and causes of mortality, and the effect of breeder loss on pack dynamics and size. This section cites to papers by Brainerd et al. (2008), Smith et al. (2010) and Borg et al. (2014), among others. We provide in Appendix D a more comprehensive treatment of the subject, in the form of a white paper co-authored by Dr. John Marzluff and Dr. Aaron Wirsing and two of their graduate students, from the University of Washington's School of Environmental and Forest Sciences.

The paper is a synthesis of findings presented at a symposium held October 29th, 2014 at the University of Washington and co-hosted by the Pacific Wolf Coalition and Professors Marzluff and Wirsing. The subject was "Tackling Wolf Management's Thorniest Issue: The Ecological and Social Complexities of Lethal Control," and the symposium consisted of presentations given by Dr. Douglas Smith, Dr. Scott Brainerd, Dr. Adrian Treves, Dr. Jeremy Bruskotter, Dr. Rob Wielgus, Dr. Donny Martorello and Carter Niemeyer. The paper provides detailed findings described by each presenter, and sums up the findings of the presenters that lethal removal can disrupt wolf pack dynamics, inhibiting recovery objectives in recolonizing populations,

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[43] Callan et al. 2013; Bouchard et al. 2013; Rooney et al. PowerPoint presentation.
[44] Wild et al. 2011.

potentially increase livestock depredations, and negatively affect human attitudes towards wolves.[45]

The Plan's Discussion of Human Social Tolerance for Wolves Should Discuss and Cite to Additional Sources.

Polls and Surveys. Part II, Chapter 3, on "Human Interactions and Current Perceptions of Wolves" includes a section discussing human perceptions and attitudes towards wolves (at pp. 47-50). Page 48 notes that "[r]esearchers have conducted a number of surveys to measure human attitudes towards wolves (ranging from positive to negative) or wolf restoration, to gauge public support for such activities. Most of these efforts were conducted prior to wolf restoration and very few occurred post wolf occupancy."

One year ago, conservation group SWG members provided the Department with surveys and polls gauging public support for wolf restoration and legal protections for wolves. Only one of the surveys we provided is discussed in this section and it relates only to people's attitudes towards wolves. None of the polls and surveys we provided which inquired about people's attitudes regarding wolf restoration and legal protections were discussed or cited to. Most of the polls and surveys we provided were recent, all were conducted after wolf restoration and occupancy occurred in several parts of the U.S., and almost all of them were polls and surveys that gathered data expressly from people living in California, Oregon and/or Washington or all three.

The polls and surveys we provided to the Department show overwhelming support by the public for continued legal protections for wolves, a view that wolves are a part of our natural heritage, and a desire to see wolves restored in the very state where the poll/survey respondee lived.

The discussion in Chapter 3 on polls and surveys should be more broadly representative of existing polls and surveys by including those we previously submitted to the Department. Citations for this literature are again provided to the Department in the comprehensive list found in Appendix C.

Wolf Conservation and Human-Caused Mortality. Part II, Chapter 9 discusses "Wolf Conservation." In section B, Threats to Wolf Conservation, on pp. 143-145, the chapter discusses threats from Human-Caused Mortality. Pages 143-144 relate the historical extirpation of wolves in the conterminous United States and describe the "sport harvest" of wolves and predator control, but fail to include a discussion of the lack of agency understanding of the key threat to wolf population viability, i.e., human tolerance.

Dr. Adrian Treves, who has authored more than 100 scientific articles on ecology, conservation and society, is director of the Carnivore Coexistence Lab at the University of Wisconsin-Madison. A significant portion of his work is devoted to research on human-carnivore conflicts

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[45] The panel discussion was also videotaped and each panelist's presentation can be viewed and listened to at http://www.pacificwolves.org/videos/

and human attitudes towards carnivores. In Chapter 3, his research team's work analyzing data from surveys taken over an 11-year period in Wisconsin is mentioned. Dr. Treves' research results found that when protections for wolves were lifted and state-sanctioned hunting seasons instituted, tolerance for wolves decreased, demands for more wolf-killing increased, and poaching increased. His findings are downplayed by the Department as being results obtained in the early stages of wolf recovery while the population was growing and hunting instituted only a few years ago. However, the Department entirely misses the boat on the overarching message, which is that the main threat to wolf population viability – i.e., human tolerance manifested through illegal take (poaching) – is not adequately understood by any federal or state agency yet and that the management actions agencies take in the absence of understanding can have serious repercussions. Per Dr. Treves, " The available evidence suggests delisting and legalizing or liberalizing lethal control is more likely to increase poaching which is the major threat to wolves in the USA than decrease it." Dr. Treves' letter to the Oregon Fish and Wildlife Commission on this critical topic can be found in Appendix B (it is the 2ⁿᵈ letter in the compilation of scientists' comment letters). We urge you to read Dr. Treves' letter to the Commission and include a discussion of this crucial topic in section B. of Chapter 9.

The Plan's Discussion of Human Perceptions and Interactions with Wolves Should Include Discussion and Citation to New Paper Establishing that More than 50% of Attacks on Humans by Carnivores is Due to Inappropriate Conduct by Humans.

Part II, Chapter 3, on "Human Interactions and Current Perceptions of Wolves" discusses Human Safety (at pp. 43-45) and Interaction with the Public (at pp. 45-47). Both describe instances of aggression or attacks by wolves on humans and/or contexts for those interactions. One or both of these sections should cite to and include a discussion of a recently published paper which finds that about half of all well-documented reported attacks by carnivores (black bears, brown bears, mountain lions, wolves and coyotes) in Europe and North America have involved risk-enhancing human behaviors, and that prevention and information that can encourage appropriate human behavior when sharing the landscape with large carnivores is of paramount importance to reduce both dangerous human-carnivore encounters and their consequences to carnivores. A discussion of this paper would be beneficial to any reader who lives, recreates or works in landscapes where there are bears, mountain lions, coyotes and wolves in California. It provides published research demonstrating that humans can choose to take actions which are risk-enhancing or risk-reducing and that it benefits us and California's carnivores to be thoughtful and do the latter.[46]

Evidence of Historical Wolf Presence in California as Indicated Languages, Tales, Practices and Ceremonies of Native Peoples Deserves a Heading Other than "Anecdotal Observations."

In Part II, Chapter 1, Wolf Life History and Background is discussed. At pp. 20-24, historical distribution and abundance of wolves in California, museum specimens and anecdotal observations are described. We are disappointed to see included under the heading "anecdotal

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[46] Penteriani et al. 2016.

observations" the information which comes from the languages, tales, practices and ceremonies of California's native peoples. Given the 10,000 year history of native inhabitation of California well before the arrival of European explorers, settlers, market hunters, gold rush miners and others, it seems truly and culturally inappropriate to characterize evidence from 10,000 years of culture as mere "anecdotes." If anything should be characterized in the Plan as anecdotes, it should be the ranchers' and hunters' fears, perceptions, attitudes, and beliefs, given no one in California has systematic, scientific observations of wolves to make.

During the SWG meetings, the environmental caucus requested that the Plan distinguish the evidence from California tribes in a separate section. Possibly it could be entitled "Evidence from Traditional Ecological Knowledge." If that is not an accurate characterization of evidence from language, tales, practices and ceremonies, we feel certain the Department could come up with another suitable, distinct heading.
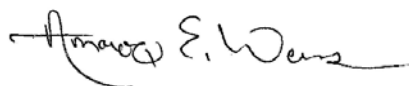
CONCLUSION

As detailed in the comments above, our organizations greatly appreciate the Department's open, transparent and inclusive approach to planning for wolf conservation and management in California as the species makes its return after a nearly century-long absence. CDFW has a legal obligation to manage wildlife on behalf of all citizens of California. Promoting coexistence between wolves and livestock producers will be of critical importance to the successful management of wolves in our state, and many of our organizations stand ready to assist the Department in its effort to successfully recover gray wolf populations in California.
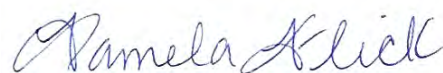
Numerous concerns remain about various aspects of the Draft Plan, however, including but not limited to the Department's suggested population thresholds and duration of management phases, reducing protections at state and federal levels, lack of prioritization of actions and missing information. It is our collective hope that the Department will thoroughly review these comments and thoughtfully incorporate our suggestions to make a stronger and more comprehensive Wolf Plan that will guide recovery, conservation and management of the species well into the future.

We appreciate this opportunity to provide these comments and recommendations regarding the Department's Draft Wolf Plan. Please do not hesitate to contact any of us if you have questions about what we have provided to you.
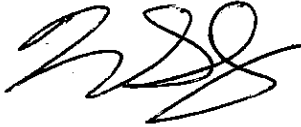
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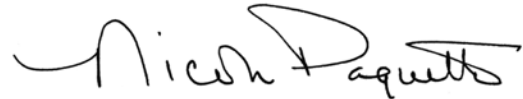Environmental Protection Information Center (EPIC)
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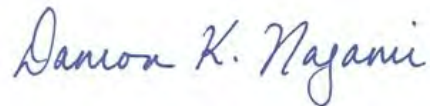Living with Wolves
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(pdfs of listed items are in Appendix E, except Gowan et al. 2015 is in Appendix D.)

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Oregon

ORS §§ 496.171 - 996

ORS § 498.014(a)(A)

OAR 635-110-0010(8)(b)(B)

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Washington

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WAC 232-12-297, § 4.2

Federal

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Appendix A

PROPOSED REGULATORY LANGUAGE FOR REQUIREMENTS

BEFORE RESORTING TO LETHAL CONTROL

Additional Criteria, in Phase II and III for Lethal Control of Wolves to Address Chronic Livestock Depredation (if existing state and federal law allow lethal control)

Lethal take to address chronic livestock depredation. CDFW may authorize its personnel or authorized agents to use lethal force on a wolf or wolves it reasonably believes are responsible for chronic depredation upon livestock where each of the conditions in sections (1) through (6) of this rule is satisfied. CDFW shall limit lethal force to the wolf or wolves it deems necessary to address the chronic depredation situation.

Conditions for Lethal Take by CDFW. CDFW's discretionary authority for use of lethal force pursuant to this rule may be exercised if CDFW:

1. Designates an Area of Known Wolf Activity (AKWA) and upon designation timely coordinates with potentially affected livestock producers to provide information about the California Wolf Plan, wolf behavior/management/conservation, how to document and report wolf activity to CDFW including livestock depredations, nonlethal measures/ incentives /assistance for minimizing conflicts between wolves and livestock/domestic animals in the AKWA.

2. CDFW confirms an incident of depredation by a wolf or wolves.

3. Within 14 days of CDFW's confirmation of first wolf depredation incident, designates an Area of Depredating Wolves (ADW).

4. Concurrent with designation of ADW, prepares and publicly discloses area-specific wolf-livestock conflict-deterrence plan in coordination with potentially affected parties that identify appropriate non-lethal measures most likely to be effective for the particular circumstances.

5. Confirms a total of at least 5 separate qualifying incidents of livestock depredation on separate days within the previous 3 months by the same wolf or wolves.

6. Each of the documented depredation incidents has resulted in livestock mortality or injury.

7. Issues and makes publicly-available, prior to exercise of lethal force, written determination by CDFW Director or their designee to use lethal force to address specified situation of chronic depredation, with supported findings that (a) criteria (1)-(6) above and (8)-(13) below have been met, (b) livestock producers in ADW have worked to reduce wolf-livestock conflicts and are in compliance with wolf protection laws and conditions of any harassment or take permits, (c) the situation of depredation by wolves on livestock in ADW is likely to remain chronic despite use of additional non-lethal conflict deterrence measures and (d) wolf or wolves identified by CDFW for removal are those which CDFW finds to be associated with the qualifying depredations and CDFW finds that their removal will decrease risk of chronic depredation in ADW.

8. **Qualifying Contingencies and Counting Incidents.** An incident of depredation is a single event resulting in the injury or death of one or more lawfully present livestock that is reported to CDFW for investigation and, upon investigation by CDFW or its agent(s), CDFW confirms to have been caused by a wolf or group of wolves.

A qualifying incident of depredation is a confirmed incident of depredation for purposes of this rule only if:

    A. If the depredation is outside an AKWA or ADW, only the first confirmed depredation by a wolf or wolves counts as a qualifying depredation. As soon as a depredation by a wolf or wolves outside of an AKWA or ADW is confirmed by CDFW, the agency must immediately designate an ADW and an AKWA and take the steps described in (1)-(4) above. If additional depredations occur outside the AKWA or ADW before the agency has acted pursuant to (1)-(4), these subsequent depredations will not count as qualifying depredations.

    B. If the depredation is within an AKWA or within an ADW, the landowner or lawful occupant has, at least 7 days prior to the depredation removed, treated or disposed of all intentionally placed, known or reasonably accessible unnatural attractants such as bone or carcass piles or disposal sites; and prior to and on day of depredation incident been using non-lethal measures CDFW deems appropriate to protect the specific livestock operation there.

    C. After the first depredation incident, the livestock producer has applied for or already has in place a Wolf Depredation Prevention Cooperative Agreement (WDPCA).

9. **Human Presence.** Human presence, when used as non-lethal measures, is presence that CDFW could reasonably expect to deter wolf-livestock conflict under the circumstances and if it occurs at proximate time prior to and in an area proximate to a confirmed depredation per CDFW and indicates timely response to wolf location information in situations of potential wolf-livestock conflict.

10. **Transparency and Public Disclosure.** Prior to using lethal force to address chronic wolf depredation, and with adequate notice to the public, CDFW shall document and make publicly available on at least its website (a) the determinations and supported findings referenced in section (7) above (b) but with any personal information of landowners, lawful occupants or other relevant individuals redacted from public disclosure.

11. **Duration of Chronic Depredation Lethal Take Authority.** Chronic depredation lethal take authority expires (a) when wolf or wolves identified for lethal removal have been removed by CDFW; (b) 45 days after issuance of the take authority unless within that time period another qualifying depredation incident occurs by same wolf or wolves identified for lethal removal and non-lethal methods have continued to have been implemented; or (c) if CDFW determines wolf or wolves identified for lethal removal have left the ADW for more than just a short-term or seasonal movement outside the area's boundary.

Appendix B

SCIENTISTS' LETTERS TO

OREGON FISH AND WILDLIFE COMMISSION

April 14, 2015
Letter to Oregon Department of Fish and Wildlife
From Scientists on Wolf Recovery

We, the undersigned scientists, are writing to express our concern that now is not the time to delist the gray wolf in Oregon. Continued state Endangered Species Act (ESA) protections are essential for allowing existing populations to stabilize and expand into other suitable habitat. Milestones should be celebrated, but meaningful recovery is not complete in significant portions of suitable habitat in the state. Prematurely weakening gray wolf protections is likely to reverse years of progress, put recovery in jeopardy, and exacerbate conflict.[i][ii][iii]

We urge ODFW to:

Maintain ESA status for gray wolves and foster coexistence by getting ahead of – rather than reacting to – conflict. Some suggestions for doing this are to:

- *Focus on positive aspects of wolf recovery, native predators, and healthy landscapes*

- *Conduct and facilitate research regarding wolves and conflict deterrence measures and*

- *Provide landowners with information that will assist in reducing potential conflicts*

Like all native wildlife, wolves are an enormous asset to the biological diversity of our state, ecosystem services, and quality of life. Wolf recovery is overwhelmingly supported by Oregonians. After years of making excellent progress toward recovery, it would be a shame to stop before the final goal is accomplished.

We offer our expertise and support for such an effort and extend our thanks to you for your leadership on wildlife conservation issues.

Signed:

Marc Bekoff, Ph.D.
Ecology and Evolutionary Biology
University of Colorado, Boulder
Science Advisory Board, Project Coyote

Robert L. Beschta, Ph.D.
Professor Emeritus
Forest Ecosystems and Society
Oregon State University

Barbara Brower, Ph.D.
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Robert Crabtree, PhD
Victoria, British Columbia
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Michael Paul Nelson, Ph.D.
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Paul Paquet, PhD
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Senior Scientist Carnivore Specialist, Raincoast Conservation Foundation
Science Advisory Board, Project Coyote

David Parsons, M.S.
Wildlife Biologist - U.S. Fish and Wildlife Service, Retired
Science Advisor for Project Coyote

William J. Ripple, Ph.D.
Distinguished Professor of Ecology
Oregon State University

Jeffrey W. Snyder, Ph.D.
Department of Biology
Western Oregon University

Michael Soulé, PhD
Professor Emeritus
Dept. Environmental Studies, University of California, Santa Cruz
Co-founder, Society for Conservation Biology
Science Advisory Board, Project Coyote

Adrian Treves
University of Wisconsin-Madison
Science Advisory Board, Project Coyote

Jennifer Wolch, PhD
Berkeley California
Dean, College of Environmental Design
Science Advisory Board, Project Coyote

[i] Tad Larsen and William J. Ripple, "Modeling Gray Wolf (Canis lupus) habitat in the Pacific Northwest, U.S.A," *Journal of Conservation Planning* Vol 2 (2006) 17-33.

[ii] Oregon Department of Fish and Wildlife," Oregon Wolf Population," http://dfw.state.or.us/Wolves/population.asp, (January 27, 2015)

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28 October 2015

To the Oregon Fish and Wildlife Commission:

The following comments relate to the proposal to delist gray wolves in Oregon, entitled "Updated biological status review for the Gray Wolf (Canis lupus) in Oregon and evaluation of criteria to remove the Gray Wolf from the List of Endangered Species under the Oregon Endangered Species Act (Oregon Department of Fish and Wildlife (ODFW), October 9, 2015)" hereafter "ODFW Review 2015".

I have been studying wolf-human interactions for 16 years and ecology generally for >25 years. I've published >50 scientific articles on ecology, conservation and human dimensions. **My lab group is the only one in the world to have measured changes in individual humans' tolerance for wolves over time and attitudes under changing policies on lethal management and delisting.** We have also studied poaching (illegal take) iin several peer-reviewed scientific publications. More information about my lab and our work on wolves can be found on our webpage: http://faculty.nelson.wisc.edu/treves/.

My comments address human tolerance for wolves, illegal take, and the public trust. I restrict my comment to two points:

(1) **Oregon's delisting criteria have not been met**,
    and
(2) **The main threat to wolf population viability is not adequately understood by any state or federal agency yet, therefore the expected benefits of delisting are unlikely to manifest and the likely costs are not well addressed by current regulatory mechanisms.**

By Oregon law ORS 496.17, state delisting can occur if all of five conditions are met. I address the first and fifth here.

1. The species is not now (and is not likely in the foreseeable future to be) in danger of extinction in any significant portion of its range in Oregon or in danger of becoming endangered; and

5. Existing state or federal programs or regulations are adequate to protect the species and its habitat.

Comment 1.   **The criteria for state delisting have not been met.**

The phrase "**The species is not now… in danger of extinction in any significant portion of its range in Oregon**" has two implications. The first relates to historic range and the second to not being endangered.

The historic range of the wolf in Oregon was the entire state (*1*) as the ODFW Report 2015 correctly noted and visible in Appendix A for map of historic range in the U.S. Habitat suitability analyses for wolves confirm that prey availability and human-caused mortality are the major factors limiting wolves from recolonizing a region, e.g., (*2*). If one limits the geographic extent considered to be wolf range to those areas where people want wolves to live, one opens the door to illegal and otherwise unacceptable human-caused mortality determining where wolves can live. The legal and biological flaws in this line of

thinking have been described and rejected for federal delisting of the gray wolf (*3*). In simple terms, the ODFW **should not define wolf range based on interest group anger or some unquantified social acceptance, because that opens the door to a form of extortion by intolerant communities**, "We'll kill wolves that move here." Threats posed by people are something to combat.

Instead available range should be defined by the biological capacity of wolves to find what they need to reproduce in an area and the acceptable recolonization might be determined by legal standards (see below).

With this biological logic in mind, the gray wolf is currently present in less than 6% of the state's land area now (ODFW Review 2015), approximately equivalent to Douglas County, OR. Now imagine if the 3% of Oregon's human population in Douglas County were the only ones to benefit from the presence of an endangered species (e.g., Washington Ground Squirrel or Lower Columbia River Coho Salmon). Wouldn't other counties' residents demand access without extreme efforts? Currently, too few citizens have access to the benefits generated by wolves in Oregon, which include aesthetic, ecological, and uses that deplete the asset (if that depletion leaves the asset unimpaired). Furthermore, future generations of Oregonians have a right to those benefits also. That point is emphasized by the case law upholding the public trust doctrine in Oregon. Wildlife belongs to all state citizens by Oregon law as a trust asset [1]. That trust obligation limits the allocation of assets such as wildlife to private interests, e.g., livestock producers demanding lethal control of wolves (*1*). That trust obligation also curbs the eagerness of administrative agencies to allocate assets,

> "In *Morse v. Department of State Lands*,[2] the 1979 Oregon Supreme Court remanded the director's decision to issue a permit authorizing a fill for an airport runway extension because he failed to determine whether the public need for the project outweighed damage to public use of trust resources…" (p. 686, section 6.2) in (*4*)

Therefore I recommend the Commission consider all current citizens and the rights of future generations for whom the trust is held.

I recommend that 'a significant portion of range' be interpreted so as to defend against litigation. **I recommend 'a significant portion of range' be defined as one of the following geographic extents: at least one breeding pair in every county or breeding pairs in a majority of counties.**

Furthermore, the current population size of wolves in Oregon "As of July 2015, there were 16 known groups or packs of wolves containing a male-female pair (Table 2), and the mid-year minimum population (non-pup) was 85 wolves." (ODFW Review 2015). A recent illegal shooting has probably lowered that number while emphasizing the role of negligent hunters in illegal take (http://www.statesmanjournal.com/story/news/2015/10/19/man-shot-and-killed-wolf-could-face-charges/74223524/). At a population size <85, the addition of a few extra wolf deaths in a year can stop

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[1] State v. McGuire, 33 P. 666 (Or. 1883)

[2] *Morse*, 590 P.2d at 715; After *Morse*, the Oregon legislature amended the Submerged and Submersible Lands Act to require the director to find that the "public need" for the project outweighs harm to public rights of navigation, fishery, and recreation. OR. REV. STAT § 196.825(3) ("The director may issue a permit for a project that results in a substantial fill in an estuary for a nonwater dependent use only if the project is for a public use and would satisfy a public need that outweighs harm to navigation, fishery and recreation and if the proposed fill meets all other criteria ... [in the Act].").

or reverse population growth. As the ODFW Review 2015 noted, wolves are highly susceptible to human causes of mortality and many of these mortalities go undetected and unreported (cryptic poaching). The ODFW Review 2015 reported illegal take was the leading cause of death among wolves in a small sample of recovered mortalities. For a quantitative example from another state, we estimated an average of 44% (SD 4%) of Wisconsin wolves aged >7.5 months died each year after delisting procedures began and the state regained intermittent authority for lethal control (*6*). **The majority of those wolf deaths went undetected and nearly half of all deaths were poached wolves. If that pattern applies after delisting in Oregon, one should expect 34–41 yearlings and adult wolves to die in the year that follows. Most will go undetected.** Overcoming such high mortality rates would require higher than average population growth seen in the Oregon population (Table 2, ODFW Review 2015). Chronic, undetected, human-caused mortality challenges the success of Oregon's wolf recovery.

Moreover hopes that delisting or state authority for lethal control will reduce poaching have been fostered by a flawed analysis (*7*), see (*1*) and (*6*) for why it is flawed. The actual conclusion should be just the opposite, namely delisting and legal culling authority increased poaching in Wisconsin[3].

In sum, the Oregon wolf population has not met the first criterion for delisting, whether measured by geographic distribution or population size.

The next comment speaks directly to the fifth requirement that, "**Existing state or federal programs or regulations are adequate to protect the species**"

Comment 2.   **The main threat to wolf population viability is not adequately understood by any state or federal agency yet, therefore the expected benefits of delisting are unlikely to manifest and the likely costs are not well addressed by current regulatory mechanisms.**

The ODFW correctly identifies the major threat to wolf population viability is human tolerance manifested through illegal take (poaching) mainly, "Since human tolerance has been and remains the primary limiting factor for wolf survival, building tolerance for this species will require acceptance of the Plan's approach to addressing wolf conservation and human conflicts." (p. 3, ODFW Wolf Conservation and Management Plan, December 2005 and Updated 2010)" hereafter "ODFW Plan 2010") and same sentence on p. 34 of the ODFW Review 2015. One should expect the major threat to a listed species to be well understood and abated if delisting will succeed. Unfortunately the threat is neither **well understood nor abated currently**. Our evidence that **illegal take has not been abated** comes from the section above and data on illegal take in the past as well as the likely prospect that **illegal take is likely to increase** as we explain below. The evidence that **human tolerance is not well understood by the ODFW** comes from the ODFW Review 2015 and the ODF Plan 2010.

The ODFW Plan 2010 and ODFW Review 2015 are not up-to-date on research relating to human tolerance for wolves despite 36 instances in which those documents mentioned "tolerance" or "attitude". There are over 100 scientific, peer-reviewed articles on human attitudes to wolves (*3*), and >10 recent studies from the USA address what to expect in human tolerance for wolves after intervention or after policies change (*3, 8-16*). The ODFW Review 2015 does not cite a single one of those studies or anything by the leaders in the field, which suggests that **the ODFW has not considered the scientific evidence for the major threat to Oregon wolves**.

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[3] Please contact the author for evidence to support this assertion in a report under review.

Instead, the ODFW Review 2015 cites wolf biologists who have never collected human dimensions data when making a claim about human tolerance, "There are many references which relate human tolerance to successful wolf management (Mech 1995, Bangs et al. 2004, Smith 2013)." Had the ODFW reviewed the expert scientific literature rather than biologists' opinions, they would have learned the following:

Public acceptance for lethal control has declined significantly since the 1970s and the public prefers non-lethal methods for managing wildlife. Tolerance for carnivores and inclinations to poach them are not well predicted by wealth or economic losses but rather by peer networks and social norms that foster resistance to authority and anti-establishment actions. Those inclined to poach tend to justify their actions by over-estimating how many of their neighbors and associates do so. Tolerance for bears declined when messaging was purely negative or concerns hazards posed by wildlife. Tolerance for wolves declined after delisting and legalization of lethal management, probably because people perceived the government was sending a signal that wolves have less value or illegal take will not be enforced. The implementation of lethal control did not raise tolerance for wolves after 8 years and the inauguration of public wolf-hunting did not raise tolerance for wolves after one year. Messaging that includes a sizeable component of information on benefits is more likely to raise tolerance for carnivores than messaging that focuses on costs and risks.

The available evidence suggests delisting and legalizing or liberalizing lethal control is more likely to **increase poaching which is the major threat to wolves in the USA** than decrease it.

Despite the latest results described above, the scientific community still does not know enough to abate poaching, which we believe is generated by intolerance. Perpetrators of poaching are poorly studied. That creates uncertainty about who would poach a wolf, under what conditions, and where. It is widely believed that the average human's tolerance in areas inhabited by wolves will predict behaviors that harm or help wolf conservation. If that hypothesis is false, concerns with social tolerance are misplaced and attention should focus on a few perpetrators and their social networks that promote law-breaking, rather than on the general public

I conclude that state delisting might have costs that the ODFW has not anticipated and is currently ill-equipped to understand let alone abate.

Furthermore the ODP Plan 2010 is liable to lead to an increase in poorly understood take in the wake of delisting. "A delisting decision by the Commission is not expected to significantly affect the management of wolves. This is because the Wolf Plan and associated OAR's guide the management of wolves regardless of OESA listing status, and a delisting decision would not inherently alter the management aspects of the Wolf Plan." (ODFW Review 2015). That is unfortunate because **delisting should lead to a change in management to reduce legal AND illegal killing and increase messages about the benefits of wolves to Oregon ecosystems and citizens.**

Of particular concern is whether the ODFW has correctly described the future costs and benefits of its management efforts that affect wolf survival and reproduction. Lethal management raises such concerns because there has never been a rigorous scientific experiment to test if killing wolves actually prevents future wolf predation on livestock (*17-19*).

Also Oregon's state delisting would presumably activate the hunting and trapping of wolves as a "special status game mammal" under ORS 496.004 (9). (While the state wolf Plan indicates that controlled take of wolves could not occur until wolves enter into Phase III, ODFW has publically indicated that the

population goals established in the Plan for moving into Phase III could be met as early as 2017. The Plan also advises that it is expected that wolves will have been delisted by the time Phase III management regimes and the availability of controlled take of wolves begins. With these guidelines and the timeline ODFW has indicated, controlled take of wolves will follow delisting in short order but without scientific basis.) The expectation that "controlled take of wolves would be permitted as a management response tool to assist ODFW in its wildlife management efforts" presumes public hunting is a useful management response. **Setting aside private hunters desires to hunt or revenue generation from hunting, what conservation purpose does hunting play in a population recovering from extirpation?**

Reviews of this question find little or no benefit of public hunting and trapping for conserving large carnivores (*20-24*). Furthermore, studies of cougars suggest public hunting can exacerbate problems with domestic animal owners (*25*). It may seem obvious that killing a wolf in the act of chasing, biting or otherwise attacking livestock will save that animal but the vast majority of lethal management is done far from the livestock and long after an attack has occurred. Under such indirect circumstances, lethal management is not clearly effective. Consider the unsettled dispute about lethal management of Northern Rocky Mountain wolves despite twenty years of lethal management (*26, 27*). Another concern is that the ODFW over-states the problem of livestock depredation in the following quote, "The challenges of wolves in areas with livestock are well documented, and wolves prey on domestic animals in all parts of the world where the two coexist". This over-states the challenge posed by livestock predation because it ignores years of evidence that a minority of wolf packs are involved in domestic animal depredations and the geographic locations of such attacks are predictable (*14, 28, 29*). Moreover it ignores the many non-lethal methods that are more effective than lethal control and have not had detectable side-effects and counter-productive results such as higher livestock predation.

I recommend the ODFW pay close attention to research by independent scientists with academic freedom (not USDA-WS which has a financial conflict of interest and not hunter interest groups for the same reason) who have reviewed the evidence on whether killing wolves – either through public hunting or by USDA-WS contract – will prevent livestock predation. Otherwise, and until the scientific community finds consensus on this evaluation, any such killing authorized and condoned by ODFW is not based on best science. Indeed it is being conducted in the absence of scientific justification and may be in violation of the public trust duties of the state, as mentioned previously.

In conclusion, I find (**1) Oregon's delisting criteria have not been met**, and (**2) The main threat to wolf population viability is not adequately understood by any state or federal agency yet, therefore the expected benefits of delisting are unlikely to manifest and the likely costs are not well addressed by current regulatory mechanisms.**

Thank you for reading my comments.

Adrian Treves, PhD

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Appendix A.

Blue area is the historic range of the gray wolf in the conterminous United States. Hatched gray areas are the current range of breeding pairs of wolves as of 2013. The dark polygons show relative human population density (*1*).
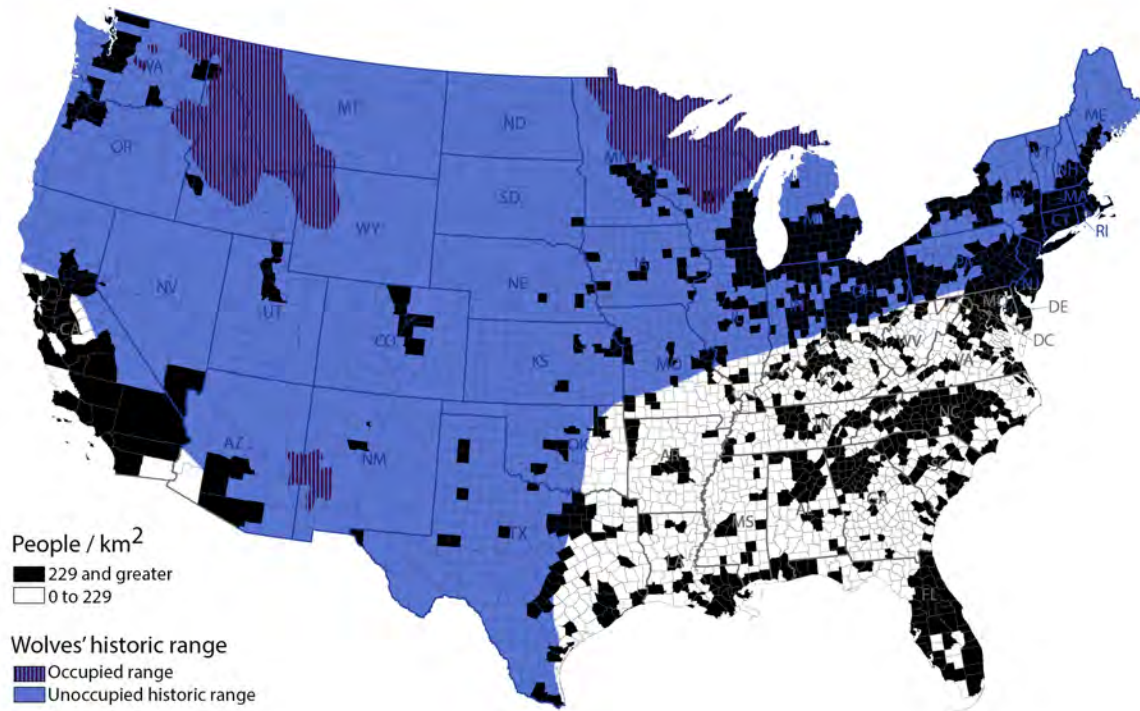
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October 27, 2015

Dear Commissioners,

Soon the Commission will decide whether to remove wolves from the Oregon state list of endangered species. For reasons outlined below, we urge the Commission to refrain from removing wolves from Oregon's endangered species list at this time.

Because Oregon state law requires delisting decisions be based on the best-available science, the Oregon Department of Fish and Wildlife has made a concerted effort to perform scientific analyses to evaluate the appropriateness of removing wolves from Oregon's endangered species list. That analysis is reported in a document entitled, *Updated biological status review for the Gray Wolf (Canis lupus) in Oregon and evaluation of criteria to remove the Gray Wolf from the List of Endangered Species under the Oregon Endangered Species Act*. Hereafter we refer to that document as ODFW (2015).

While the analyses described in ODFW (2015) are important, those analyses are also, by themselves, an insufficient application of best-available science. A sufficient application of best-available science also requires analyses, like those reported in ODFW (2015), to be adequately vetted by the scientific community through an independent review process. To our knowledge, that vetting has not to have taken place. In particular, we are especially concerned that the extinction risk analysis and its interpretation has not been adequately vetted.

This scientific vetting is especially critical because discourse arguing for state delisting is enabled only because the U.S. Congress removed wolves from the federal list of protected species in 2011. But delisting action was based entirely and overtly on political circumstances, not best-available science. That circumstance heightens the need for Oregon to offer due diligence with respect to best-available science, where the federal government has failed.

ODFW (2015) includes analyses which strongly suggests that wolves should remain listed at this time. In particular, ODFW (2015) indicates

1) that Oregon has 106,853 km^2 of currently suitable range for wolves. That is, range with sufficient prey and habitat where wolf-human conflicts are relatively minimal (as indicated by road density and land uses such as agriculture and developed areas).
2) wolves currently occupy about 12,582 km^2.

ODFW (2015) also implies that former range of wolves (i.e., range occupied before humans drove wolves to an endangered status) would have been greater than the current suitable range.

To summarize, ODFW (2015) indicates that wolves in Oregon currently occupy *less than* 12% of their former range and only about 12% of current suitable range. Comparing that circumstance conditions with Oregon's Endangered Species Act provides important context for informing Oregon's listing judgment. In particular, the Act states that an endangered species is one that is "…in danger of extinction throughout any significant portion of its range within this state." By that standard wolves are endangered because the species remains extirpated from nearly 90% of its currently suitable range (and extirpated from an even greater proportion of the range that wolves occupied before human persecution).

Oregon state law does not require wolves to occupy all of their former range. Oregon state law does not even require wolves to occupy all of the currently suitable range. However, it is untenable to think that being extirpated from nearly 90% of current suitable range (a subset of former range) would qualify the species for delisting.

This comparison between the language of Oregon's law and wolves' circumstance in Oregon is robustly supported by considerable scholarship and judicial opinion. Some of that peer-reviewed scholarship and judicial opinion is presented in Vucetich et al. (2006); Tadano (2007); Enzler & Bruskotter (2009); Geenwald (2009); Kamel (2010); Carroll et al. (2010), Bruskotter et al. (2013). If the Commission would be interested in a more detailed account of this scholarship for itself or its constituents, we would happily provide such an account upon request.

We fully understand that wolves can be a challenging species to manage. And we appreciate that delisting may seem a solution to that challenge. However, two very important considerations suggest otherwise. *First*, Oregon already has many tools for managing wolf-human conflicts. Vigilant and judicious use of those tools is the key to effectively managing wolf-human conflicts. That much is clearly demonstrated by the good work of the Commission and ODFW. However, it is difficult to envision how wolf-human conflicts would be more effectively managed as a result of premature delisting.

Second, the consequences of acting in haste or inconsistently with principles outlined here increase the risk that other decisions pertaining to delisting and natural resource management in general would be made out of political convenience rather than principle of law and science.

For these reasons, we urge you to refrain from removing wolves from Oregon's list endangered species at this time.

Sincerely,
John A. Vucetich, Professor of Wildlife, Michigan Technological University

Jeremy T. Bruskotter, Associate Professor, School of Environment and Natural Resources, The Ohio State University

Michael Paul Nelson, Ruth H. Spaniol Chair of Renewable Resources and Professor of Environmental Ethics and Philosophy, Oregon State University

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To the Oregon Fish and Wildlife Commission:

I am submitting these comments regarding the ODFW gray wolf biological status review (ODFW 2015). I am a professional quantitative ecologist and principal scientist with the Wild Nature Institute. I have a Bachelor's degree in Anthropology from University of California, Santa Barbara, a Master's degree in Wildlife Natural Resource Management from Humboldt State University, and a PhD in Biological Sciences from Dartmouth College.   I am an expert population biologist who has co-authored two population viability analyses (PVA) for the U.S. Fish and Wildlife Service:

1. N. Nur, R.W. Bradley, D.E. Lee, P.M. Warzybok, and J. Jahncke. 2013. Population Viability Analysis of Western Gulls on the Farallon Islands in relation to potential mortality due to proposed house mouse eradication. Report to the National Fish and Wildlife Foundation and the US Fish and Wildlife Service. PRBO Conservation Science, Petaluma, California.

2. N. Nur, D.E. Lee, R.W. Bradley, P.M. Warzybok, and J. Jahncke. 2011. Population Viability Analysis of Cassin's Auklets on the Farallon Islands in relation to environmental variability and management actions. Report to the National Fish and Wildlife Foundation and the US Fish and Wildlife Service. PRBO Conservation Science, Petaluma, California.

I co-authored a comprehensive review of demography and population dynamic models (including PVA) that was part of the California Current Seabird Management Plan for U.S. Fish and Wildlife Service:

N. Nur and D. E. Lee. 2003. Demography and Population Dynamic Models as a Cornerstone of Seabird Conservation and Management in the California Current. *in* California Current System Seabird Conservation Plan (eds. W.J. Sydeman, K.

Mills and P. Hodum). Report to the US Fish and Wildlife Service. PRBO

Conservation Science, Stinson Beach, California.

Eight, relevant, peer-reviewed scientific articles that I have had published from my

research include the following:

1. D.E. Lee, J. Bettaso, M.L. Bond, R.W. Bradley, J. Tietz, and P.M. Warzybok. 2012. Growth, age at maturity, and age-specific survival of the Arboreal Salamander (*Aneides lugubris*) on Southeast Farallon Island, California. Journal of Herpetology 46:64-71.

2. D.E. Lee, R.W. Bradley, and P.M. Warzybok. 2012. Recruitment of Cassin's Auklet (*Ptychoramphus aleuticus*): Individual age and parental age effects. Auk 129:1-9.

3. D.E. Lee. 2011. Effects of environmental variability and breeding experience on Northern Elephant Seal demography. Journal of Mammalogy 92:517-526.

4. A.C. Brown, D.E. Lee, R.W. Bradley, and S. Anderson. 2010. Dynamics of White Shark predation on pinnipeds in California: effects of prey abundance. Copeia 2010 No. 2:232-238.

5. D.E. Lee and W.J. Sydeman. 2009. North Pacific climate mediates offspring sex ratios in Northern Elephant Seals. Journal of Mammalogy 90:1-8.

6. D.E. Lee, C. Abraham, P.M. Warzybok, R.W. Bradley and W. J. Sydeman. 2008. Age-specific survival, breeding success, and recruitment in Common Murres (*Uria aalge*) of the California Current System. Auk 125:316-325.

7. D.E. Lee, N. Nur, and W.J. Sydeman. 2007. Climate and demography of the planktivorous Cassin's Auklet *Ptychoramphus aleuticus* off northern California: implications for population change. Journal of Animal Ecology 76: 337–347.

8. S.F. Railsback, B.C. Harvey, R.R. Lamberson, D.E. Lee, N.J. Claasen, and S.
    Yoshihara. 2001. Population-level analysis and validation of an individual-based
    Cutthroat Trout model. Natural Resource Modeling 15:83-110.

I have also acted as an independent consultant offering expert advice on questions of
population management and population viability for management authorities and stakeholders
involved in the multi-national Action Plan under the Agreement on the Conservation of
Albatrosses and Petrels.

As part of my PhD work at Dartmouth College, I conducted a PVA to explore
metapopulation dynamics of giraffe in a fragmented ecosystem in Tanzania:

D.E. Lee. 2015. Demography of Giraffe in the Fragmented Tarangire Ecosystem.
PhD Dissertation. Dartmouth College.

My expertise has mostly focused on seabirds and other marine predators, in addition to
giraffe, but the mathematics and the biological concepts relevant to PVA are universal and well-
established. The universality of the concepts is apparent in the variety of taxa population
biologists like me are able to apply our expertise to. For example, my work has encompassed
taxa as diverse as cutthroat trout, woodrats, mice, seabirds, seals, salamanders, spotted owls,
and giraffes.

I have examined the Oregon wolf PVA and found that details of the model's
construction are vague or confused about fundamental aspects of the model, and some outputs
seem to disagree with conclusions in the text. The model includes many relevant factors
important to wolf population dynamics, but excludes or underestimates others such that I
believe that the PVA as it was used is too simplistic and lacks sufficient detail of important
demographic processes to realistically estimate probabilities of " conservation failure" or
"biological extinction" over time.

It is my expert opinion that the existing PVA is fundamentally flawed and does not provide an adequate or realistic assessment of the Oregon wolf population to meet Criterion 1 or 2 or 4, therefore the delisting requirements are not supported by the results of the PVA as it was performed.

My primary concerns with the Oregon wolf PVA are:

1. The base model seems to produce unrealistically stable and high population growth.

2. Density-dependent survival and reproduction are not included.

3. Dispersal and territory establishment are poorly modeled.

4. Environmental and Demographic stochasticity were not explained clearly enough to convince me that the model was properly constructed.

5. Environmental stochasticity was poorly modeled.

6. Impacts of human-caused mortality were downplayed.

7. Sensitivity analyses were insufficient.

1) The **base model seems to produce unrealistically stable and high population growth**. Perhaps due to unrealistically high estimates of vital rates, or due to unrealistic levels of vital rate variability or covariances of vital rate variability (see below), the population growth rate of the base model is unrealistically high and stable. Page 16 of Appendix B says, "Using our baseline model, simulated wolf populations increased an average of 7% ($\lambda = 1.07 \pm 0.17$ SD) per year." This high growth rate (λ = finite rate of population growth) and its variation are comparable to recent estimates from three populations of wolves over 10 years in the northern Rocky Mountains (Gude et al. 2011). However, a recent meta-analysis of three protected and circumscribed populations monitored over 28–56 years showed population growth rates were very close to $\lambda = 1.0$, with much greater variation (SD = 0.33 to 0.51) than the Oregon wolf

PVA described (Mech and Fieberg 2015). A summary in Fuller et al. (2003) of 19 exploited (hunted) wolf populations monitored for 2–9 years described the average finite population growth rate as $\lambda = 0.995 \pm 0.21$ SD. This leads me to believe that the Oregon wolf PVA underestimated the risk of conservation failure and biological extinction due to structural issues in the model, or due to underestimates of variability or covariation in vital rates.

2) Density dependence in survival, reproduction, and dispersal success should have been included in the model structure. What the PVA authors called density dependence was actually a simply calculated carrying capacity, or theoretical maximum wolf population size, given the current elk population, but was not in any way a realistic modeling of density dependent effects on the growing wolf population. Furthermore, wolf carrying capacity was computed in the PVA using summer elk range, when winter range, the period of greatest food limitation and the greatest limitation on elk spatial distribution, is the more realistic and conservative period during which to estimate carrying capacity.

True **density-dependent** effects would have recognized the documented cumulative effects of an increasing or decreasing wolf population on vital rates of survival, reproduction, and dispersal and territory establishment. It has long been known that intraspecific competition related to territoriality seems to regulate wolf density below that predicted by food availability (Stenlund 1955; Pimlott 1967, 1970; Cariappa et al. 2011).   Without true density dependence in vital rates, the Oregon wolf PVA assumes wolf vital rates are the same whether wolf habitat is nearly empty of wolves, or when wolves have nearly filled all the habitat. That true density

dependence affects wolf populations was well demonstrated in Cubaynes et al. (2014) where

adult survival decreased as wolf density increased, independent of prey density in the area (see
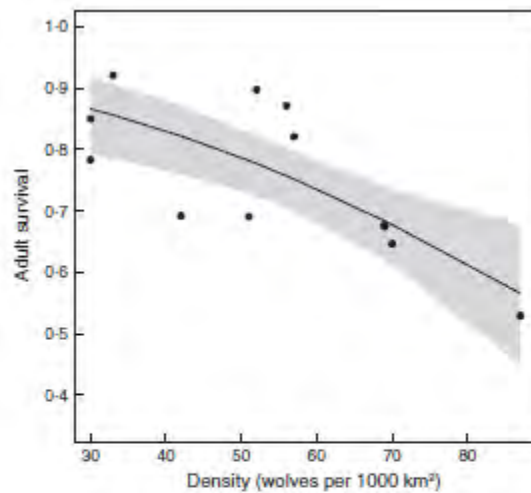

Fig. 3. Annual survival rates of adult wolves in the Northern Range as a function of wolf density in April. The intercept and slope were obtained from a model in which adult survival was modelled as a function of wolf density in April (Model 23), the zone filled with gray represent 95% confidence. Points represent mean survival estimates obtained from a model in which survival was time-dependent (Model 29).

Fig. 3 from Cubaynes et al. 2014, depicted here).

3) Dispersal and territory establishment should have been modeled as a spatially

explicit process using a similar spatial simulation as was used for emigration, combined with the

habitat model supplied in Appendix A. The PVA uses simple probabilistic rates of dispersal

and successful territory establishment. This is unrealistic given that wolves occupy exclusive,

defended territories in explicit spatial arrangements, so new territories cannot be established

where one already exists (Fuller et al. 2003). This relates also to the unrealistic density

dependence mentioned above. Also, wolves dispersing through non-habitat will not have the

same survival as wolves dispersing through suitable wolf habitat. A more realistic dispersal

process would use the existing wolf habitat map and established wolf territories, keep track of

additional territories as the PVA simulation progresses, and when a dispersing individual ends

up in an occupied area, it must disperse again until it ends up out of the state, or in unoccupied

habitat. Additionally, when wolves are travelling through non-habitat, their survival rates

should be lowered to reflect this reality. Human-caused mortality also should be increased

when wolves dispersed through non-habitat. Finally, dispersal and territory establishment

should have included an environmental stochasticity component.

      4) Environmental and demographic stochasticity are two of the most important

aspects of population viability analyses, but environmental and demographic stochasticity were

poorly described, and even the authors of the Oregon wolf PVA seem confused about this topic.

      Appendix B states, "We incorporated environmental stochasticity in our model by

randomly drawing vital rate values from a uniform distribution with a predefined mean and

standard deviation at each time step of the simulation." What this describes is <u>not</u>

environmental stochasticity, this is **demographic stochasticity**, as is stated in the next sentence

of Appendix B, "…vital rates were applied at an individual level, which inherently incorporated

demographic stochasticity into our model." This confusion over demographic and

environmental stochasticity is very disturbing. Nevertheless, we can establish that some level of

individual demographic stochasticity is included in the model, but the authors of the PVA are

unclear about the details. Drawing from a uniform distribution means all values between the

lower and upper boundaries are equally likely to be selected. The authors say the values for

vital rates were "from a uniform distribution with a predefined mean and standard deviation",

but this is somewhat nonsensical. What I think they mean is that they drew from a uniform

distribution where the interval's lower and upper boundaries were defined by the estimate of the

vital rate's mean, plus and minus 2 SD, however in Table 1 they say," Values used at each time

step of the analysis were randomly drawn from a uniform distribution within the specified

standard deviation (SD)." So I am confused about a fundamental aspect of the PVA's

construction regarding demographic stochasticity. This is a critical point as defining the

uniform distribution as the vital rate's mean ± 1SD would make demographic stochasticity

much less than if the uniform distribution's interval was defined as the vital rate's mean ± 2SD.

5) The effects of **environmental stochasticity** are included in the model as two 'catastrophes,' and a prey multiplier effect. The first catastrophe resulted in complete reproductive failure for that year at the pack level to simulate diseases such as canine parovirus, and occurred with an annual probability of 0.05. The second catastrophe was modeled at the population level "to represent extremely rare, range wide events that may affect wolf populations (e.g., disease, abiotic conditions, prey population crashes)," that occurred with a probability of 0.01 and resulted in a population-wide reduction in survival of 25%. These sorts of catastrophe are indeed useful to include because rare phenomena with large demographic effects are real and often have significant effects on populations. Indeed, in the PVA as constructed, these catastrophes were important effects during early years of the simulations, before population size was large enough to be resilient to catastrophes.

Unfortunately, catastrophes are not realistic proxies for true **environmental stochasticity** in abiotic conditions or prey availability that are typically due to stochastic annual variation in weather patterns. True environmental stochasticity would recognize that all wolf vital rates of age-class specific survival and reproduction usually co-vary among years because they are all correlated with certain weather phenomenon (such as extremely cold, wet winters) either directly, or indirectly through the weather's effects on prey species. Environmental stochasticity should have been modeled as a population-wide, or climate zone region-wide effect whereby all demographic parameters rise or fall together according to either a documented relationship between weather and vital rates, or a relationship between weather and prey species that indirectly affects wolf demographic vital rates.

The Oregon wolf PVA did include a prey multiplier effect (page 12) as environmental stochasticity, where, "Each year of the simulation, the prey multiplier had a 1 out of 3 chance of increasing, decreasing, or remaining the same, respectively. In years the prey multiplier increased or decreased, the maximum change was restricted to 0.10." However, this effect

seems too small, or perhaps too limited by not affecting reproduction and dispersal, to realistically simulate true environmental variation.

Several studies have documented that the wolf populations are regulated by food, as a function of prey abundance and their vulnerability to predation (Packard and Mech 1980; Keith 1983; Peterson and Page 1988; Fuller et al. 2003). Because prey condition is highly dependent on weather conditions (Mech and Peterson 2003), wolf demography is also dependent on weather (Fuller et al. 2003). "In Denali National Park, Alaska, where humans also have little effect on the wolf population, the trend in wolf numbers from 1986 through 1994 … was driven by snow depth, which influenced caribou vulnerability (Mech et al. 1998)… As snow depth and caribou vulnerability increased, adult female wolf weights also increased, followed by increased pup production and survival and decreased dispersal (Mech et al. 1998)… In the east central Superior National Forest of Minnesota…from about 1966 to 1983, the wolf population trend followed that of the white-tailed deer herd, which was related to winter snow depth. Thus snow was seen as the driving force in the wolf-deer system (Mech 1990)." From Fuller et al. (2003). In Isle Royale National Park, wolf population growth depended mainly on the number and age structure of the prey population, although density dependence, winter severity, and catastrophic events like disease outbreaks also play important roles (Peterson and Page 1988; Peterson et al. 1998; Vucetich and Peterson 2004).

6) Human-caused mortality impacts were significant, but conclusions downplayed the effect of human-caused mortality. The section on lethal control (page 26, Appendix B) addressed the issue of legal and illegal human-caused mortality, and concluded that reasonable levels of human-caused mortality could result in conservation failure and/or biological extinction. Probability of conservation-failure increased to 0.40 and 1.00, for mean human-caused mortality rates of 0.15 and 0.25, respectively. These results highlight the importance of anthropogenic mortality to population viability of wolves. Probability of biological-extinction was relatively low for all simulations with mean human-caused mortality rates ≤ 0.15.

Additionally, human-caused mortality is likely to increase as the wolf population increases, possibly leading to additional density-dependent mortality. Illegal human-caused mortality has been recorded as 30–34% of total mortality (Liberg et al. 2012; Board 2012).

Oregon Legislative Assembly changed the status of wolves to "special status game mammal" under ORS 496.004 (9). Under this classification, and when in Phase III of the Wolf Plan, controlled take of wolves would be permitted as a management response tool to assist ODFW in its wildlife management efforts. This rule would effectively allow the legal killing of all wolves in excess of the conservation objective of 4 breeding pairs. Reducing the population to such a low number would undeniably result in the impairment of wolf viability in the region. A PVA scenario should be run to quantify the probability of conservation failure and extirpation under this legally permitted management action.

7) The **sensitivity analyses** was simplistic and insufficient in my opinion to characterize true sensitivity of demographic parameters under different scenarios of management and environmental conditions. The PVA was supposed to focus on "determining effects of key biological processes, uncertainty in model parameters, and management actions on wolf population dynamics and viability." I recommend a more detailed and systematic sensitivity analysis where specific parameters are individually varied ± 5, 10, and 15% to determine their impact on population growth rate. Additionally, I recommend that after the model structure and parameter values and variation has been corrected as I suggested above, several realistic management and ecological scenarios be explicitly examined to document realistic probabilities of conservation failure and biological extinction.

Sincerely,

Derek E. Lee

Principal Scientist

Wild Nature Institute

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Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

Grimsö Wildlife Research Station

Comments re: ODFW's gray wolf delisting recommendation and status review

October 29th 2015

To the Oregon Fish and Wildlife Commission:

This comment concerns the document "Updated biological status review for the Gray Wolf (*Canis lupus*) in Oregon and evaluation of criteria to remove the Gray Wolf from the List of Endangered Species under the Oregon Endangered Species Act (Oregon Department of Fish and Wildlife (ODFW), October 9, 2015)" in particular to the Appendix B "Assessment of Population Viability of Wolves in Oregon" hereafter termed "the PVA".

My name is Guillaume Chapron, I am Associate Professor in quantitative ecology at the Swedish University of Agricultural Sciences and my research focuses on large carnivore conservation and management, with a particular emphasis on modeling and viability analysis. I have more than a decade of experience in this field and my research has been published in the top U.S. and international peer-reviewed scientific journals (see e.g. Chapron et al. 2014. *Science* 346 (6216): 1517-1519, Bauer, Chapron et al. 2015. *PNAS*. 10.1073/pnas.1500664112).

I submit this comment to help the commission in meeting the requirement outlined in OR ESA that listing decisions be based on "documented and verifiable science".

My first comment is to congratulate ODFW for providing details on the PVA and sharing the R source code of the PVA. Such openness and transparency are not so common among agencies and deserve to be praised, as they open up for the possibility of constructive criticism. My comments are the following:

1) The PVA is not statistically correct.

A PVA typically functions by running multiple stochastic (i.e. random) trajectories of a simulated population and counting the resulting number of extinct trajectories. For example, if one would simulate 1000 trajectories and obtain 137 extinct trajectories among these 1000, the extinction probability would be 13.7%. A critical part of a viability model is therefore how stochastic processes are modeled. I have reviewed the source code of the PVA written in the R language and the way stochasticity is modeled is not correct. Taking the example of survival events, stochasticity is modeled by generating a random number from a uniform

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distribution between 0 and 1 (as I understand it, this amounts to demographic stochasticity), and then comparing that number with another number. This latter number is randomly generated from a uniform distribution with parameters (mean-SD, mean+SD) and, as I understand it, this amounts to environmental stochasticity. This approach is fundamentally wrong for two reasons. First, the breadth of the latter distribution is restrained and values lower than mean-SD and larger than mean+SD are by default impossible (which roughly means 32% of all possible values, see the "68–95–99.7 rule", noting that excluding the lowest values will have the most severe impact on extinction risk). Second, all values are equally likely, which is typically not the case when estimating parameters from field data as one gets a normal (or bell-shaped) parameter distribution. The PVA therefore restricts possibilities of extinction and adds noise in parameters that could be more informative. The proper way to model environmental and demographic stochasticity for survival is by using a beta-binomial mixture where beta distributed values (with shape parameters obtained through the method of moments with mean and SD) are randomly generated to serve as parameters of the binomial distribution.

The same problem is also present for litter size, where the PVA uses a uniform distribution between 2 and 8. This means that litter sizes of 1 are impossible and that litter sizes of e.g. 2, 3, 4, etc till 8 are all equally likely. This approach is simply inconsistent with wolf biology. One could use a Gamma-Poisson mixture to generate stochastic integer numbers with some environmental stochasticity.

Environmental stochasticity in the PVA is in practice implemented by sampling a vector with stride of 0.01 or 0.001. However I noticed the stride was different between environmental (0.001) and demographic (0.01) stochasticity for poaching and this is also not correct.

Finally, because the model has a quite a few parameters, I believe that running 100 trajectories is not enough to get informative and converging estimates of extinction risk and 1000 trajectories would have been a minimum. I consider the points raised in this section justify the rejection of the PVA without further consideration.

2) The PVA is not properly validated.

Calibrating and validating a complex Individual Based Model is important but can also be challenging. For the OR wolf PVA this seems to have been done by comparing simulations with a time series of 5 years. I do not believe this is statistically rigorous. Modern algorithms such as Approximate Bayesian Computation with prior-posterior inference or Pattern Oriented Modeling would be more suitable here. Note that the PVA has probably quite a few weakly identifiable parameters (pairs of different parameter values giving the same model fit). Importantly, it is not because the model was published in a peer-reviewed journal that this implies the model is validated or correct (see previous point showing it is not) and I recommend the OR wolf PVA and its R source code be peer-reviewed in

an open and transparent process. Finally, I would like to point to the fact that the initial population is randomly assigned across age and social classes, which suggests the population did not start at an asymptotic stage, and early oscillations of the population structure may have affected simulations and the results of the sensitivity analysis.

3) The PVA does not use realistic parameter values or scenarios.

The PVA is parameterized with a very low poaching rate. This is not in line with what has been found in other wolf or large carnivore populations. Using a hierarchical Bayesian state-space model I have found that half the mortality of wolves in Sweden was due to poaching and that two third of poaching was not observed (Liberg, Chapron, et al. 2015. Proceedings of the Royal Society B 279 (1730): 910-915). There has been several documented cases of illegal take in OR and the total number is likely higher as illegal activities are typically under-reported. The PVA also assumes that survival rates were not influenced by social status of the animal but I question whether this is realistic as some social classes are exposed to higher mortality risks by being more active in hunting large prey.

A critical assumption of the PVA is that the past is a proper representation of the future, in particular regarding human induced mortality rates. However, the PVA in this case is actually being used to make a decision making the future different from the past (delisting). Therefore, justifying delisting based on a PVA assuming that parameters will remain constant for the next 50 years is inadequate as parameters are likely to change as soon as and if delisting happens—especially if the state moves to initiate legal hunting and/or trapping of wolves. Indeed, the PVA actually documents the effect of such changes and finds that the probability of conservation failure dramatically increases with legal mortality. A proper interpretation of the actual PVA results would actually support not delisting the wolves in OR.

Another critical assumption in the PVA is the annual immigration of 3 wolves in OR. This raises two questions. First, a population is generally considered as viable when considered as a stand-alone population and not through the regular addition of individuals. Second, the persistence of this flow of immigrants is doubtful as, for example, adjacent states are attempting to dramatically reduce their wolf populations.

4) A PVA is not the appropriate tool.

The PVA completely ignores long-term viability and the ability of OR wolves to adapt to future environmental change. However, there is a substantial amount of literature of the need for populations to have a genetically effective population size of at least Ne=500 to be considered as genetically viable and a large number of viability analyses in the conservation literature have used a package called VORTEX to include genetics aspects in viability estimates. It is unfortunate the PVA ignores such aspects and this precludes using the PVA to reach conclusions

on the long-term viability of OR wolves and hence meet the requirement of OR ESA.

Worth noting is that under no possibility could a population of ~85 individuals be considered as not warranting listing under the IUCN Red List, which is a globally recognized authority in assessing species extinction risks. Similarly, the Mexican wolf population is today larger than the OR wolf one but is not at all considered as recovered by Federal authorities. There appears to be little substance for ODFW to consider a population of ~85 wolves as being recovered.

ODFW finds that the wolf is not now (and is not likely in the foreseeable future to be) in danger of extinction throughout any significant portion of its range in Oregon. However, ODFW makes this statement by implicitly removing "any significant portion of its range", as only the outcome of a non-spatial PVA is considered sufficient. The reality is that the wolf is past being in danger of extinction throughout many significant portions of its range in OR because it occupies only 12% of its suitable habitat (so is extinct in 88% of its suitable habitat). The interpretation of this section of OR ESA by ODFW is an illegitimate interpretation that implies the suitable habitat where the species has become extinct is no longer considered as part of the species range and included in recovery targets. This interpretation also runs contrary to recent scientific literature on significant portion of range.

Finally, there has been an impressive amount of research on the ecological role wolves can play in shaping ecosystems and the report by ODFW does not consider fulfilling this role as a criteria for delisting.

Based on the points raised above, I conclude that the PVA does not provide support for delisting wolves in OR.

Yours sincerely

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RE: Oregon wolf management plan and proposal to delist gray wolf

To Whom it May Concern:

We welcome the opportunity to address Oregon Department of Fish and Wildlife 's (ODFW) proposal to remove Endangered Species (ES) protection from the State's gray wolves (*Canis lupus irremotus*). The State's wolf plan emphasizes the need to employ the best peer reviewed and most current data available.

ODFW is seeking public input on three potential options for wolf management. The first would remove the wolf from the State's Endangered Species designation—ODFW's preferred option. A second option would remove the wolf from the State's Endangered Species designation in the eastern portion of the state but retain the Endangered Species designation in the western part of the state. The third option, our preference, maintains the wolf in protected status on the State's Endangered Species list. The decision by Oregon will be based on the following criteria: 1) the species is not in danger of extinction in any portion of its range; 2) the species' reproductive potential is not in danger of failure; 3) populations are not undergoing imminent or active deterioration of range or primary habitat; 4) over-utilization of the species or its habitat is not occurring or likely to occur; 5) existing state or federal programs or regulations are adequate to protect the species and its habitat. In our opinion, the five criteria for Oregon's delisting options to be met have not been achieved and/or are based on untested assumptions at this time.

1

Status of the Gray Wolf in Oregon

ODFW (2015) estimates there are 77 wolves in Oregon and expects to maintain this figure with four breeding pairs per annum, as a MVP (minimum viable population) size. The wolf has been in Oregon for the past eight years and occupies, by one broad-brush estimate, approximately 15% of the State, mostly in the east. However, analysis of ODFW's own data indicates that actual areas of current wolf use comprise only 12% of the suitable wolf habitat in Oregon (Weiss 2015). If delisted, wolves would be protected for three additional years with the exception that animals deemed a threat to livestock could be lethally controlled.

State Wolf Management Plans & Implementation

The U.S. Fish and Wildlife Service (FWS) began removal of the gray wolf from the protection of the Endangered Species Act (ESA) in 2009. The FWS, by implementing questionable management decisions, has abrogated its conservation obligations under the ESA for gray wolves (Alderman 2009, Bruskotter et al. 2014). In lieu of federal oversight, for a historically exploited species that remains extirpated from the majority of its range, management authority has been left to the states where the species is considered federally recovered. States are required to develop wolf management plans to maintain viable populations

Oregon considers their wolf population to be recovered in spite of evidence to the contrary, consisting of very low population count and habitat saturation. By law Oregon has been mandated to develop a management plan for the species. The plan Oregon has developed is of questionable merit to maintain a viable population. Unfortunately, many state wolf management plans have failed to meet the intent, as meant by Congress, for scientifically based recovery in the short or long term (Anderson 2004, Harbine 2009). State wildlife agencies,

which have been given broad discretion, have frequently acted to appease vocal and politically active anti-wolf interests, traditionally members of the agricultural, hunting and property rights constituencies who prefer low wolf populations through large harvests and liberal regulations to cull "problem" wolves (Anderson 2004, Bergstrom 2011, Bergstrom et al. 2009, Haber 1996, Harbine 2009). Beyond livestock interests and some ungulate focused sportsmen groups, the preponderance of the public and stakeholders have clearly expressed their sentiments to see government planning maintain long term viable wolf populations able to survive predictable and stochastic factors far beyond the foreseeable future into the next century (Alderman 2009, Anderson 2004, Harbine 2009, Kellert et al. 1996).

Conversely, several state wolf plans take a myopic view. Creel and Rotella (2010) document many shortcomings of these recent plans:

> "Rocky Mountain wolves were removed from the ESA in May, 2009. Idaho and Montana immediately established hunting seasons with quotas equaling 20% of the regional wolf population [combining] ...hunting and predator control...37.1% of the Northern Rocky Mountain (NRM) wolves were killed in the first year of delisting….unprecedented for a species to move so rapidly from the ESA to direct harvest...strong association between human offtake [with] additives in total mortality....in North American [wolves]...".

Creel and Rotella (2010) explain that even substantially lower harvests than allowed by the government have been detrimental to wolves. Liberal wolf harvest quotas by Idaho's Department of Fish and Game have killed at least 1,100 wolves. Such a magnitude of removal has surpassed the number considered necessary to maintain the MVP, yet Idaho continues its unabated hunting and culling leading to the conclusion that, "open hostility toward wolves is official state policy" (Harbine 2009).

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Idaho's actions are blatantly not focused on maintaining wolves, but it is by no means an outlier among the states with wolf management plans. The Northern Rocky Mountain states exemplify several worst case scenarios of unscientifically and politically motivated wolf management. These attitudes, enabled by some state governments, extirpated the western wolf by the 1930's. Given tolerance for legal and illegal killings of wolves, the lack of repercussions for poaching and weakly written and unenforced recovery goals, the wolf's recovery remains uncertain in some states (Anderson 2004, Bruskotter et al. 2014, Harbine 2009)   .

Recognizing the weakness of some state plan,s the judiciary has intervened on behalf of wolves. Federal courts in Wyoming and Michigan have ordered protection reinstated for gray wolves within their jurisdictions. The courts have described management in those States as being characterized by, "lack of planning" and "reckless[ness]" (Alderman 2009).

A weakness in many of these recent state management plans is that the political process and special interest groups have promoted and fostered limited recovery actions for the species. For many years, the FWS and states have discounted the concerns expressed by many scientists about the inadequacies and perils of the government's wolf management plans (Bergstrom 2011, Bergstrom et al. 2009, Haber 1996, Morrell 2008). Most plans remain unchanged and several are characterized by unrealistically low MVPs (Alderman 2009, Harbine 2009, Reed et al. 2003). It is important that Oregon in its planning and implementation avoid many of these problems exhibited by other states and regions, including removing protected status too early.

Criterion 1: "Species is Not Endangered in Any Portion of its Range."

The gray wolf in Oregon is more than "endangered" in significant portions of its range; it is in fact absent from 88% of suitable wolf habitat in the state of Oregon (Weiss 2015). Oregon's

suggested MVP not only is inadequate to protect the species, but if kept this low it will not serve as an effective source of dispersers to fill the rest of the suitable wolf range in Oregon. Well established principles of conservation biology hold that populations need robust numbers of individuals for long-term viability. Recovery, as defined by ODFW, appears premature considering that the gray wolf's return to Oregon has been for an unusually brief time and that it has not in this brief time repopulated most of the suitable habitat available.

In contrast to the current situation in Oregon, the neighboring NRM had populations establishedfor 13 years before delisting, consisting of at least several hundred animals and at least 45 breeding pairs (Fallon 2008, Reed et al. 2003). These animals had been repatriated into almost ideal conditions consisting of large tracts of wilderness and sparsely human inhabited ecosystems and optimal prey, the vast Northern Range elk (*Cervus elaphus*) herd, which had been so unchecked that they were instrumental agents of habitat destruction. The Upper Midwest (Minnesota, Wisconsin and Michigan) is characterized by healthy, functional and ecologically viable wolf populations of approximately 3,700 animals, which were established in a protected status for at least several decades (Bruskotter et al. 2014, Fallon 2008, Leonard and Wayne 2008, FWS 2014). Their range includes large tracts of protected lands that stretches into Canada. The present status of Oregon's wolf population is significantly less secure than in these cases.

Canid populations of fewer than 100 are insufficient to sustain a long term viable population. Alaska's Alexander Archipelago subspecies (*Canis lupus ligoni*) suffered a major population crash, which in one year cut its size from 221 to 89 (Edwards and Noblin 2015, Person and Larson 2013). Their fate is contingent upon whether or not the FWS lists them as protected. At Alaska's Denali National Park, the National Park Service (NPS) was forced

prematurely to terminate wolf harvests, also due to a precipitous population decline (Arthur 2015). The Southwest's Mexican gray wolves (*Canis lupus baileyi*) had been subject to significant levels of illegal take necessitating at times recapture to protect them (Povilitis el al. 2006, U.S. Fish and Wildlife Service 2008).

Use of MVP as a strict conservation tool for species has value but should not be employed as an absolute for precise population targets; the limitations of modeling and the information they are based on require that we err on the side of caution when setting population objectives for rare species (Brook et al. 2006, Vucetich et al. 2000). Very few wildlife and plant species would be considered for delisting that have populations below 100 (Brook et al. 2006, Bergstrom et al. 2009, Morrell 2008, Thomas 1990, Traill et al. 2007, Vucetich et al. 1997, Wabakken et al. 2001).

Criterion 2: "Species' Reproductive Potential is Not in Danger of Failure."

Just as the examples cited above for long-established wolf populations, the future reproductive potential of Oregon's wolf population and its ability to increase is unknown. Examples from some other areas/regions have demonstrated conditions where recovering populations have not increased or declined largely due to anthropogenic factors (Liberg et al. 2011, Morrell 2008, Murray et al 2015, Povilitis el al. 2006, U.S. FWS 2008, Vucetich and Paquet 2000). At this stage of recovery for the population in Oregon, it is too early to determine or predict its future reproductive potential with any certainty as well as the key factors that may influence it.

If removal from protection occurs for Oregon wolves, potential culling/harvest will affect the species' reproductive potential. Culling and harvest, which will likely transpire upon

delisting, is a documented stress factor to packs. The concomitant physiological increase in cortisol levels hampers fecundity in surviving animals (Bryan et al. 2014). Reproductively viable wolf populations are characterized by a stable social hierarchy in a known territory with an adequate prey base. Culling and harvest disrupts this social behavior and structure (Borg et al. 2015). Adult wolves that are killed are unavailable to teach hunting techniques and maintain control over their pack structure, leading to a reduction in reproductive output and young adult wolves that disperse prematurely, entering unknown areas, which may increase mortality particularly from anthropogenic sources.

It is not known with certainty if the species' reproductive potential is secure enough to maintain a viable population and how that may change if protected status is eliminated. Wolf populations elsewhere have exhibited significant volatility due to legal take, illegal take, disease and habitat loss (Haber 1996, Haydon et al. 2002, Liberg et al. 2012, Sparkman et al. 2011, Wilmers et al. 2006).

Recovery and protection planning require a goal of maintaining not only a minimum population number, but also adequate genetic diversity (Wayne and Hedrick 2011). Larger populations can avoid the deleterious effects of inbreeding, which in certain cases can be a precursor to extinction (Liberg et al. 2005, Peterson and Krumenaker 1989, Wayne et al. 1991). On Isle Royale a population of over 50 wolves is now down to three, a partial result of inbreeding effects. Low populations of other large predators have demonstrated the impacts of the loss of genetic diversity to population vitality (Florida panthers, *Puma concolor* and cheetahs, *Acinonyx jubatus*) (Hedrick and Fredrickson 2010, Johnson 2010, O'Brien et al. 1985).

Wayne and Hedrick (2011) state that, "isolated populations of less than 100 individuals...have a high chance of extinction...genetic loss could be consequential...these

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populations could lose 2.5% [genetic heterozygosity] per generation." A generally accepted number of 500 animals is considered an acceptable baseline estimate for a Minimum Viable Population (MVP) to avoid inbreeding depression in the short term (Brook et al. 2006). Preferably, the MVP would be 1,200-2,500 (Fallon 2008). Wolves in the NRM specifically should have 1,403 individuals with a goal of 6,332 at 40 generations to better ensure a genetically diverse, robust population to last for a century (Reed et al. 2003).

Oregon's option for removal of the gray wolf from protection at this time does not provide safeguards for the genetic diversity of the population, which could have deleterious drift effects and inbreeding depression, nor a large enough population for maintaining reproductive potential in the long-term.

Criterion 3: "Populations are Not Undergoing Imminent or Active Deterioration of Range or Primary Habitat."

A diverse array of suitable prey and habitat exists for wolves in Oregon (Larsen and Ripple undated), yet only about 12% of it is currently occupied by wolves (Weiss 2015). Western Oregon is heavily urbanized with a continuously growing human population, a frequent deterrent for many of the West's exploited wolves as well as a potential for increased cause of mortality due to transportation infrastructure and potential for higher levels of human disturbance. Conversely, rural Eastern Oregon is characterized by agricultural and timber resources where those interests frequently view wolves in a negative manner, which in some circumstances results in unregulated take (Anderson 2004, Liberg et al. 2011).

The importance of travel corridors between subpopulations of wolves in the State is also not well known or documented at this time due to their limited number. Travel corridors are

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considered essential for maintaining disjunct wolf populations (Haight et al. 1998). Paquet et al. (2009) stress the significance of avoiding anthropogenic impacts to wildlife movement. Wolves are what Paquet et al. (2009) refers to as "passage species," which "need corridors to allow individuals to pass directly between two areas in discrete events of brief duration (e.g. dispersal of a juvenile, seasonal migration, or moving between parts of a large home range)." Oregon is considered to have less contiguous habitat and more patches spread out than in the NRM, which would require wolves to cross areas of unsuitable habitats (Larsen and Ripple undated). Essential corridors for wolf populations and habitat patches within Oregon are poorly known and understood, because the species is still in an early stage of recovery.

Criterion 4: "Over-utilization of the Species or its Habitat is not Occurring or Likely to Occur."

Wolves were efficiently extirpated in the contiguous U.S. by the 1930s. FWS describes the event as, "wolves were hunted and killed with more passion and zeal than any other animal in U.S. history" (FWS 1998). Given our modern technology and increased network of roads even in protected lands, anyone can access wolf habitat and cause the take of wolves. Many individuals have access to year-round use of off-road vehicles, aircraft, drones, traps and high-powered guns. As just one example of the ability for rapid reductions, in Canada, the government permitted the taking of several hundred wolves in several days by hunters on snowmobiles with firearms, indicating the ease of making large reductions in a short period of time (Cluff 2003). Key habitat areas and components, as well as essential travel corridors and their level of protection, are poorly understood and should be addressed before delisting occurs.

Poaching has been estimated to comprise 30% of known mortality in some wolf populations (Liberg et al. 2012), and roadkill as much as 11% (Fuller 1989).

Criterion 5: "Existing State or Federal Programs or Regulations are Adequate to Protect the Species and its Habitat."

The gray wolf has only recently returned to Oregon. It still occurs in isolated populations and occupies only a fraction of its former range. Eliminating existing state protection under its current status is not justified at this stage. Setting the regulatory environment to increase "take" or modifying the current status of protected habitat when the population is at an early stage of recovery is not justified for meeting a goal of maintaining a viable population. There are many examples where wolf populations have declined or where recovery has been delayed/slowed due to a lack of or limited government protection (Bergstrom 2011, Bruskotter et al. 2014, Edwards and Noblin 2015, Liberg et al. 2011, Morrell 2008, Murray et al. 2015, Polivitis et al. 2006, Vucetich and Paquet 2000).

Comments on the population viability analysis (PVA)

Although we have not examined the PVA in great detail, we do have a few concerns and questions about the reliability of some assumptions made about wolf vital rates, and the lack of application of the best and most recent science on these specific issues. First, it appears that the modelers assumed that current population growth rates of the Oregon wolf population, which are indicative of an expanding population filling vacant habitat, will continue indefinitely. If so, that is unrealistically optimistic. The reality for the gray wolf population of Yellowstone National Park (YNP) after reintroduction was that density peaked at > 170 animals in the early-mid 2000s,

and then fell to around 100 or fewer for the last 5 years

(http://www.nps.gov/yell/learn/nature/wolfmgnt.htm). In other words, density dependent self-regulation took control some years after establishment (demonstrated in a statistical analysis of this population; Cubaynes et al. 2014), causing first a negative population growth rate and ultimately an equilibrial density that was considerably lower than peak density. The latter would constitute a more realistic model of what happens to wolf population dynamics when the habitat fills up.

Second, we think that 88% adult survival is unrealistically high, given that the most recent analysis of the unhunted YNP population revealed a natural mortality rate of 20% (95% C.I. ranging from 5-50%, and with higher mortalities at higher densities when inter-pack aggression increased). The same study also indicated an 8.4% mortality due to roadkill. To the extent that the PVA incorporates human-caused mortality, it should not be assumed that such mortality is largely compensatory (i.e., trades off with natural mortality, or is compensated for by increased recruitment as a response). Any rigorous sensitivity analysis within PVA would be remiss if it did not model the effects on wolf population growth rates of human-caused mortality acting in an *additive* and even *super-additive* manner. Creel and Rotella (2010) found that in the Northern Rocky Mountain (NRM) metapopulation, human offtake was indeed super-additive. Similarly, Ausband et al. (2015) found for NRM wolf populations that not only did recruitment not increase to compensate for human-caused mortality, but it actually decreased (again, the super-additive effect).

Finally, poaching is likely to be a significant source of mortality, which is often overlooked or underestimated, and therefore must be modeled. Although difficult to determine, 2 recent estimates of the proportion of total mortality in wolf populations that is due to poaching

are 30% for Sweden (Liberg et al. 2012) and 34% for Wisconsin (Natural Resources Board 2012).

Our Recommendations

Even though we feel that the USFWS-imposed threshold for listing (relisting) of the gray wolf in each of the three neighboring NRM states—150 wolves and 15 breeding pairs sustained for at least 3 consecutive years—is unjustifiably low given the science we have briefly reviewed above, Oregon's current population is only half that. Therefore, it would be preferable if Oregon not entertain the prospect of delisting the gray wolf at least until that landmark was achieved for 3 or more consecutive years. That should also allow the gray wolf to increase its utilization of suitable habitat in the state beyond its current 12%. In the meantime, the species should be closely monitored and information collected to aid in the continuing refinement of the state's wolf management plan, specifically identifying and protecting key habitat and travel corridors, developing innovative policy and guidance for agricultural interests to reduce the need for removal/culling (Niemeyer 2012, Shivik 2006, Wielgus and Peebles 2014), and providing a focus on maintaining a population at a level for a functional ecosystem role (Licht et al. 2010).

Cordially,

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October 25, 2015

Oregon Department of Fish and Wildlife Commission
4034 Fairview Industrial Drive SE
Salem, OR 97302
ODFW.commission@state.or.us

Chair Finley and Commissioners:

My name is Robert Beschta, I am emeritus professor in the Department of Forest Ecosystems and Society at Oregon State University (professional affiliation provided for informational purposes only). For more than four decades I have participated in research, teaching, and extension activities assessing the effects of land use practices on watersheds and plant communities. Much of that effort was in Oregon but more recently I have done research in Yellowstone National Park and other areas of the American West.

When wolves were extirpated from Yellowstone National Park, increased herbivory by elk soon began to impact plant communities. Over time, and over a wide range of elk densities, the park's aspen, willow, cottonwood, alder, and a wide range of berry-producing shrubs were less able to establish and grow above the browse level of elk; tall forbs and native grasses were also impacted. As a consequence, streams eroded and incised, riparian habitat for birds and other wildlife became limited, and beaver disappeared.

After seven decades of absence, wolves were returned to the park in the mid-1990s thus completing the wild predator guild. With the return of this apex predator, changes to previously browsing-suppressed plant communities began to occur. Initially these effects were small and local but over time the effects have become more widespread. Increasingly aspen and riparian plant communities have become more robust, increasingly plants are growing above the browse level of elk, stream banks are stabilizing, more birds have habitat, and beaver are returning. These effects did not happen overnight, but have become more pronounced over the last several years. It is important to note that Yellowstone is not a unique, stand-alone experiment. Improving plant communities have also been observed in other areas of western North America where formerly extirpated wolves have returned.

Like Yellowstone, wolves were extirpated from Oregon and were absent over many decades. Elk numbers, which had been reduced to only a few thousand in the early 1900s have since increased greatly and in 2011 Oregon's total elk numbers were 3rd highest of 11 western states (based on estimates of the Rocky Mountain Elk Foundation). And, like Yellowstone, wolves have returned.

Oregon's wolf conservation and management plan indicates "Wolves need to be managed in concert with other species and resource plans." Most people would likely assume "other species" simply means elk. I would strongly suggest that we need to look deeper.

Deciduous woody plant communities on public lands in eastern Oregon, plant communities such as those associated with aspen and riparian areas, have experienced major declines over much of the 20th century with adverse consequences to terrestrial wildlife species as well as aquatic species, such as salmon. While outmoded livestock practices have been a major reason for this decline, herbivory by wild ungulates, principally elk, is now a significant factor in many areas and may limit recovery of degraded plant communities even if livestock impacts are minimized.

Whether the positive ecosystem effects found in Yellowstone and other areas following the return of wolves will occur in Oregon is not yet known. However, if wolves are going to be a factor in the recovery of degraded aspen stands and riparian plant communities on public lands in eastern Oregon, I would strongly indicate that delisting this keystone species is a move in the wrong direction.

Sincerely,

Robert L. Beschta

Robert L. Beschta, PhD

4005 NW Princess St.

Corvallis, OR 97330

Klamath Center for Conservation Research

Via email to:

Russ Morgan

Wolf Program Coordinator

Oregon Department of Fish and Wildlife

107 20th Street

La Grande, OR 97850

October 28, 2015

<u>Scientific peer review comments on Oregon Department of Fish and Wildlife Review of the Biological Status of the Gray Wolf</u>

Thank you for your invitation to submit comments on the updated biological status review document of October 9, 2015. My research as a wildlife ecologist with the Klamath Center for Conservation Research in Orleans, California, has focused on habitat, viability, and connectivity modeling for a diverse group of threatened and endangered species ranging from large carnivores to rare and endemic plant species. I have also served on the Science and Planning Subgroup of the Mexican Wolf Recovery Team. I welcome the opportunity to use this expertise to evaluate the document.

Firstly, I wanted to commend the Oregon Department of Fish and Wildlife (ODFW) for its work over the past decade to advance wolf recovery in Oregon, and specifically on the work that went in to preparation of the biological status review document. On the whole, the document is well-written, factual, and informative. However, there are several areas where the document could be improved to better reflect current science. Although the document states that a change in status (delisting) of Oregon wolf populations will have little practical short-term effect on management of the species in the state, it is nonetheless important that any status determination reflect best available science.

The population viability analysis (PVA) completed by ODFW to support the status report provides relevant information concerning some factors effecting population status. The PVA results support the intuitive conclusion that the relatively high reproductive rate shown in many colonizing wolf populations

make them fairly resilient to extirpation in the short term in the absence of high human-associated mortality rate (such as from hunting or lethal control programs). This conclusion can be drawn from simple deterministic PVA models. The PVA associated with this status review expands on this conclusion by using a stochastic individual-based model to evaluate factors (such as disease outbreaks or other chance events) that may threaten small populations, even if these populations on the whole show positive population growth. However, I have two areas of concern with the PVA, and with the resulting conclusion as to the resilience of the current Oregon wolf population:

1) the manner in which stochastic factors are parameterized in the PVA is overly optimistic;

2) the PVA does not incorporate the effects of small population size and isolation on genetic threats to population viability. Instead the status review relies on a brief qualitative discussion which does not accurately represent what is currently known about genetic threats to small wolf populations.

Treatment of stochastic factors

The ODFW PVA incorporates stochastic factors such as disease outbreaks or prey decline in two ways (PVA p 14):

1) An effect on reproduction via a 5% chance per pack of reproductive failure in any year. Importantly, these reproductive failures were not correlated between packs, so population-level reproductive output did not experience "bad years".

2) An effect on population-level survival where survival was reduced by 25% on average once in 100 years.

The PVA does not document the source of these parameter estimates, but they appear highly optimistic when compared to data from well-studied wolf populations such as in the Yellowstone region. In terms of stochastic factors affecting reproduction, effects of disease outbreaks on fecundity (considered broadly to include pup survival) are often correlated between packs in a population, which increase the effect of this factor on viability. Additionally, the ODFW PVA's mean interval of 100 years between catastrophes likely underestimates the frequency of events impacting population-level survival rates. If

only rare "catastrophic" events are considered, then a 25% decrement likely underestimates the effect of such an event on survival. In contrast to the parameters used in the ODFW PVA, Almberg et al. 2010 concluded based on data for the Yellowstone region that "wolf managers in the region should expect periodic but unpredictable CDV-related population declines as often as every 2–5 years".

Treatment of genetic issues associated with population size and isolation

Recent wolf PVAs (e.g., Carroll et al. 2013) have explicitly incorporated the effects of genetic factors on population viability. In contrast, the ODFW PVA omits quantitative consideration of genetic factors, which may cause its results to be overly optimistic. The status review relies on statements such as "In context of a larger meta-population, Oregon's wolf population is neither small, nor isolated" (p 20). This statement is so general as to be uninformative. Wolves were historically present throughout their range in the lower 48 states as a largely continuous population with some degree of genetic isolation by distance (Vonholdt et al. 2011). The current Oregon wolf population is small and relatively isolated when compared to historic conditions, and thus genetic factors are of potential concern. This is true even when Oregon's wolves are considered in a metapopulation context. The fact that wolves are good dispersers even in the current landscape may reduce genetic effects associated with small population size but will not eliminate these effects.

The review implicitly assumes that wolf populations in other states within the metapopulation will remain at their current size and continue to be a robust source of dispersing individuals. For example, on page 18, the document states "We contend that high levels of genetic diversity in Oregon wolves will be maintained through connectivity to the larger NRM wolf population." However, one cannot assume that populations in adjacent states will remain at current levels. The Idaho wolf population could potentially be reduced fivefold from its recent peak level, to a minimum of 150 wolves, under current state management regulations. Any such reduction would reduce dispersal into Oregon below that evident in the last decade. Additionally, if, in the longer term, hunting is permitted after delisting of Oregon wolves, this increased human-caused mortality, even if sustainable from a demographic perspective, would be expected to reduce immigration from the NRM population.

More generally, the document's statement (p 17) that "Small populations of wolves are unlikely to be threatened by low genetic diversity" is not consistent with the latest research on small wolf populations. For example, the wolf population in Isle Royale National Park has long been used as an example of the ability of a small, isolated wolf population to persist. However, recent developments have demonstrated the high risks associated with genetic inbreeding in this population (Raikkonen et al. 2009), which as of early 2015 had dwindled to 3 individuals (Vucetich and Peterson 2015). Similarly, the Finnish wolf population has decreased in size in recent years to the point where it has become genetically depauperate (Jansson et al. 2012).

Given these potential risks, a precautionary management approach is appropriate in order to avoid undermining the progress to date in recovering Oregon's wolf populations. Management of wolves in the Eastern Wolf Management Zone (WMZ) should ensure that the rate of dispersal to western Oregon during the period in which the western population is still being established is not reduced, so that wolf populations in the Western WMZ can be founded with the broadest sample of genetic representation from the larger metapopulation, in order to avoid future genetic problems. Continued frequent dispersal into the Western WMZ will also facilitate the establishment of wolf populations is all "significant portions of range" in western Oregon where habitat remains suitable for wolves.

Sincerely,

Carlos Carroll,

Klamath Center for Conservation Research,

e-mail: carlos@klamathconservation.org

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Appendix C

LIST OF ALL PUBLISHED LITERATURE

PROVIDED BY SWG ENVIRONMENTAL CAUCUS

TO CDFW ONE YEAR AGO

CITATIONS PREVIOUSLY PROVIDED TO CDFW IN JANUARY 2015
(pdf copies of cited materials were supplied to CDFW at that time)

In December 2014, CDFW provided an internal version of the draft wolf plan to SWG members, to review and provide feedback to the Department. SWG members replied with comments/text edits/literature citations in January 2015.

The environmental caucus of the SWG provided 56 citations to published, peer-reviewed research, reports, news articles, legal cases and agency website links, along with our comments and recommended edits. For each citation, we indicated the chapter of the plan in which it should be included and discussed. However, in the public version of the draft wolf plan CDFW released for public comment in December 2015, only one of the 56 citations has been included and discussed.

The 2015 public comment version of the plan is structured slightly differently than the 2014 internal version. The list below is of all 56 citations, indicated by chapter of relevance in the 2015 public version of the plan.

DRAFT WOLF PLAN, PART I

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Natural Resources Defense Council v. Fish and Game Com. (1994) 28 Cal.App.4th 1104, 1117-18

THE FOLLOWING CITATIONS ARE FOR CHAPTERS IN DRAFT WOLF PLAN, PART II

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CHAPTER 2 – DISEASES AND WOLVES
None

CHAPTER 3 – HUMAN INTERACTIONS AND CURRENT PERCEPTIONS OF WOLVES

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CHAPTER 5 – WOLF INTERACTIONS WITH OTHER WILDLIFE SPECIES

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http://www.wildlifeadaptationstrategy.gov

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http://www.jhnewsandguide.com/news/top_stories/gyc-sees-wolf-solution/article_ae0425ba-380c-5c2a-90dc-067e41c6d026.html

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CHAPTER 7 – EFFECTS OF WOLVES ON LIVESTOCK AND HERDING/GUARDING DOGS

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http://www.climatechange.ca.gov/adaptation/documents/Statewide_Adaptation_Strategy_-_Chapter_5_-_Biodiversity_and_Habitat.pdf

Hunter kills wolf in Utah, saying he thought it was a coyote
http://www.sltrib.com/news/1999741-155/utah-hunter-kills-wolf-near-beaver

CHAPTER 10 – PUBLIC INFORMATION AND OUTREACH
None

CHAPTER 11 – FUNDING NEEDS AND OPPORTUNITIES
None

CHAPTER 12 – PLAN EVALUATION AND REPORTING
None

Appendix D

WHITE PAPER FROM UNIVERSITY OF WASHINGTON
OCTOBER 29, 2014 SYMPOSIUM ON ECOLOGICAL AND SOCIAL
COMPLEXITIES OF LETHAL CONTROL OF WOLVES

Tackling Wolf Management's Thorniest Issue: The Ecological and Social Complexities of Lethal Control

Catherine H. Gowan[1], Carol Bogezi[2], John M. Marzluff[3], and Aaron J. Wirsing[4]

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The presence of gray wolves (*Canis lupus*) evokes intense emotions and attitudes throughout the species' range (Lute et al., 2014, Treves and Karanth, 2003). Therefore, the return of the gray wolf to the Pacific Northwest has thrilled conservationists but has at times been challenging for some residents, especially hunters and livestock producers, who share turf with these carnivores. In Washington State, wolf recolonization has heightened urban-rural divisions and management efforts to satisfy diverse stakeholders, including conservation groups, livestock producers, and hunters have been complicated. Between 2008, when the first wolf pack was established in Washington, and 2015, two packs in Washington have repeatedly depredated livestock and in response have been targeted with lethal control. In 2012, the Wedge Pack was removed for depredating cattle and in 2014, the breeding female of the Huckleberry Pack was removed after the pack depredated 24 sheep. Both uses of lethal control were controversial and led to extensive public comment, highlighting the need for scientific data to inform the use of lethal control as a management tool.

Understanding the social acceptability of the presence and management of predators is vital to their conservation in a human-dominated world. Although approximately 64% of Washington

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State residents are in favor of wolf recovery (Responsive Management, 2014), the wolf debate remains intense and management decisions by the Washington Department of Fish and Wildlife (WDFW) are under heavy scrutiny. Approximately 63% of Washington residents support some level of lethal removal to protect livestock, while 28% are opposed (Responsive Management, 2014). Residents' values concerning wolves often determine their attitudes toward wolf recovery and the management of wolves in the State. In a survey of Washington residents' attitudes towards wolves, respondents whose views of wildlife were either focused solely on utilization or open to multiple views of nature and conservation were less accepting of wolf recovery than other value orientation types (Dietsch et al., 2011). In general, residents living in the eastern half of the State were less supportive of wolf recovery and more in favor of lethal control of wolves, whereas most residents in the western half of the state were in favor of wolf recovery and less in favor of lethal control of wolves. These divergent values and management priorities have made wolf management in Washington a contentious topic. WDFW is consequently in the position of resolving wolf conflicts that are based as much, if not more, on social values than the biological reality of wolves.

Conflicts over the continued presence of wolves can, at times, be aggravated more by human values, perceptions, and attitudes towards wolves than by economic losses stemming from wolf depredations (Treves and Bruskotter, 2014; Dickman, 2010). At the same time, there is growing concern that management actions aimed at reducing the impacts of predators like wolves on humans interests (e.g., predation on livestock and wild game) could disrupt the social behavior and/or alter the ecological role of these top predators (Wallach et al., 2009; Ordiz et al., 2013). Thus, reconciling the interests of wolf conflict mitigation and conservation requires understanding the social dynamics of both wolves and humans. Fortunately, Washington State is in the early stages of wolf recolonization efforts and can draw upon a growing body of research on the ecology and behaviors of wolves in the wild as well as human dimensions of wolf recovery conducted in other states to inform its own management strategy.

To this end, on October 29th, 2014, University of Washington Professors John Marzluff and Aaron Wirsing and the Pacific Wolf Coalition (pacificwolves.org) hosted a panel discussion of scientists researching issues surrounding one of wolf management's most controversial aspects –

lethal control of wolves. The purpose of this panel discussion was to understand some of the complexities of lethal wolf removal, both social and ecological, in order to inform Washington's wolf management policies with the best natural and social science available. This effort involved panelists from a wide range of disciplines and life experiences where wolves and people have had extensive interactions. The panelists included: Dr. Scott Brainerd, from the Alaska Department of Fish and Wildlife (ADFG); Dr. Douglas Smith, from Yellowstone National Park; Dr. Robert Wielgus, from Washington State University; Dr. Jeremy Bruskotter, from Ohio State University; and Dr. Adrian Treves, from the University of Wisconsin-Madison.

Dr. Scott Brainerd is the Research Coordinator for the Interior and Northeastern Arctic Region of the Division of Wildlife Conservation with ADFG in Fairbanks, Alaska. He has done extensive research on the impacts of breeder loss on wolf pack social structure in Alaska and Scandinavia. His studies highlight the importance of breeding wolves in maintaining group unity at the pack level.

Dr. Douglas Smith is a senior wildlife biologist for the National Park Service in Yellowstone National Park, Wyoming, and has studied wolf biology for more than 30 years. He has co-authored multiple papers studying how human-induced mortality of individual wolves affects wolf social dynamics and connectivity.

Dr. Robert Wielgus is an associate professor and the director of the Large Carnivore Conservation Lab at Washington State University in Pullman, Washington. He has done extensive research on the impacts of hunting and lethal control on cougars in Washington State. Most recently, he has been studying the effects of lethal control of wolves as a means of reducing livestock depredations.

Dr. Jeremy Bruskotter is an associate professor in the School of Environment and Natural Resources at Ohio State University in Columbus, Ohio. His research areas include natural resources and recreation conflicts and the use of psychology and communication theories in natural resource management and policy.

Dr. Adrian Treves is an associate professor at the University of Wisconsin–Madison in Wisconsin. His research has focused primarily on public attitudes toward wolves and wolf policy in Wisconsin, behavioral ecology of carnivores and the risks for people living near them, and methods for mitigating human-wildlife conflicts.

Overview of Wolves in the Pacific Northwest

The purpose of the panel was to inform wolf management actions in Washington State. Thus, it began with an up-to-date overview of wolf management in Washington and the surrounding recovery area. Dr. Donny Martorello, from the WDFW, provided some local context, covering current wolf policy in Washington and Oregon, and Carter Niemeyer, retired U.S. Fish and Wildlife Service (USFWS), covered the broader northern Rockies recovery area and the current wolf population and harvest numbers in Montana, Idaho, and Wyoming. At the time this panel was held, Dr. Martorello was the Carnivore Section Program Manager at the WDFW and he has been at the forefront of assessing the status and management of wolves in Washington since their return to the state in 2008. He currently holds the title of Wolf Policy Lead and oversees much of the ecological recovery and management of wolves in Washington.

Dr. Martorello began the session by giving a brief history of what the WDFW has been doing since wolves arrived in Washington State. In 2007, prompted by the eminent likelihood of wolves recolonizing the state in the next few years, the WDFW Director appointed a 17-member citizen advisory group (the Wolf Working Group or WWG) to advise the development of a state wolf management plan. In addition to the WWG, the WDFW received almost 65,000 public comments on the draft plan and held 23 public meetings around the State for input into the wolf plan. The plan went through a rigorous scientific peer review process. The WDFW Commission approved the Wolf Management and Conservation Plan in 2011 (from here forward referred to as the Wolf Plan). The Wolf Plan is the policy document used to guide recovery and management of wolves in Washington State. Components of the Wolf Plan that involve lethal control of wolves are not implemented in the western two-thirds of the state, since wolves currently remain federally-listed there.

In 2013, the WDFW created the Wolf Advisory Group (WAG) to help inform management and guide implementation of the Wolf Plan. The WAG has been asked to review and recommend conflict-reducing strategies and they have also been tasked with being the review board for livestock compensation programs. It is comprised of a diverse group of stakeholders appointed by the WDFW Director. For 2013-2014, there were nine members representing: Quad-county commissioners, the Farm Bureau, Washington Cattlemen's Association, Cattle Producers of Washington, Conservation Northwest, Humane Society of the United States, Wolf Haven International, Sierra Club, and Hunter's Heritage.[5] The population trend of wolves in Washington is on the rise, going from one confirmed pack in 2008 to 16 confirmed packs in 2014. The WDFW has been capturing and instrumenting wolves with GPS collars to enable monitoring and assessment of their recovery progress. Washington is seeing a pattern similar to that observed in many Northern Rocky Mountain (NRM) States; namely, relatively high wolf population growth rates, with less than 20% of the wolf packs depredating livestock. Two depredation events, mentioned previously, have occurred in northeastern Washington, resulting in the removal of eight total wolves. In both incidents, the WDFW implemented lethal removal of the problem wolves, in accordance with the Wolf Plan (page 80).[6] The WDFW has a checklist for non-lethal preventive measures to be followed before lethal control efforts are considered. The checklist is composed of the following five preventive non-lethal tools that livestock owners are advised to implement before lethal control is used: removing livestock carcasses, removing sick and/or injured livestock, securing bone yards, calving or lambing away from wolves, and hazing wolves if they are encountered. These preventive non-lethal tools are required before WDFW implements any lethal control action on wolves, but it is only recommended that they be in place before depredations occur (Appendix, Figure 1).

In 2008, WDFW began allocating resources toward hiring conflict-specialists, employees acting as liaisons between the WDFW and landowners on wildlife conflict issues, for every region, setting up a compensation program for livestock loss due to wolves, and entering into cooperative, cost-share agreements with livestock owners to implement preventative measures

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[5] In the fall of 2014, WDFW decided to expand the membership of the WAG and, as of 2015, there are now 17 individuals on this advisory body, including representatives from additional organizations.

[6] Conservation groups disagreed with WDFW actions in both lethal removal instances, citing literature contained in the Wolf Plan (81).

(known as depredation prevention cooperative agreements). Thus far there are 13[7] conflict specialists (Appendix, Figure 2) working with livestock owners and the general public in areas with the highest level of wildlife conflict (either predator or elk and deer related conflict). There are currently 41 active damage prevention cooperative agreements in the state. These agreements can provide funds for improved fencing, sanitation, guard animals, range riders, and other preventative measures.

Dr. Martorello also presented a snapshot of the Oregon Wolf Management Plan on behalf of Russ Morgan, the Oregon Department of Fish and Wildlife (ODFW) Wolf Program Coordinator. The ODFW developed a wolf conservation and management plan in 2005 and updated it in 2010. As in Washington, there was extensive public input on the wolf management plan, and a Wolf Advisory Group consisting of 14 members who represent its primary stakeholder groups was assembled to advise ODFW during the creation of the plan. The recovery trends are similar to Washington State and the NRM States. With 10 packs and about 64 wolves in Oregon as of October 2014, ODFW expects to reach their recovery objective of 4 successful breeding pairs for three consecutive years by 2015.[8] As of 2013, there was an addendum to the wolf plan with new rules on the use of lethal control and harassment of wolves: the new rules set the bar at four qualified depredations by the same pack over the course of six months before lethal control can be considered. Livestock owners must not have unnatural attractants and must implement one non-lethal measure before a depredation will be considered qualified. It is mandatory for ranchers to implement at least one non-lethal wolf control measure as part of their animal husbandry (including removal of any possible wolf attractants including dead animals and any calving afterbirth remains) at least seven days prior to and on the day of the depredation (ODFW Wolf Plan, 2010). In Oregon, when a depredation is suspected, the livestock operator must then implement at least one non-lethal site-specific measure before any additional depredations are considered qualified for potential lethal action against the wolf pack. If the livestock operator implements appropriate non-lethal measures for a period of six months and three depredations by the same wolf or wolf pack occur, ODFW will assess whether the offending wolf or wolf pack is likely to continue depredating, regardless of increased implementation of non-lethal measures.

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[7] At the date of this publication, there are 19 conflict specialists, 11 of whom work with livestock producers in areas with wolf packs.

[8] ODFW's 2014 wolf count observed 77 individuals.

After this assessment lethal control may be approved. In addition to these new rules, the ODFW is making an effort to be as transparent as possible, using the agency website (http://www.dfw.state.or.us/wolves/) to post information about preventative measures, depredation investigations, and pack locations and timelines[9].

Wolf recovery in the Northern Rocky Mountain (NRM) recovery areas

Carter Niemeyer has been a primary player in wolf recovery since wolves were first reintroduced in Yellowstone. He is retired from the USDA Wildlife Services and US Fish & Wildlife Service (USFWS) in Idaho where he worked from the mid-1980s until 2006. Mr. Niemeyer was part of the team that captured and reintroduced the wolves in Yellowstone National Park and Idaho in 1995/1996. He gave a summary of events in the broader recovery area and the wolf population trends and harvest numbers in Montana, Idaho, and Wyoming from 1982 to 2013. Recovery in the NRM was achieved in 2002, and currently there are at least 1,657 wolves and 282 packs. In most NRM states wolf populations have remained stable and are federally delisted, with the exception of Wyoming whose limited state regulation to protect wolves outside of Yellowstone National Park has resulted in re-listing their wolf population as endangered. Mr. Niemeyer emphasized that the use of non-lethal management tools is not mandatory in most States, Washington included, except for the consideration of lethal control. Consequently, he found that it is not readily implemented by many producers. However, by all biological measures the NRM wolf population remains secure under state management and he called gray wolf reintroduction "an amazing success story."

Summary

In summary, numbers of wolves and breeding pairs in Oregon and Washington are increasing steadily, promising the real possibility of achieving the two states' recovery goals by 2015 and 2021, respectively. Challenges remain in the continued use of the best available science to solve human-wolf conflicts in Washington, as in other western states where wolves are recovering.

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[9] The Oregon Wolf Plan has a three-phased approach and the new rules described here apply only during Phase I of the Wolf Plan. Once wolves in Oregon reach population and breeding pair thresholds that move them out of Phase I and into Phase II, these new rules no longer apply.

This discussion panel served to address the difficulties highlighted by Dr. Martorello and Mr. Niemeyer.

Review of Current Research by the Panelists

Dr. Scott Brainerd

Dr. Scott Brainerd based his talk on two recent articles concerning the effects of breeder loss on wolf populations (Brainerd et al., 2008; Borg et al., 2015). The first article, a meta-analysis of 148 breeding wolves in both national parks and unprotected areas, showed that more than half of breeder loss was from anthropogenic causes. The authors found that pups survived in 84% of the cases where breeders were lost, regardless of the sex of the breeder, and that pup survival was better in larger packs (greater than six wolves) where the pups were over six months of age. The loss of both breeders was far more detrimental to reproduction than just the loss of one; 56% of packs that only lost one breeder reproduced subsequently whereas only 9% of packs that lost both breeders subsequently reproduced. Also, relatively few of the packs dissolved after losing one breeder (38.2%), while a much larger proportion dissolved after losing both breeders (>80%). In areas where wolf populations were saturated, it took less time for packs to replace breeders (10 months) than in areas where wolves were recolonizing (~20 months).

Borg et al. (2015) based their article on a 36-year dataset on wolves in Denali National Park where much of the breeder loss was from natural causes, primarily from other wolves. In Denali, breeder loss accounted for 77% of pack dissolution. Packs were more likely to dissolve if breeder loss was due to anthropogenic causes than natural ones. However, there was no demonstrable effect of breeder loss on the overall population of wolves in Denali.

Dr. Robert Wielgus

Dr. Robert Wielgus presented the results of his research assessing the efficacy of wolf lethal control in preventing livestock depredations using data collected from 1987 to 2012 in Idaho, Montana, and Wyoming (Wielgus and Peebles, 2014). He highlighted the unexpected relationship between lethal control of wolves and livestock depredation rates. Specifically, his team used the annual USFWS wolf harvest reports from 1987-2012 and the United States Department of Agriculture National Agricultural Statistics Service (USDA NASS) records of

cattle and sheep depredation counts from wolf occupied counties to determine the correlation between lethal control and livestock depredation incidents. The results of the analysis showed that an increase in livestock, breeding pairs, and wolf numbers was correlated with increased instances of depredation. However, countering common wisdom that wolf removal decreases livestock depredations, Wielgus and Peebles found that there was a 5% increase in depredation (both for cattle and sheep) for every wolf that was killed. This phenomenon is possibly caused by an increase in breeding pairs to compensate for lethal wolf removal (Wielgus and Peebles, 2014). Ultimately, it seems that lethal control might decrease depredation on a local scale, but may not control widespread livestock loss unless over 25% of the wolf population is lethally removed.

Dr. Douglas Smith

Dr. Douglas Smith began his talk by emphasizing that wolves in Yellowstone National Park allow us to study the ecology of these carnivores in an environment mostly free of human interference. Since the reintroduction of wolves into the park in 1995 and 1996, Dr. Smith has been studying pack size and complexity to determine how unexploited packs behave in the wild. Dr. Smith has found that, in the absence of management, wolf packs quickly become socially complex and retain multiple age groups. Having a variety of age groups in a pack is important for the segregation of hunting duties, although not necessarily hunting success (MacNulty et al., 2012; Mech, 1999); females and younger males are faster, while older males are bigger and stronger (MacNulty et al., 2009). In contrast, many of the wolf packs outside of Yellowstone protected area are simple packs composed of breeders and offspring (Smith, *unpublished data*). Wolf packs are generally composed of primarily younger wolves even in protected areas due to intraspecific strife (Mech, 1994). However, more complex packs are more likely to survive territorial disputes and hunt efficiently than simple packs (Smith, *unpublished data*). Smith and his colleagues are also finding that pups act as social glue for wolf packs; the more pups born to a pack, the less likely it is that subordinate wolves will disperse (Smith, *unpublished data*). In addition, dispersal patterns are seasonally dependent inside Yellowstone National Park, whereas outside the park there is no observable seasonal pattern (Smith, *unpublished data*). At this time, more research is needed to explain why this disparity might exist.

Dr. Smith concluded that it appears that killing wolves reduces social cohesion within a pack. For example, removal of the breeder female was shown to result in higher reproductive rates in a

pack due to the breeder male mating with more than one remaining female in the pack. Killing of wolf pups can cause stress in the family pack, and packs whose pups are killed are more likely to disperse than to stay together. Dispersing wolves are more likely to cause livestock conflicts as they find new geographic areas to occupy. In addition, killing wolves may reduce the packs to sizes that cannot efficiently hunt game species and resort to easy prey such as sheep.

Dr. Adrian Treves

Transitioning from the ecological to the social sciences, Dr. Adrian Treves presented his research on common assumptions that lead to lethal removal of wolves. Generally, there are two main justifications for lethal removal of wolves: prevention of property damage and improvement of attitudes towards carnivores (Treves et al., 2009). Dr. Treves believes both of these assumptions need to be evaluated, especially in light of the recent finding by Wielgus and Peebles (2014) that lethal management of wolves is correlated with increased frequency of livestock depredations. One of the ways Dr. Treves studied this issue in Wisconsin was by developing a risk map to determine which areas were most likely to have wolf-livestock conflict. By examining differences between sites with and without depredations, Dr. Treves determined that areas with more grassland and pasture, closer to known wolf pack ranges, and farther from forest coverage were at the highest risk for depredations (Treves et al., 2011). This risk map proved over 90% effective at predicting depredation sites. A highly predictive risk map allows managers to anticipate and plan for, rather than react to, conflicts. Additionally, risk maps can be used to guide local action and reduce the perceived risk of wolf conflicts among residents living close to wolf territories. Dr. Treves found that lethal removal has mixed results in terms of protecting private property. Namely, he found that the time period between recurring depredations is actually shortened after lethal removal than after use of non-lethal control measures in Michigan (Treves, 2013).

Thus far, lethal removal has also not been found to improve attitudes toward wolves. Treves conducted two surveys of two different citizen panels. The first panel from 2001 was chosen for wolf experience and hunting (Naughton-Treves et al., 2003), the second from 2004 was a random sample (Treves et al., 2009) and both were resampled in 2009. In the years between the surveys, wolf numbers and depredations increased and lethal control of wolves was increased. There was a significant amount of media attention centered on wolf issues. Instead of showing a

positive trend in attitudes with increased use of lethal control, a significant portion of citizens became more negative about wolf populations; 37% of respondents reported an increase in the likelihood they would shoot a wolf if they saw it, 44% reported an increased agreement with the statement that Wisconsin's wolf population threatened deer hunting opportunities, and 46-47% of the respondents showed increased agreement to hunting wolves (Treves et al., 2013). On the other hand, support for government-sponsored lethal removal increased. Attitudes continued to decline after one year of a public hunting and trapping season (Hogberg et al., 2013). It appears that legalizing the killing of wolves devalued the wolf in the eye of the public in Wisconsin (Treves and Bruskotter, 2014).

Dr. Jeremy Bruskotter

Even if attitudes towards wolves on a local scale are becoming more negative in areas where wolves are present, attitudes towards carnivores and other traditionally maligned animals are becoming more positive on a national scale. Dr. Jeremy Bruskotter presented his work on the psychology underlying reactions to large carnivores (Bruskotter et al., 2007; Bruskotter, 2011; Slagle et al., 2013). Dr. Bruskotter (2011) replicated a study by Kellert (1978) surveying the general public about their feelings toward 26 different species of animals. The results showed a marked increase in positive feelings towards wolves; there was a 9% increase of participants indicating they felt "very positively" about wolves and a 3% decrease in respondents who felt "very negatively" about wolves. It is important to study the mental processes, such as perceived risks and benefits and emotional responses, which go into our cognitive construction of animals like wolves because they affect both policy and behavior, potentially leading to intolerance or coexistence. With this in mind, Dr. Bruskotter surveyed readers of an active wildlife blog, www.thewildlifenews.com, about their perceived risks and benefits of wolves and their affective responses to wolves. He found that perceived benefits, such as healthier riparian areas, were more predictive of support of wolves than perceived risks, such as dangers to livestock and children, and that there was a large indirect effect of emotional reactions to wolves on perceived benefits (Slagle et al., 2012). In other words, positive feelings towards wolves strongly affect the belief in perceived benefits and subsequent tolerance for wolves. However, negative emotional responses lead directly to intolerance towards wolves, rather than simply an increase in perceived risks (Treves and Bruskotter, 2014). Dr. Bruskotter posited that an individual's perception of

wolves is rooted in group identity and membership. Therefore, social conflict must be taken into account when managing wolves. For example, the residents in the NRM can be split into the "new west" (animal rights advocates, environmentalists, conservationists, wildlife advocates) and the "old west" (hunters, gun rights advocates, farmers/ranchers, property rights advocates), and this delineation predicts beliefs about positive impacts of wolves (Bruskotter, *unpublished data*). Because individual perceptions of wolves can be influenced by group membership, elite cues-- such as a message from an influential member of the community-- can have enormous impact on the individuals in the group and shape how they view wolves as well as other groups. In terms of management implications, it is important to focus on shared goals and improvements (rather than just solutions to problems), build trust through cooperative efforts and avoid "demonizing" the other side, and try to avoid power structures that favor some groups over others (Bruskotter, 2014).

Implications for Washington State

The research findings presented by the panelists can be incorporated into management decisions and help inform future wolf management and conservation strategies in Washington State. The following section will cover the take-away points of the discussion panel and what they mean for Washington State going forward. However, before these specifics, we wish to point out a more general suggestion. The wolf research community is large and scientifically-focused. As such, the WAG would benefit from regular consultation with outside scientists, and might consider expanding its membership to include at least one wolf researcher.

A common scientific finding is that lethal management of wolves has many unintended consequences on wolves and human perceptions of wolves. Although Dr. Brainerd's research showed the remarkable resilience of wolves faced with breeder loss, there are still negative effects on wolf packs, such as simplification of social structure, pack dissolution and short-term reproduction decreases, especially when wolves are newly recolonizing an area (Brainerd et al., 2008; Borg et al., 2015). Furthermore, removal of wolves may increase future livestock depredation and has been found to lower the public's valuation of a wolf's life (Wielgus and

Peebles, 2014; Treves and Bruskotter, 2014). These findings suggest five lessons Washington managers can apply to minimize human-wolf conflict.

1. Consider the needs of a recolonizing population.

One aspect of Dr. Brainerd's work that is highly relevant for wolf management in Washington is the finding that wolf packs in areas that have already been recolonized and saturated replaced their lost breeders more quickly than wolf packs in recolonizing areas. By implication, wolf packs in areas that have high connectivity with other wolf packs may be more resilient to breeder loss than wolf packs in recolonizing areas (Brainerd et al., 2008, Borg et al., 2015). It is possible, in light of Dr. Brainerd's work, that the shooting of the Huckleberry Pack female breeder in August 2014 will cause the Huckleberry pack to dissolve into solitary sub-adult wolves seeking their own territories[10]. However, the Huckleberry pack's proximity to the wolves in NRM recovery area and Canada will likely diminish the effects of breeder loss because new females can be recruited from nearby packs fairly rapidly. More isolated packs in the central portion of the state, such the Teanaway or Lookout packs, will need to be managed more carefully. Breeder loss may increase the chance of wolves coming into conflict with livestock due to two highlighted mechanisms: (1) either inexperienced young wolves lacking the pack complexity to hunt large ungulates such as elk (Smith, *unpublished*) will prey on sheep, or (2) as a result of compensatory reproduction due to non-breeding females breeding in the absence of the breeder female (Borg et al., 2015). Therefore, unintended consequences of lethal control could include a delay in achieving wolf recovery goals and an increase in livestock conflicts. For example, in late October of 2014 the breeding female of the Teanaway pack, which had not depredated any livestock, was illegally poached. Later in the summer of 2015, the pack was attributed with having depredated a calf, possibly as an unintended consequence of killing the alpha female. Wielgus and Peebles (2014) found that 25% of wolves must be removed to decrease livestock depredation. For wolves in the recovery phase, this percentage is high and if implemented the recovery goals will take longer to achieve and wolves will continue to be federally listed.

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[10] In August of 2015, Dr. Martorello briefed WAG members on the status of the Huckleberry pack and noted that it is the WDFW's belief that the Huckleberry pack has split into two packs – a northern pack which contains the original breeding male and several other wolves, and a southern pack, which contains remaining members of the original pack.

2. Provide wild space for wolves.

Washington wolf managers may want to consider, as Dr. Smith suggested, what it means to manage for "naturalness" in wolf populations. Between the effects of breeder loss, the tendencies of wolves to form complex rather than simple packs, the importance of key individuals for hunting success, and the unexpected relationship between increased lethal removal and increased livestock depredations (Brainerd et al., 2008; MacNulty et al., 2011; Wielgus and Peebles, 2014), the science is painting a complicated picture for management agencies using lethal control. Given the complexities of managing wolves with lethal control and the risks of such control during the early phases of recolonization (Brainerd et al., 2008; Borg et al., 2015), it would be reasonable to first manage for recovery by allowing wolves sufficient wild space. Washington State is highly populated, however, and while there are wilderness areas that can provide habitat for wolves, they are not as extensive as those in other western states. Consequently, Washington may benefit from a zonal approach that expands on refuges for wolves with management that mimics wild space. These strategic areas could provide extensive protection for wolves, even after delisting, while other areas would allow for more active wolf management (lethal control and/or regulated hunting).

3. Develop a predictive map of the risk of human-wolf conflict.

A risk map (see Treves et al. 2011 for an example) of Washington's wolves showing which ranchers are most likely to experience depredations would be helpful to streamline efforts to work proactively with ranchers. Most ranches, even those with wolf packs in their proximity, do not experience depredations often and as such may not be motivated to enroll in WDFW cooperative agreements or implement non-lethal measures. Livestock producers and WDFW officials could use a risk map to assess whether or not to request extra assistance in implementing non-lethal control. If the rancher is in an area predicting high risk, they may enter into a cooperative agreement or if they are in an area with low risk continue to use their regular predator-prevention measures. In the Q&A session after the presentations, many of the panelists stressed the need for further scientific studies of the effects of lethal removal and the potential benefits of creating a risk map for Washington.

4. Rethink how lethal control is implemented.

The ecological research on social behavior in wolves (Brainerd et al.; 2008; Borg et al.; 2015; Smith, *unpublished*) provided information that could refine how lethal management is employed in Washington State. Currently, lethal removal of wolves in Washington State is done by USDA Wildlife Services through sharpshooters from helicopters, or by staff on the ground, who find the wolves by following a GPS collared wolf and killing wolves suspected to be problem animals. The age and sex of the wolves are identified after the wolves are shot. Given the current best science on wolf social structure, managers should consider means to allow for selective removal of identified culprits in cases of repeated depredations by the same pack in an area. As this may be extremely difficult, especially in cases where landscape features render individual wolves difficult to identify, the best option may be following Brainerd et al.'s (2008) time and location recommendations for decreasing the impact of lethal removal. It also may be beneficial to revise the requirements concerning non-lethal measure implementation, focusing on designing site-specific preventative plans and making it obligatory to have those plans in place before depredations occur in order to consider lethal removal, similar to the ODFW system (ODFW, 2013). The continued implementation and refinement of the WDFW's conflict specialist program can aid in coordinating with ranchers on pre-depredation preventative measures. In addition, a redefined temporal scale on the wolf-management checklist showing the amount of time non-lethal measures should be in place between depredations before lethal control is employed could provide the time to consider ecologically-based management options without the immediate pressure to remove wolves.

With the creation of a risk map, it may also be possible to establish targeted areas with a high probability of livestock depredation where more decisive implementation of lethal removal could be beneficial. However, the work by Brainerd et al. (2008) suggests that, to the extent possible, lethal removal should be limited to solitary individuals and territorial pairs, wolf packs that are large with older pups, wolf packs that are close to other packs, and when it is not breeding season (Borg et al., 2015).

5. Understand the human dimension.

Dr. Martorello emphasized that one of the biggest struggles for the WDFW was a gap in understanding the human dimensions of wolf recovery. The ecological recovery of wolves may

be progressing, but increasing efforts will need to be made to understand and work within the social constraints of wolf management. Overall, there is a marked lack of trust between the management agencies, conservation groups, and livestock producers in Washington. Dr. Bruskotter's research on the importance of elite cues in identity conflicts may be helpful in informing efforts to address this issue and foster coexistence. For example, the use of lethal control and lack of mandatory use of non-lethal control against wolves prior to depredations may send cues to the livestock producers that lethal control is efficient and endorsed. In contrast, efforts by state agencies to translocate problem animals (e.g. black bears) instead of shooting them could send cues to the public that the species being moved is important and wanted in the backcountry.

Most of the panelists highlighted the necessity of trust between the management agencies and the general public, stressing one-on-one efforts to build relationships, being transparent, and decreasing polarization by focusing on common goals. Both Dr. Bruskotter and Dr. Treves mentioned the importance of talking about the potential benefits of carnivores and reframing the ongoing conflict. Right now, much of the general public, as well as some natural resource managers, are asking the question, "How do we live with animals that can kill us and the things we value?" It may be that the way to move forward is to instead focus on the potential positives associated with wolves, and other carnivores, rather than on the conflict they can create. This is especially so given all of the trappings of modern life that people use and interface with daily which are far more likely to cause death (e.g., driving an automobile, falling from a ladder, etc.) yet which people readily accept and engage in without fear or forethought. The current frame surrounding carnivore management suggests a rational approach to dealing with animals, but it seems that our behavior is at least partially determined by our emotions. Additionally, a new frame and perspective may create spaces of common ground to promote conflict resolution between traditionally opposed groups (Asah et al., 2012). Because wildlife is a public resource, it is also important for management to focus on all the legal uses of wildlife and preserve natural resources for future generations.

Summary

Lethal removal can disrupt wolf pack dynamics, inhibiting recovery objectives in recolonizing populations, potentially increase livestock depredation, and negatively affect human attitudes towards wolves (Brainerd et al., 2008; Borg et al., 2015; Wielgus and Peebles, 2014; Treves et al., 2009; Treves and Bruskotter, 2014). Thus, understanding the effects of lethal control in Washington State will require rigorous ecological and social science research of the kind presented at this panel discussion. Based on the information provided, it seems that Washington State could benefit from the construction of a risk map for increased precision in targeting potential problem areas for wolf depredations (Treves et al., 2011). Furthermore, human dimensions research on wolf recovery in Washington State is needed in order to gain a more nuanced understanding of the ways in which individuals and groups are viewing wolves and the potential reasons behind those perceptions. Stakeholders must play an integral part in wolf management. Trust and relationship-building efforts between all the stakeholders is critical; transparency in management is necessary. The results from the panel show that the needs of recolonizing and isolated wolf packs must be carefully assessed when considering lethal removal. In order to implement the best available science, we must know more about the effectiveness of various preventative measures, the habits and trends of wolves within Washington, and the needs and desires of the people involved.

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Appendix:

Figure 1. WDFW decision process for implementing lethal control of wolves, Martorello, 2014.

Wolf Conflict Management Flowchart
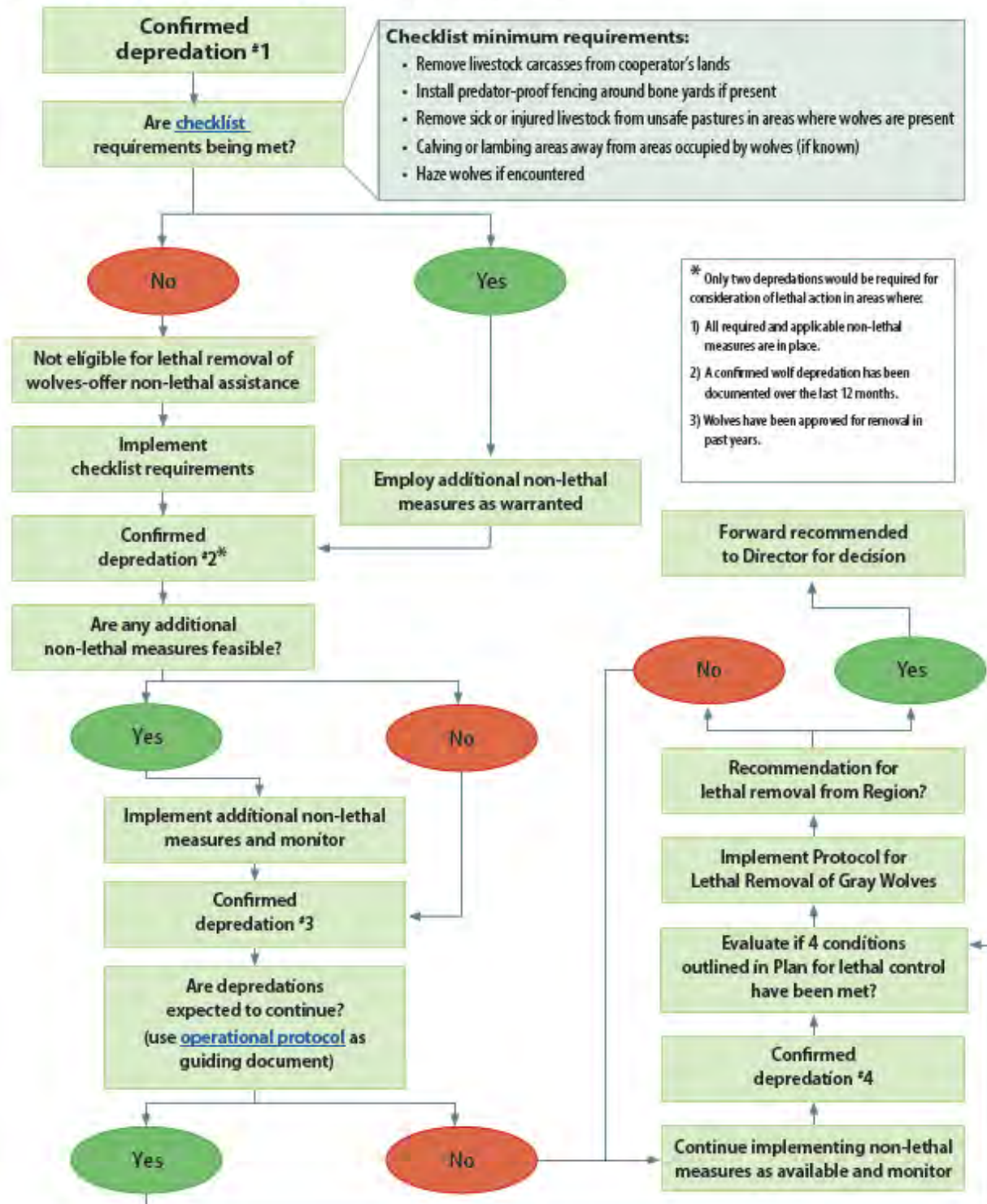
Figure 2. Washington confirmed wolf pack locations and corresponding conflict specialists, Martorello, 2014.
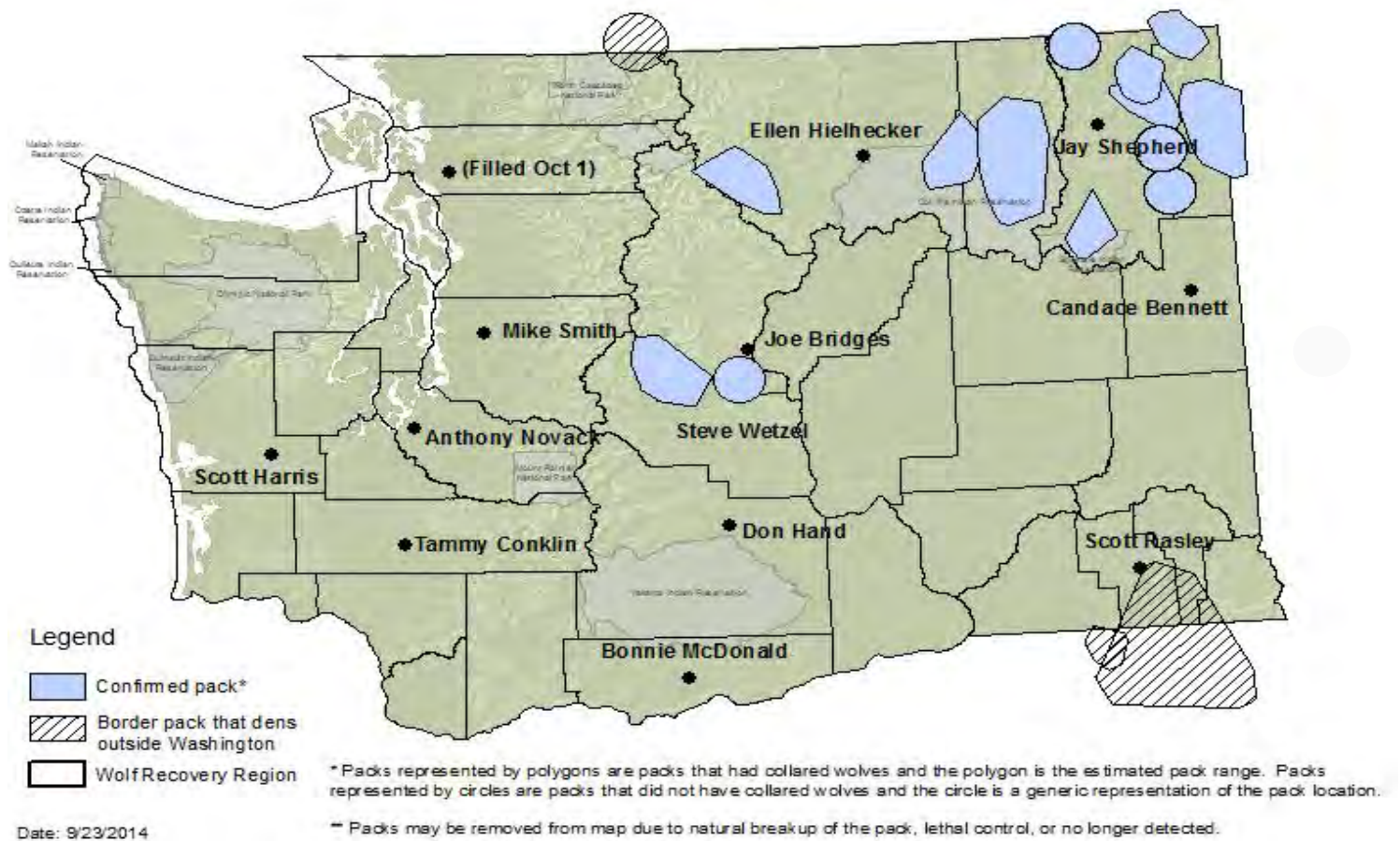
Appendix E

COPIES OF NEW CITATIONS REFERENCED IN THIS

JOINT CONSERVATION GROUPS'

DRAFT WOLF PLAN COMMENT LETTER TO CDFW

Wolves facilitate the recovery of browse-sensitive understory herbs in Wisconsin forests

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We asked whether wolf re-colonization would facilitate increased growth and reproduction of three browse-sensitive plant species. We hypothesized plant size and the proportion of reproductive individuals would be lowest in areas with no wolves, intermediate where wolves had been present for 4–6 years, and highest where wolves had been present for 12–13 years. Two plant species exhibited significantly greater reproduction where wolves were present for 12–13 years. Mean leaf size of indicator plants was significantly greater in areas where wolves were present for 12–13 years, as compared with that in areas where wolves were not present or were present for 4–6 years, but the effect size appears small. While the return of wolves to this region is likely to benefit browse-sensitive plant species, our findings suggest that wolf recovery will not generate a trophic cascade of sufficient magnitude to halt or reverse the loss of plant diversity in the Great Lakes region in the near term.

Introduction

Following the extermination of predators and the enactment of restrictive game laws, white-tailed deer (*Odocoileus virginianus*) populations grew and their browsing resulted in major changes in forest community composition and structure throughout eastern North America (Côté *et al.* 2004). Deer browsing have been implicated in shifting community compositions reducing the abundance of palatable and non-resistant species to less palatable and resistant species (Gill 1992, Husheer *et al.* 2003, Rooney 2009). Repeated browsing of palatable and non-resistant herbaceous species can result in shorter stature,

reduced growth and reproduction, truncated size structures, and population declines (Anderson 1994, Rooney and Gross 2003, Balgooyen and Waller 1995). Changes in plant community structure and composition following deer browsing can indirectly alter composition of animal assemblages, as is seen in birds (Allombert *et al.* 2005, Martin *et al.* 2011).

Wydeven *et al.* (2009) provide a brief history of gray wolves (*Canis lupus*) in Wisconsin. Prior to European settlement, there was sufficient prey to support 3000–5000 wolves in the state. Wolves were extirpated by 1960, and began recolonizing from Minnesota in the mid-1970s. Between 1980 and 2007, the wolf popu-

lation grew from 25–28 individuals to 540–577 individuals (35.5 wolves per 1000 km²). Wolves are now widely distributed across the northern third of the state. Pack locations and sizes have been mapped and monitored using radio-collars and winter track surveys since 1979 (Wydeven *et al.* 2009). The combination of extensive data and monitoring of a recovering wolf population, regionally-high deer densities, and impacted plant populations (Rooney *et al.* 2004) makes Wisconsin an ideal natural experiment for investigating trophic cascades.

Studies from western North America have demonstrated the effects recovering wolf populations can have on tree recruitment dynamics (Beschta and Ripple 2009). The reintroduction of wolves to Yellowstone National Park, for example, appears to have released aspen (*Populus tremuloides*) and willow (*Salix* spp.) from elk (*Cervus elaphus*) herbivory. The question of whether wolves generate trophic cascades in midwestern forests is largely unexamined. In years with high snowfall, wolves have influenced the growth rate of balsam fir (*Abies balsamea*) on Isle Royale by depressing moose abundance on the island (McLaren and Peterson, 1994, Post *et al.* 1999). However, it is unclear whether this trophic cascade is the exception or the rule in mainland Wisconsin forests.

In this study, we determined whether the recolonization of wolves could facilitate increased growth and reproduction of browse-sensitive plant species. To do this, we compared vegetation in areas that had wolves for three different periods of time. We compared areas without wolves with areas that established wolf packs for 4–6 years and for 12–13 years. We measured individual plant size, population size-structure, and the proportion of reproductive individuals of three herbaceous deer browse indicator species: *Polygonatum pubescens*, *Clintonia borealis*, and *Trillium grandiflorum* (Anderson 1994, Balgooyen and Waller 1995, Augustine and Frelich 1998, Kirschbaum and Anacker 2005, Rooney and Anderson 2009). We hypothesized plant size, size structure variation, and the proportion of reproductive individuals would be lowest in areas with no wolves and highest where wolves had been present for 12–13 years.

Material and methods

Site selection

Wolf pack locations have been mapped annually by the Wisconsin Department of Natural Resources (WIDNR) since 1979, and are maintained in a geographic information system. Annual shapefiles were overlayed in ArcGIS in order to determine how long an area was occupied by a wolf pack. Individual packs were selected for study based on a time criteria (either wolves continuously occupied the area for 4–6 years or 12–13 years). This created three treatments: no wolf impact, low wolf impact, and high wolf impact. Once a pack was selected, random points within its boundaries were chosen using ArcGIS and the coordinates recorded.

Each potential site was visited and cruised to determine that forest types were similar in age and composition, and contained populations of *P. pubescens*. *Polygonatum pubescens* is common throughout northern Wisconsin and was initially used as a focal species. Where they co-occurred, we collected data from *Clintonia borealis* and *Trillium grandiflorum* populations (measurement details are provided below). However, the absence of one or both of these species did not constrain our site selection procedure. Once the sites were deemed suitable, we randomly selected two packs from our list of wolf occupancy for 4–6 years, and two packs from our list of wolf occupancy 12–13 years. We established two sites within the territorial boundary of each pack.

Wolf-free sites were selected in a manner similar to sites with wolves. We used an ArcGIS map overlay to identify and select potential non-wolf sites. Potential non-wolf sites were selected in areas where the closest wolf pack boundary was located at least 5 km away. Forest types were similar in age and composition, and contained populations of *P. pubescens*. Four non-wolf sites were chosen for inclusion in the experiment.

Field methods

Surveys were conducted in June 2008 and 2009. A transect consisting of five 10 × 10 m plots

each separated by 20 m. Each transect was located at least 30 m from the nearest road or ATV trail road, with most transects established parallel to a road or trail. Plots were systematically sampled for *P. pubescens* until either all *P. pubescens* plants were measured (*see* details below), or alternatively, when 200 plants were measured. We required a minimum of 50 individuals per site for analysis. Consequently, not all sites were used in each analysis. A total of 1268 *P. pubescens* were surveyed at eight sites (three no-wolf, two 4–6 year wolf, and three 12–13 year wolf sites). We used the same procedure when sampling *T. grandiflorum* and *C. borealis*. In total, we measured 476 *T. grandiflorum* total at three sites (1 per wolf occupancy treatment) and 558 *C. borealis* at 4 sites (two no-wolf, one 4–6 year, and one 12–13 year).

Within each plot, we counted the number of leaves for each *P. pubescens* and recorded if the plant was reproductive. The number of leaves per plant (x) is directly related to total leaf area, y ($y = 1.50x$, $r^2 = 0.70$, $n = 49$; Bouchard 2009), so we used leaf count as a proxy for leaf area and hence plant size. We collected more detailed measurements to estimate leaf area of *T. grandiflorum* and *C. borealis*. For both species, the length and width of each leaf (in mm), which were converted into total leaf area using regression analysis ($y = e^{1.00\ln(\text{length} \times \text{width}) - 0.58}$, $r^2 = 0.99$, $n = 29$ for *T. grandiflorum*; $y = e^{1.06\ln(\text{length} \times \text{width}) - 0.91}$, $r^2 = 0.96$, $n = 57$ for *C. borealis*). The number of reproductive plants was also tallied for *T. grandiflorum* and *C. borealis*.

Data analysis

To determine the top-down influence of wolves on plant reproduction, we pooled flowering data across all sites within each wolf treatment. We assessed differences among treatments were analyzed using Yates' χ^2 goodness of fit tests.

To determine the effects of wolf occupancy duration on average leaf area of each species, we computed mean leaf area (A) in each wolf treatment. Measurements for each plant species were pooled for each wolf treatment. We performed analyses for three pairwise comparisons: "no

wolves" and "wolves present 4–6 years," "no wolves" and "wolves present 12–13 years," or "wolves present 4–6 years," and "wolves present 12–13 years." In each case, we assume that areas with wolves for a longer period of time reflect a greater wolf impact, and areas without wolves or with wolves for a shorter period of time reflect a lower wolf impact. We then computed the log response ratio L for the leaf area of each species where $L = \ln(A_{\text{more wolf impact}}/A_{\text{less wolf impact}})$. When $A_{\text{more wolf impact}} = A_{\text{less wolf impact}}$, $L = 0$. Negative values of L indicate smaller plants in areas with less wolf impact, while positive values indicate larger plants in areas where wolves have been present for a longer period of time. A 95% confidence interval (CI) was calculated for each species L to determine if it differed from zero.

We combined results from all plant species to examine the used techniques developed for meta-analysis. Data from each species were combined to create a mean effect size, following the procedures outlined in Hedges *et al.* (1999). To account for among-species variation in effect sizes, we combined effect sizes from each plant species to calculate the mean effect size, or overall effect. The effect size of each plant species was first weighted by their inverse sampling variance plus a constant, q. The computation of q is derived from homogeneity analysis and represents variability across population effects (Hedges *et al.* 1999). To determine if the mean effect size differed from zero, we constructed 95% CIs. We considered top-down effects from wolves statistically significant if 95% CIs did not include zero.

Results

As compared with areas without wolves, plants growing in areas with wolves for a period of 4–6 years generally did not show any directional trends. The mean size of *P. pubsecens* plants was 36% greater in the 4–6 year wolf treatments than the non-wolf treatment. This difference was significant ($p < 0.05$; Fig. 1). However, the proportion of reproductive *P. pubescens* plants (27 of 327, or 8.3%) in the 4–6 year wolf treatments was not significantly different than the propor-

No wolves vs. wolves 4-6 yrs.

No wolves vs. wolves 12-13 yrs.

Wolves 4-6 yrs. vs. wolves 12-13 yrs.
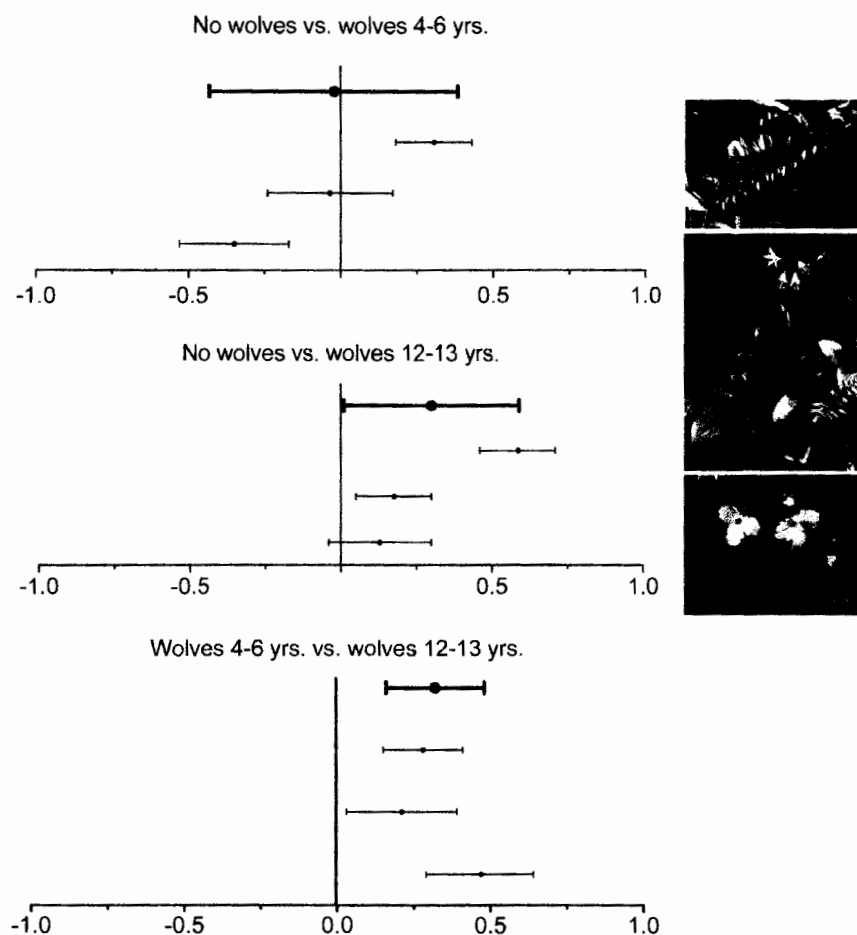
Fig. 1. Log response ratio (ratios of leaf area at sites with wolves for a longer time period relative to a shorter time period or wolf absence) and 95% confidence intervals for all species combined (thick line), *Polygonatum pubescens* (top thin line), *Clintonia borealis* (middle thin line), and *Trillium grandiflorum* (bottom thin line). Positive values indicate larger plants where wolves have been present for a longer period of time. Confidence intervals that intercept zero indicate no significant difference ($p > 0.05$).

tion (37 of 479, or 7.2%) in the no-wolf areas ($\chi^2 = 0.1$, df = 1, $p = 0.78$). The mean leaf area of *C. borealis* plants was 3% smaller in the 4–6 year wolf treatments than the non-wolf treatment, but this difference was not statistically significant (Fig. 1). None of the 94 plants were reproductive in the 4–6 year wolf treatments, compared to zero of 301 in the non-wolf treatment. The mean leaf area of *T. grandiflorum* plants was 30% smaller in the 4–6 year wolf treatments than the non-wolf treatment, and this difference was statistically significant ($p < 0.05$; Fig. 1). There were no reproductive *T. grandiflorum* plants in the 4–6 year wolf treatment, but 7.8% of the 191 plants were reproductive in no-wolf areas ($\chi^2 = 12.7$, df = 1, $p < 0.001$).

As compared with areas without wolves, plants growing in areas with wolves for a period of 12–13 years showed some signs of recovery. Mean size of *P. pubsecens* plants was 80% greater in the 12–13 year wolf treatments than

the non-wolf treatment (Fig. 1). This result was statistically significant. Additionally, the proportion of reproductive *P. pubescens* plants (79 of 433, or 18.2%) in the 12–13 year wolf treatments was more than twice the proportion (37 of 479, or 7.2%) in the no-wolf areas ($\chi^2 = 21.7$, df = 1, $p < 0.001$). Mean size of *C. borealis* plants was 13% greater in the 12–13 year wolf treatments than the non-wolf treatment (Fig. 1). This result was statistically-significant. However, only 1 plant of 200 was reproductive in the 12–13 year wolf treatment. Zero of 338 plants was reproductive in the no wolf treatment. Mean leaf area of *T. grandiflorum* plants in the 12–13 year wolf treatments was also 13% greater in than the non-wolf treatment, but this was not significantly different (Fig. 1). Of 191 *T. grandiflorum* plants in the 12–13 year wolf treatment, 7.3% (14 of 191) were reproductive. This did not significantly differ from the 7.8% reproductive (15 of 191) in no-wolf areas ($\chi^2 = 0.0$, df = 1, $p = 1.0$).

As compared with areas with wolves for 4–6 years, plants growing in areas with wolves for a period of 12–13 years were generally larger and more likely to flower. Mean size of *P. pubsecens* plants was 30% greater in the 12–13 year wolf treatments than the 4–6 year wolf treatment (Fig. 1) and were 2.2 times more likely to flower ($\chi^2 = 14.66$, df = 1, $p < 0.001$). Mean size of *C. borealis* plants was 24% greater in the 12–13 year wolf treatments than the 4–6 year wolf treatment ($p < 0.05$; Fig. 1). Because only a single plant was in flower, the influence of wolves on reproduction could not be assessed. Mean size of *T. grandiflorum* plants was 61% greater in the 12–13 year wolf treatments than the 4–6 year wolf treatment (Fig. 1), and plants were more likely to flower ($\chi^2 = 5.8$, df = 1, $p = 0.02$). No *T. grandiflorum* plants flowered in the 4–6 year wolf treatment.

Meta-analysis allowed us to combine the data across species and examine the net effect. When the mean leaf sizes of plants were combined into a single effect size, there was no significant effect of the 4–6 year wolf treatment on plant size relative to areas without wolves ($p > 0.05$; Fig 1). The combined effect size of all three indicated a significantly larger leaf size when wolves were present for 12–13 years relative to no wolves, as the lower bound of 95%CI was greater than zero (Fig. 1). The largest differences in mean leaf size were found between the 4–6 year wolf treatment and the 12–13 year wolf treatment. The mean leaf size was significantly greater in the 12–13 year wolf treatment for all three species, and the combined effect size was significant (Fig. 1).

Discussion

The re-colonization of the Great Lakes region by wolves can be represented as a type of chronosequence (Rooney and Anderson 2009). Packs became established in some areas 15 years ago, while other areas have been colonized in the past few years. Time since re-colonization by wolves was associated with a modest increase in growth and reproduction of browse-sensitive indicator plant species. Mean leaf size of indicator plants was significantly greater in areas where wolves

were present for 12–13 years, as compared with that in areas where wolves were not present. The magnitude of the effect appears small.

Reproduction of browse-sensitive species usually declines in response to herbivory (Côté *et al.* 2004, Kirschbaum and Anacker 2005), but reproduction was a poor indicator of a response in this study. While over 1000 plants were sampled across the three species, we were unable to draw statistically-reliable conclusions about reproduction of *C. borealis*. Our other species were most likely to flower in areas with wolves for 12–13 years.

Meta-analysis of plant sizes indicated that plants growing in the 12–13 year wolf treatment were significantly larger than plants growing in the no-wolf treatment, but there was significant heterogeneity among species. There was an even greater difference between growing the 12–13 year wolf treatment relative to plants growing in the 4–6 year wolf treatment. Browse-sensitive plant species performed most poorly at sites with wolves present for 4–6 years. Indeed, it appears that plants growth and reproduction is higher with no wolves at all, relative to wolves present for 4–6 years. Initially, this result puzzled us. In retrospect, however, we realized that our initial hypothesis was faulty. When colonizing a new area, wolves select areas with high deer densities (Fuller 1989, Potvin *et al.* 2005). Our "no wolves" sites were probably located areas with fewer deer than elsewhere in the landscape. We would have been wiser to sample vegetation in areas that had wolves for a brief period of time, such as 1–2 years, instead of areas with no wolves. Such areas may have served more effectively as "high deer impact" sites within the wolf re-colonization chronosequence we wished to explore.

The magnitude of plant recovery from deer browsing is much less than that found in the aspen and cottonwood of Yellowstone after wolves were re-introduced (Ripple *et al.* 2001, Ripple and Beschta 2003, Beschta and Ripple 2009). The differences in the magnitudes of vegetation response between our study and those from Yellowstone could simply be the result of a few factors. Herbaceous plants growing in a shaded forest understory do not show the same growth rate as woody species growing in sunny riparian areas when released from herbivory. Elk

concentrate their foraging in discrete areas of the landscape with high quality forage. White-tailed deer have high quality food distributed more evenly across the landscape, which could make their daily movements more unpredictable to predators (Rooney and Anderson 2009). It is quite possible that trophic cascades are not biologically important in the Great Lakes. Alternatively, 12–13 years is an insufficient amount of time for trophic cascades to become apparent.

There were two key limitations of our study design that could have affected our results. First, we did not statistically control for differences in wolf pack sizes in our study areas. Wolf pack sizes are estimated every year, but pack sizes change seasonally and from year to year. Between 1995–2007, mean pack size was 3.1 ± 0.3 wolves (Bouchard 2009). Second, we did not have good deer population density estimates from our study areas. Wisconsin estimates deer densities for a deer management unit, and these units are ~1000 km². Between 1995–2007, overwintering densities averaged 11.2 ± 1.3 deer km⁻² in the study area (Bouchard 2009). We have no information about deer density at the spatial scale of study plots. Both limit the strength of inferences we can draw.

High deer densities throughout much of the upper Great Lakes region continue pose a challenge to conservation efforts. Deer browsing contributes to the erosion of plant diversity (Rooney *et al.* 2004). This in turn could lead to additional indirect effects on insects, birds, and other species (Rooney and Waller 2003). While the return of wolves to this region is likely to have modest benefits that accrue to plants (Callan *et al.* 2013), our findings do not suggest that the current wolf population is sufficient to halt or reverse the loss of plant diversity in the Great Lakes region in the near term. The recovery of browse-sensitive understory herbs in Wisconsin forests is dependent on the severity of previous browsing and the degree to which browsing is reduced (Kirschbaum and Anacker 2005, Rooney *et al.* 2004).

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CALIFORNIA FISH AND GAME COMMISSION
NOTICE OF FINDINGS AND NOTICE OF PROPOSED RULEMAKING
Gray Wolf
(*Canis lupus*)

NOTICE IS HEREBY GIVEN that the California Fish and Game Commission (Commission), at its June 4, 2014 meeting in Fortuna, California, made a finding pursuant to California Fish and Game Code section 2075.5(e), that the petitioned action to add the gray wolf (*Canis lupus*) to the list of endangered species under the California Endangered Species Act, Fish & G. Code, § 2050 *et seq.* (CESA) is warranted.[1] *See also* Cal. Code Regs., tit. 14, § 670.1, subd. (i)(1).

NOTICE IS ALSO GIVEN that the Commission, consistent with Fish and Game Code section 2075.5, proposes to amend Title 14, section 670.5, of the California Code of Regulations, to add the California gray wolf to the list of species designated as endangered under CESA. *See also id.*, tit. 14, 670.1, subd. (j).

I.   BACKGROUND AND PROCEDURAL HISTORY

On February 27, 2012, the Center for Biological Diversity (Center), Big Wildlife, the Environmental Protection Information Center, and Klamath-Siskiyou Wildlands Center petitioned (Petition) the Commission to list the gray wolf as an endangered species under CESA. Cal. Reg. Notice Register 2012, No. 15–Z, p. 494. The Commission received the Petition on March 12, 2012, and referred it to the Department of Fish and Wildlife (Department) for an initial evaluation on March 13, 2012. Cal. Reg. Notice Register 2012, No. 15-Z, p. 494. On June 20, 2012, the Commission granted a request by the Department for an additional thirty (30) days to complete its initial evaluation of the Petition.

On August 1, 2012, the Department submitted its Initial Evaluation of the Petition to List the Gray Wolf (*Canis lupus*) under the California Endangered Species Act (CESA) (August 1, 2012) (hereafter, the 2012 Candidacy Evaluation Report), recommending that the Petition provided sufficient information such that listing may be warranted and, therefore, that the Commission accept the Petition for further evaluation under CESA. Fish & G. Code, § 2073.5, subd. (a)(2); Cal. Code Regs., tit. 14, § 670.1, subd. (d).

On October 3, 2012, the Commission voted to accept the Petition for further evaluation and to initiate a review of the status of the species in California pursuant to Fish and Game Code section 2074.2, subdivision (e)(2). Upon publication of the Commission's notice of determination, the gray wolf was designated a candidate species on November 2, 2012. Cal. Reg. Notice Register 2012, No. 44-Z, p. 1610 (2012 Candidacy Evaluation Report).

Consistent with the Fish and Game Code and controlling regulation, the Department commenced a 12-month status review of the gray wolf following published notice of its designation as a candidate species under CESA. As part of that effort, the Department solicited data, comments, and other information from interested members of the public and the scientific and academic community; and the Department submitted a preliminary draft of its status review for independent peer review by a number of independent reviewers who possess the knowledge and expertise to critique the validity of the report. Fish & G. Code, §§ 2074.4, 2074.8; Cal. Code Regs., tit. 14, § 670.1, subd. (f)(2).

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[1] The definition of an "endangered species" for purposes of CESA is found in Fish and Game Code section 2062.

The effort culminated with the Department's final Status Review of the gray wolf (*Canis lupus)* (February 5, 2014) (Status Review), which the Department submitted to the Commission at its meeting in Sacramento, California, on February 5, 2014. The Department recommended to the Commission that designating gray wolf as an endangered species under CESA is not warranted. Fish & G. Code, § 2074.6; Cal. Code Regs., tit. 14, § 670.1, subd. (f).

The Commission considered the Petition, the Department's 2012 Candidacy Evaluation Report, the Department's Status Review, and other information included in the Commission's administrative record of proceedings at its meeting in Ventura, California on April 16, 2014, and at its meeting in Fortuna, California on June 4, 2014. Fish & G. Code, § 2075; Cal. Code Regs., tit. 14, § 670.1, subds. (g) and (i). After receiving additional information and oral testimony, the Commission determined, based on the requirements of CESA and the evidence before it, that listing gray wolf as an endangered species under CESA is warranted. Fish & G. Code, § 2075.5(a); Cal. Code Regs., tit. 14, § 670.1, subd. (i)(1)(A). In so doing, the Commission directed its staff to prepare findings of fact consistent with its determination for consideration and ratification by the Commission at a future meeting. The Commission also directed its staff, in coordination with the Department, to begin formal rulemaking under the California Government Code to add the gray wolf to the list of endangered species set forth in Title 14, section 670.5, of the California Code of Regulations. Fish & G. Code, § 2075.5(e)(2); Cal. Code Regs., tit. 14, § 670.1, subd. (j); Gov. Code, § 11340 *et seq.*

II.   STATUTORY AND LEGAL FRAMEWORK

The Commission has prepared these findings as part of its final action under CESA to designate the gray wolf as an endangered species. As set forth above, the Commission's determination that listing the gray wolf is warranted marks the end of formal administrative proceedings under CESA prescribed by the Fish and Game Code and controlling regulation. *See generally* Fish & G. Code, § 2070 *et seq.*; Cal. Code Regs., tit. 14, § 670.1. The Commission, as established by the California Constitution, has exclusive statutory authority under California law to designate endangered and threatened species under CESA. Cal. Const., art. IV, § 20, subd. (b); Fish & G. Code, § 2070.[2]

As set forth above, the CESA listing process for gray wolf began in the present case with the Center's submittal of its Petition to the Commission in March 2012. Cal. Reg. Notice Register 2012, No. 15–Z, p. 494. The regulatory process that ensued is described above in some detail, along with related references to the Fish and Game Code and controlling regulation. The CESA listing process generally is also described in some detail in published appellate case law in California, including:

> *Mountain Lion Foundation v. California Fish and Game Commission,* 16 Cal.4th 105, 114–116 (1997);
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> *California Forestry Association v. California Fish and Game Commission*, 156 Cal.App.4th 1535, 1541–1542 (2007);

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[2] Pursuant to this authority, standards, and procedures, the Commission may add, remove, uplist or downlist any plant or animal species to the list of endangered or threatened species, or to notice that any such species is a candidate for related action under CESA upon acceptance of a listing petition. Fish & G. Code, § 2074.2(a)(2); s*ee also* Cal. Code Regs., tit. 14, § 670.1, subd. (i)(1)(A)–(C). In practical terms, any of these actions may be commonly referred to as subject to CESA's "listing" process.

Center for Biological Diversity v. California Fish and Game Commission, 166
    Cal.App.4th 597, 600 (2008); and

Natural Resources Defense Council v. California Fish and Game Commission, 28
    Cal.App.4th 1104, 1111–1116 (1994).

The "is warranted" determination at issue here for the gray wolf is established by Fish and Game Code section 2075.5. Under this provision, the Commission is required to make one of two findings for a candidate species at the end of the CESA listing process; namely, whether the petitioned action is warranted or is not warranted. Here, with respect to gray wolf, the Commission made the finding under section 2075.5(2) that the petitioned action is warranted.

The Commission is guided in making this determination by the Fish and Game Code, CESA, other controlling law, and factual findings. The Fish and Game Code, for example, defines an endangered species under CESA as a "a native species or subspecies of a bird, mammal, fish, amphibian, reptile, or plant which is in serious danger of becoming extinct throughout all, or a significant portion, of its range due to one or more causes, including loss of habitat, change in habitat, overexploitation, predation, competition, or disease." Fish & G. Code, § 2062. As established by published appellate case law in California, the term "range" for purposes of CESA means the range of the species within California. *California Forestry Ass'n v. California Fish and Game Comm'n, supra*, 156 Cal.App.4th at 1540, 1549-1551. The Fish and Game Code, CESA, and other controlling law do not require a species to have a continuous presence or a breeding population in California in order to meet the definition of "endangered" or "threatened."

The Commission is also guided in making its determination regarding gray wolf by Title 14, section 670.1, subdivision (i)(1)(A), of the California Code of Regulations. This provision provides, in pertinent part, that a species shall be listed as endangered or threatened under CESA if the Commission determines that the species' continued existence is in serious danger or is threatened by any one or any combination of the following factors:

1.   Present or threatened modification or destruction of its habitat;
2.   Overexploitation;
3.   Predation;
4.   Competition;
5.   Disease; or
6.   Other natural occurrences or human–related activities.

Likewise, the Commission is guided in its determination regarding the gray wolf by Fish and Game Code section 2070. This section provides that the Commission shall add or remove species from the list it establishes under CESA upon receipt of sufficient information that the action is warranted. As the Commission's findings reflect, the gray wolf's continued existence in California is in serious danger due to multiple threats.

Furthermore, CESA provides policy direction indicating that all state agencies, boards, and commissions shall seek to conserve endangered species and threatened species and shall utilize their authority in furtherance of the purposes of CESA. Fish & G. Code, § 2055. This policy direction does not compel a particular determination by the Commission in the CESA listing context. Yet, the Commission made its determination regarding gray wolf mindful of this

policy direction, acknowledging that "'[l]aws providing for the conservation of natural resources' such as the CESA 'are of great remedial and public importance and thus should be construed liberally.'" *California Forestry Ass'n v. California Fish and Game Comm'n, supra*, 156 Cal.App.4th at 1545-1546 (citing *San Bernardino Valley Audubon Society v. City of Moreno Valley*, 44 Cal.App.4th 593, 601 (1996); Fish & G. Code, §§ 2051 and 2052).

Finally, in considering these factors, CESA and controlling regulation require the Commission to actively seek and consider related input from the public and any interested party. *See, e.g., id.* §§ 2071, 2074.4, 2078; Cal. Code Regs., tit. 14, § 670.1, subd. (h). The related notice requirements and public hearing opportunities before the Commission are also considerable. Fish & G. Code, §§ 2073.3, 2074, 2074.2, 2075, 2075.5 and 2078; Cal. Code Regs., tit. 14, § 670.1, subds. (c), (e), (g) and (i); *see also* Gov. Code, § 11120 *et seq.* All of these requirements are in addition to those proscribed for the Department in the CESA listing process, including an initial evaluation of the Petition and a related recommendation regarding candidacy, and a 12-month status review of the candidate species culminating with a report and recommendation to the Commission as to whether listing is warranted. Fish & G. Code, §§ 2073.4, 2073.5, 2074.4 and 2074.6; Cal. Code Regs., tit. 14, § 670.1, subds. (d), (f) and (h).

III.   FACTUAL BASES FOR THE COMMISSION'S FINDING

CESA provides for the listing of either "native species or subspecies of a bird, mammal, fish, amphibian, reptile, or plant." Fish and G. Code, §§ 2062 and 2067. The Petition, and the Commission's finding, applies to the gray wolf in California.

The factual bases for the Commission's finding that listing gray wolf as an endangered species under CESA is warranted are set forth in detail in the Commission's administrative record of proceedings. Substantial evidence in the administrative record of proceedings in support of the Commission's determination includes, but is not limited to, the Petition, the Department's 2012 Candidacy Evaluation Report, the Department's 2014 Status Review, and other information presented to the Commission and otherwise included in the Commission's administrative record of proceedings as it existed up to and including the meeting in Fortuna, California on June 4, 2014. The Commission made its final determination under CESA with respect to gray wolf at that meeting. Fish & G. Code, § 2075; Cal. Code Regs., tit. 14, § 670.1, subds. (g) and (i).

The Commission finds the substantial evidence supports the Commission's determination under CESA that the continued existence of gray wolf in the State of California is endangered by one or a combination of the following factors:
1.   Overexploitation;
2.   Predation;
3.   Disease;
4.   Other natural occurrences or human-related activities.

The Commission also finds that there is in the record of administrative proceedings substantial evidence to establish that designating the gray wolf as an endangered species under CESA is warranted. The following Commission findings highlight in more detail some but not all of the evidence in the administrative record of proceedings that support the Commission's determination that the gray wolf is in serious danger of becoming extinct throughout all, or a significant portion, of its range:

1. It is likely that wolves historically occurred in California and were widely distributed in the State. Status Review at 10 ("While limited the available information suggests that wolves were distributed widely in California, particularly in the Klamath-Cascade Mountains, North Coast Range, Modoc Plateau, Sierra Nevada, Sacramento Valley, and San Francisco Bay Area. The genetic evidence from southeastern California suggests that the Mexican wolf may have occurred in California, at least as dispersing individuals. While the majority of historical records are not verifiable, for the purposes of this status review, the Department concludes that the gray wolf likely occurred in much of the areas depicted (CDFW 2011a) (Figure 1)); 2012 Candidacy Evaluation Report at 4 ("As to the science available at this time and the reasonable inferences that can be drawn from that information, it indicates to the Department at this time that wolves were likely broadly distributed in California historically … ."); *id.* at 10 ("In summary, historic anecdotal observations are most consistent with a hypothesis that wolves were not abundant, but widely distributed in California.").

2. There is sufficient evidence to conclude that wolves occurred historically in California. However, by the late 1920's, the species was extirpated from the state. Status Review at 4 ("2012 Candidacy Evaluation Report at 4) ("As to the science available at this time and the reasonable inferences that can be drawn from that information … humans likely purposefully extirpated the species in California early in the twentieth century.")

3. Following listing of the gray wolf under the federal Endangered Species Act in 1974 and recovery efforts during the 1990s, a population of gray wolves in the Northern Rocky Mountain states has been re-established through a federal recovery program, and dispersing wolves from this population have established territories and several packs in Washington and Oregon. 2014 Status Review at 28.

4. In September 2011, a radio-collared, sub-adult gray wolf known as "OR7" dispersed from the Imnaha pack in northeastern Oregon and arrived in California on December 28, 2011, marking the first documented individual of the species in California since the 1920s. 2012 Candidacy Evaluation Report at 4 ("a single lone wolf, a dispersing young male named 'OR7,' entered California in December 2011, remaining largely in the State since that time"); *id.* at 10 ("The first gray wolf detected in California after many decades occurred in December 2011 with the arrival of 'OR7,' a radio-collared, sub-adult gray wolf that dispersed from a pack in Oregon."); *id.* ("OR7 dispersed from the Northeastern Oregon's Imnaha pack in September 2011.")

5. The gray wolf is once again present in California, on at least an intermittent basis, and foreseeably will continue to be present in California, as discussed below. OR-7's range now includes California and Oregon. OR7 has established a range that includes portions of Northern California, as this wolf is known to have crossed back and forth across the Oregon-California border since 2011 and to have been present in California in each of those years. Status Review at 4 ("The lone radio-collared gray wolf, OR7, dispersed from northeastern Oregon's wolf population to California in December 2011 and has been near the Oregon/California border since that time, crossing back and forth."); *id.* at 18 ("As far as the Department is aware, there is one gray wolf (OR7) that is near the Oregon/California border such that it may be in either state at any time."); 2012 Candidacy Evaluation Report at 11 ("OR7 has passed back and forth over the

California/Oregon border several times over the last five months … ."); California Department of Fish and Wildlife, Gray Wolf OR7: Updates on wolves migrating to California (available at http://californiagraywolf.wordpress.com); *see also* Oregon Department of Fish and Wildlife, OR-7 Timeline of Events (available at http://www.dfw.state.or.us/wolves/OR-7.asp) (documenting OR7's presence in California in each of 2011, 2012, 2013, and 2014).

6. OR7 has utilized areas of suitable habitat, primarily on public lands, comprised of ponderosa pine forests, mixed conifer forests, lava flows, sagebrush shrublands, juniper woodlands, as well as private lands including timberlands and agricultural lands, and has exhibited normal dispersal behavior for a young male gray wolf as he has sought to find other wolves, to establish his own pack, or to become part of an established wolf pack. 2012 Candidacy Evaluation Report at 10 ("It is believed that OR7 is exhibiting normal dispersal behavior for young male wolves, seeking to find other wolves, to establish his own pack, and/or to become part of an established wolf pack."); *id.* at 11 ("OR7 has passed through ponderosa pine forests, mixed conifer forests, lava flows, sagebrush shrublands, juniper woodlands, and agricultural lands"); *id.* ("Although OR7 has used private lands (timberlands in particular), most of its route has traversed public lands.").

7. On June 4, 2014, the State of Oregon Department of Fish and Wildlife confirmed that OR7 had mated with a female wolf of unknown origin, and that the pair was denning with a litter of at least two pups on public land in southwestern Oregon. *See* Press Release, Oregon Department of Fish and Wildlife, Pups for wolf OR7 (June 4, 2014) ("Wolf OR7 and a mate have produced offspring in southwest Oregon's Cascade Mountains, wildlife biologists confirmed this week."); Comments of Pamela Flick, Defenders of Wildlife (June 4, 2014 Commission hearing) (reporting breaking news that a remote camera in southwestern Oregon has detected at least two pups).

8. As the gestation period for gray wolves is 62-63 days and OR7 was documented in northern California on February 5, 2014, it is likely that OR7's mate was traveling with OR7 in California at the time. Status Review at 10 ("The gestation period for wolves is 62-63 days."); Testimony of Amaroq Weiss, June 4, 2014 Commission Meeting (Powerpoint slides at 15) ("A breeding population is likely on the border right now and a pregnant female was likely present in California already this year."); L.D. Mech & L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois, USA (cited in 2012 Candidacy Evaluation Report and Status Review) (discussing in Chapter 2 the reproductive behavior of wolves, and how wolves spend many months together leading up to impregnation and gestation).

9. The evidence in the record regarding wolf migration and dispersal behavior at a minimum indicates that wolves other than OR7 have similarly dispersed or will disperse to California, as most wolves from Oregon packs are not collared with radio transmitters and their presence in California may not otherwise have been detected ("we have acknowledged that we know of one [wolf, OR7]" and that "there could be others that we don't know about"); U.S. Fish and Wildlife Service, Montana Fish, Wildlife & Parks, Nez Perce Tribe, National Park Service, Blackfeet Nation, Confederated Salish and Kootenai Tribes, Wind River Tribes, Washington Department

of Wildlife, Oregon Department of Wildlife, Utah Department of Wildlife Resources, and USDA Wildlife Services. 2011. Rocky Mountain Wolf Recovery 2010 Interagency Annual Report. C.A. Sime and E. E. Bangs, eds. USFWS, Ecological Services, 585 Shepard Way, Helena, Montana. 59601. (2011) at 2 (noting that "it is difficult to locate lone dispersing wolves."); Carroll (2013) (Peer Review) at 5-6 ("[n]ot all Oregon wolves are detected and collared" so "it is possible that not all wolves dispersing to California have been detected"). Petition at 15 ("… it is impossible to rule out the possibility that previous dispersal events to California may … have occurred, which simply went un-detected because it is difficult to locate and track dispersing individual wolves"); Comments of Eric Loft (April 16, 2014 Commission Hearing).

10. The presence of wolves in California is small and is likely to remain small for the foreseeable future. Eisenberg (2013) (Peer Review) at 2 ("Any wolves becoming established in California will initially constitute a small population.").

11. Dispersing wolves and small wolf populations are inherently at risk due to demographic and environmental stochasticity and in the case of wolves, of being killed by poachers, or hunters that mistake them for coyotes. Status Review at 5 ("A small population in California would be at some inherent risk although the species has demonstrated high potential to increase in other states. Dispersing individuals and small packs would likely be at highest risk due to population size."); *id.* at 19 ("It is possible that a coyote hunter could mistake a gray wolf for a coyote, particularly at a long distance."); *id.* at 22 ("With at least one gray wolf near the border of Oregon/California, and the knowledge that populations or species ranges are typically so large that they could range across both states …, an individual wolf, or a small number of wolves would be threatened in their ability to reproduce depending on the number and sex of the animals present in the range."); 2012 Candidacy Evaluation Report at 6 ("Wolves are often confused with coyotes (*Canis latrans*) and domestic dogs (*C. lupus familiaris*), and wolf hybrids, which result from the mating of a wolf and a domestic dog.").

12. Despite losses of areas of the gray wolf's historic range in California, large tracts of habitat remain in the State that are sufficient to support a wolf population, particularly in the Modoc Plateau, Sierra Nevada, and Northern Coastal Mountains. Status Review at 17 ("Habitat Suitability Modeling: There are studies that have modeled potential suitable wolf habitat in California. Carroll (2001) modeled potential wolf occupancy in California using estimates of prey density, prey accessibility and security from human disturbance (road and human population density). Results suggested that areas located in the Modoc Plateau, Sierra Nevada, and the Northern Coastal Mountains could be potentially suitable habitat areas for wolves.

13. Since entering California, there have been threats to harm or kill OR7 or other wolves found in the State. (See e.g. May 6, 2013 Center for Biological Diversity letter to Department of Fish and Wildlife, p.13.) Although many people are supportive of gray wolves as a component of wildland ecosystems, wolves are considered a threat to livestock and wild ungulates by many other people, and are considered a threat to people by some. For example, the administrative record includes reports of statements by county supervisors from Modoc, Siskiyou, and Lassen counties expressing a desire to kill wolves in the area, a sentiment which represents an

imminent threat to wolves that are dispersing to the State. Status Review at 4-5 ("It is believed that limiting human-caused mortality through federal protection has been one of the key reasons that recovery efforts in the northern rocky mountains were successful."); *id.* at 18-19 ("Public perception of wolf attacks on people, the documented losses of livestock, and the sometimes photographed killing of livestock or big game, continues to influence human attitudes toward wolves."); Lassen County Board of Supervisors Hearing (Feb. 21, 2012) (quoting Lassen County supervisor to CDFW spokesperson) ("If I see an animal in my livestock, I kill it. If I kill a wolf, you going to throw me in jail? I don't care what it is.") (from notes taken at board meeting by Amaroq Weiss, Center for Biological Diversity); Modoc County Board of Supervisors Meeting (quoting Modoc County Supervisor) ("If I see a wolf, it's dead.") (Modoc County Board of Supervisors January 24, 2012 Hearing, Audio Archive); Chair of the Siskiyou County Board of Supervisors ("People are pretty much at their wits' end trying to make a living with all the environmental protections that are being foisted upon them" and "we would like to see [wolves] shot on sight") (*Los Angeles Times* (Dec. 24, 2011)) (available at http://articles.latimes.com/2011/dec/24/local/la-me-wolf-oregon-20111225).The Commission considers these statements and others like them to be compelling evidence of a threat to the continued existence of gray wolf in California. In a small early population of the species, loss of even one individual from human causes could significantly impact the ability of the species to thrive for years to come. CESA would criminalize such behavior in a more significant way than currently exists and act as a deterrent that may assist in allowing the early members of California's gray wolf population to persist.

14. Humans are the primary factor in the past decline of wolves in the conterminous United States, including California, and humans remain the largest cause of wolf mortality as a whole in the western United States. Humans impact wolf populations through intentional predation (shooting or trapping) for sport or for protection; through unintentional killing, as gray wolves are often confused with coyotes (*Canis latrans*), domestic dogs (*C. lupus familiaris*), and wolf hybrids; through vehicle collisions; and through exposures to diseases from domestic animals.For example, the administrative record demonstrates that on more than one occasion, staff from the California Department of Fish and Wildlife have been fearful that OR7 and other unknown wolves that could be in California would be mistaken for a coyote and shot or harmed. Limiting human-caused mortality through federal protection has been one of the key reasons that the recovery effort in the Northern Rocky Mountains has been successful. Status Review at 4-5 ("It is believed that limiting human-caused mortality through federal protection has been one of the key reasons that recovery efforts in the northern rocky mountains were successful."); *id.* at 19 ("Human-caused mortality of wolves is the primary factor that can significantly affect wolf populations (USFWS 2000, Mitchell et al. 2008, Murray et al. 2010, Smith et al. 2010)"); *id.* at 20.

15. Gray wolves are susceptible to several diseases including canine parvovirus and canine distemper, which has been responsible for extremely high rates of wolf pup mortality and suppression of wolf populations and which can be contracted from domestic dogs. Wolves are also susceptible to mange; mange-associated wolf population declines in Yellowstone National Park have led to pack extinction. Status Review at 23 (Wolves are vulnerable to a number of diseases and parasites, including, mange, mites, ticks, fleas, roundworm, tape worm, flatworm, distemper,

parvovirus, cataracts, arthritis, cancer, rickets, pneumonia, and Lyme disease."); *id.* ("The transmission of disease from domestic dogs, e.g. parvovirus, is a grave conservation concern for recovering wolf populations (Paquet and Carbyn 2003; Smith and Almberg 2007). Recently, two wolves and two pups in Oregon were found to have died from parvovirus (ODFW 2013b). The disease is not thought to significantly impact large wolf populations, but it may hinder the recovery of small populations (Mech and Goyal 1993)."); *id.* ("Canine distemper and canine infectious hepatitis: Both diseases are known to occur in wolves and more recently canine parvovirus has become prevalent in several wolf populations (Brand et al. 1995)"); E.S. Almberg, P.C. Cross, A.P. Dobson, D.W. Smith and P.J. Hudson. 2012. Parasite invasion following host reintroduction: a case study of Yellowstone's wolves. *Philosophical Transactions of the Royal Society Bulletin.* 367, p. 2840-2851).").

16. Listing the gray wolf under CESA will allow the species to benefit from CESA's protections, and would further the intent of the Legislature and be consistent with the objectives of CESA, *i.e.*, the conservation, protection, restoration, and enhancement of species in their range in California. Protecting the gray wolf under CESA will also strengthen the Department's existing stakeholder process to develop a state wolf plan, by providing clarity as to the management tools and options that will be available to the Department and to stakeholders. Status Review at 33 ("If the gray wolf species is listed under CESA, it may increase the likelihood that State and Federal land and resource management agencies will allocate funds towards protection and recovery actions."); Carroll (2013) (Peer Review) at 6 ("Rather than using a dubious interpretation of CESA to decline to list a species due to its temporary and uncertain absence from state, California should follow the example of Washington and Oregon in using the relevant state statutes to protect colonizing wolves while at the same time developing multi-stakeholder plans that proactively restore wolf conservation and management issues.").

IV.   FINAL DETERMINATION BY THE COMMISSION

The Commission has weighed and evaluated the evidence presented for and against designating gray wolf as an endangered species under CESA. This information includes the Petition; the Department's Petition Evaluation Report; the Department's status review; the Department's related recommendations; written and oral comments received from members of the public, the regulated community, various public agencies, and the scientific community; and other evidence included in the Commission's record of proceedings. Based upon the evidence in the record the Commission has determined that the best information available indicates that the continued existence of the one or more gray wolves in California is in serious danger of extinction or threatened by present or threatened overexploitation, predation, disease, or other natural occurrences or human-related activities, where such factors are considered individually or in combination. (See generally Cal. Code Regs., tit. 14, § 670.1, subd. (i)(1)(A); Fish & G. Code, §§ 2062, 2067.) The Commission determines that there is sufficient evidence in the record to indicate that designating the gray wolf as an endangered species under CESA is warranted at this time and, with the adoption and publication of these findings and further proceedings under the California Administrative Procedure Act, the gray wolf shall be listed as endangered. See Cal. Code Regs., tit. 14, § 670.1, subd. (i)(1)(A).

Recolonizing wolves trigger a trophic cascade in Wisconsin (USA)

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Summary

1. We tested the hypothesis that wolves are reducing local browse intensity by white-tailed deer, thus indirectly mitigating the biotic impoverishment of understorey plant communities in northern Wisconsin.

2. To assess the potential for such a top-down trophic cascade response, we developed a spatially and temporally explicit model of wolf territory occupancy based on three decades of wolf monitoring data. Using a nested multiscale vegetation survey protocol, we compared the understorey plant communities of northern white cedar wetlands found in high wolf areas with control sites found in low wolf areas.

3. We fit species–area curves for plant species grouped by vegetation growth form (based on their predicted response to release from herbivory, i.e. tree, seedling, shrub, forb, grass, sedge or fern) and duration of wolf territory occupancy.

4. As predicted for a trophic cascade response, forb species richness at local scales (10 m^2) was significantly higher in high wolf areas (high wolf areas: 10.7 ± 0.9, $N = 16$, low wolf areas: 7.5 ± 0.9, $N = 16$, $P < 0.001$), as was shrub species richness (high wolf areas: 4.4 ± 0.4, $N = 16$, low wolf areas: 3.2 ± 0.5, $N = 16$, $P < 0.001$). Also as predicted, percentage cover of ferns was lower in high wolf areas (high wolf areas: 6.2 ± 2.1, $N = 16$, low wolf areas: 11.6 ± 5.3, $N = 16$, $P < 0.05$).

5. Beta richness was similar between high and low wolf areas, supporting earlier assumptions that deer herbivory impacts plant species richness primarily at local scales. Sampling at multiple spatial scales revealed that changes in species richness were not consistent across scales nor among vegetation growth forms: forbs showed a stronger response at finer scales ($1–100 \text{ m}^2$), while shrubs showed a response across relatively broader scales ($10–1000 \text{ m}^2$).

6. *Synthesis*. Our results are consistent with hypothesized trophic effects on understorey plant communities triggered by a keystone predator recovering from regional extinction. In addition, we identified the response variables and spatial scales appropriate for detecting such differences in plant species composition. This study represents the first published evidence of a trophic cascade triggered by wolf recovery in the Great Lakes region.

Key-words: biodiversity, determinants of plant community diversity and structure, grey wolf (*Canis lupus*), herbivory, Northern White Cedar *(Thuja occidentalis)*, species–area relationship, trophic cascades, vegetation dynamics, white-tailed deer *(Odocoileus virginianus)*, Wisconsin

Introduction

Indirect interactions between carnivores and plants, mediated by herbivores, are commonly referred to as trophic cascades (Paine 1980; Carpenter, Kitchell & Hodgson 1985). Such interactions are frequently used to justify carnivore conservation, despite limited experimental evidence of trophic cascades involving large mammalian predators (Ray 2005; Ripple, Rooney & Beschta 2010). Recent attempts to infer top-down effects of predators have drawn on comparisons

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across areas with and without predators (Berger *et al.* 2001; Terborgh *et al.* 2006), or correlative studies of vegetation response following predator reintroduction (Ripple & Beschta 2012). One of the most well-known examples of a terrestrial trophic cascade is the wolf (*Canis lupus*)/moose (*Alces alces*)/balsam fir (*Abies balsamea*) system on Isle Royale (McLaren & Peterson 1994). Despite its historical significance, cause and effect in the Isle Royale system remains speculative due to the studies' correlative nature and lack of replication or comparable control sites (Eberhardt 1997; Schmitz, Hamback & Beckerman 2000).

In addition, previously documented trophic cascades in temperate terrestrial systems represent species-level as opposed to community-level cascades (Polis 1999). These studies tested how predators affect the productivity of one or occasionally several plant species (McLaren & Peterson 1994; Berger *et al.* 2001; Ripple & Beschta 2012), but failed to test whether predator manipulations affect species composition and diversity of entire plant communities. It has been argued that terrestrial cascades are principally species-level phenomena, due to comparatively nonlinear food-web structure, trophic complexity and effective plant defence mechanisms (Halaj & Wise 2001). However, recent evidence from experimental manipulations of herbivores and carnivores in old field ecosystems suggests that predators in terrestrial systems have much stronger effects on plant species diversity than on plant biomass (Schmitz 2006). Furthermore, it is these changes in plant community composition that influence ecosystem properties.

Ecological processes (including trophic cascades) are likely to manifest differentially over a range of spatial and temporal scales (Levin 1992; Polis 1999; Bowyer & Kie 2006). Size, generation time, reproductive characteristics and dispersal ability of the organisms involved determine the scale(s) at which they perceive and respond to environmental change (Levin & Pacala 1997). Variation in these life-history traits necessitates sampling at multiple spatial scales to accurately interpret responses to top-down processes. Additionally, the effects of trophic cascades are likely to be dampened by spatial heterogeneity (van Nes & Scheffer 2005). Habitat refugia combined with spatial and temporal variability in species' distributions allow prey to escape predation (Halaj & Wise 2001), potentially creating a mosaic of cascade intensity across the landscape.

The impacts of hyperabundant white-tailed deer (*Odocoileus virginianus*) populations on understorey plant community structure and composition are well-established (Alverson, Waller & Solheim 1988; Tilghman 1989; Peek & Stahl 1997; Crete 1999; Rooney 2001; Rooney & Waller 2003; Horsley, Stout & deCalesta 2003; Rooney *et al.* 2004; Holmes, Curran & Hall 2008). However, few studies have examined how the recovery of wolves might moderate these effects. Recent studies of species interactions in Yellowstone National Park (YNP) suggest that the recovery of wolf populations can naturally ameliorate ungulate-caused ecosystem simplification (White & Garrott 2005; Ripple & Beschta 2012). In this study, we examine whether a similar trophic cascade was triggered by the recovery of the Great Lakes wolf population in northern Wisconsin. In addition, by assessing community-level responses as opposed to species-level responses and by measuring across several spatial scales of observation, we hope to inform future research by identifying the ideal response variable and spatial scale for detecting effects of top predators in similar terrestrial systems.

Ecological setting

Unlike in Yellowstone, where elk (*Cervus elaphus*) are the primary prey species of grey wolves, wolves in the Great Lakes region prey mainly on white-tailed deer. Wolves were nearly eradicated from the region during the early part of the 20th century. However, the wolf population in neighbouring Minnesota was never fully extirpated and began to recover under the protection of the Endangered Species Act. Dispersing wolves from Minnesota (and possibly Canada) first began to arrive in Wisconsin in the mid-1970s. The Wisconsin population grew slowly for the first few decades and then began to grow almost exponentially (Wydeven, Schultz & Thiel 1995; Wydeven *et al.* 2009). Wolf recovery in the Great Lakes region over the past three decades has been closely monitored by the respective Departments of Natural Resources (DNR) in Minnesota, Wisconsin and Michigan. The Wisconsin DNR (WiDNR) has annually mapped all known wolf pack territories in the state since 1979. The high quality of this data set provided the information we needed to examine the spatial and temporal patterns in wolf occupancy throughout the state and thus answer the following question: Is the recovery of wolves releasing some understorey plant communities from over-browsing by white-tailed deer?

Aldo Leopold reported irruptions (abrupt population rise) of deer in Wisconsin as early as 1947 (Leopold, Sowls & Spencer 1947). Based on land cover conditions, pre-settlement white-tailed deer densities in northern Wisconsin are thought to have ranged between 4 and 6 km^{-2} (McCaffery 1995). The combination of predator extirpation, protective hunting laws and habitat management has contributed to current deer densities ranging between 4 and 15 km^{-2} (WiDNR 2010). Densities as low as 1–2 deer km^{-2} have been prescribed to improve recruitment of browse-sensitive plant species (Alverson, Waller & Solheim 1988). Is the recovering wolf population in Wisconsin even capable of maintaining deer densities this low?

In the Great Lakes region, wolves require 15–18 deer 'equivalents' per wolf per year (Fuller 1989). Hence, the current Wisconsin wolf population, which has grown to *c.* 690 individuals (in winter) since their placement on the endangered species list (Wydeven & Wiedenhoeft 2010), has the capacity to take *c.* 12 000 deer per year. Given the current estimated deer population of 340 000 in the Northern Forests of Wisconsin (WiDNR 2010), region-wide effects of wolf recovery on deer populations are unlikely to manifest in the short term. In addition, whether wolf kills represent primarily compensatory or additive mortality for white-tailed deer is in

part dependent on stochastic environmental variables such as winter severity (Mech & Peterson 2003). However, localized influences of wolf predation on deer populations are more probable, and drastic local herd reductions have been observed in Minnesota (Nelson & Mech 2006).

Hoskinson & Mech (1976) found higher white-tailed deer survival on the edges of wolf territories as compared to their centres. Wolves are less likely to hunt in these buffer zones so as to avoid potentially fatal encounters with neighbouring wolf packs (Mech 1977). At local scales, the distribution of deer in northeastern Minnesota was found to be negatively correlated with wolf territory extents, and deer were found primarily in buffer zones (Lewis & Murray 1993). Thus, buffer zones surrounding wolf pack territories may act as refugia for white-tailed deer (Mech 1994). By extension, consistently occupied wolf pack territories may act as refugia for understorey plants that are preferred by white-tailed deer.

Exclosure studies combined with resampling of historic vegetation plots from the 1950s (Curtis 1959) strongly implicate the hyperabundance of white-tailed deer as the causal factor driving local losses in plant species diversity (Rooney & Waller 2003; Rooney *et al.* 2004). This decline in rare and uncommon species is contributing to the biotic homogenization of understorey plant communities in northern Wisconsin (Frelich & Lorimer 1985; Cote *et al.* 2004; Rooney *et al.* 2004; Wiegmann & Waller 2006). Consistent with this pattern, populations of northern white cedar (*Thuja occidentalis*) have suffered region-wide recruitment failure due primarily to decades of over-browsing (Rooney, Solheim & Waller 2002).

White cedar forests are used intensively by white-tailed deer during the winter months, subjecting the highly nutritious and palatable seedlings to excessive herbivory (Habeck 1960; Van Deelen, Pregitzer & Haufler 1996). Historically, these coniferous wetlands have supported extremely diverse plant communities (Curtis 1959; Pregitzer 1990) providing habitat for a variety of rare lilies and orchids (USDA Forest Service 2004). Unique shrub and forb species restricted to conditions found in white cedar wetlands are also susceptible to over-browsing. Without recruitment to the canopy, existing mature stands of white cedar may become increasingly isolated as older stands senesce, accelerating the associated loss of understorey plant species restricted to this unique habitat type (Alverson, Waller & Solheim 1988; Cornett *et al.* 2000) via the process of 'relaxation' described by Diamond (1972).

Given that northern white cedar wetlands are very sensitive to herbivory and are heavily used by white-tailed deer, we anticipated that recovery from over-browsing would be more easily detected in these ecosystems than in other forest cover types. Thus, the tri-trophic cascade that we are testing for is comprised of wolves, white-tailed deer and understorey plant communities of northern white cedar wetlands (Fig. 1). The objective of this study was to develop species–area curves to test whether differences in plant species richness occur between high and low wolf areas (as defined by years of wolf pack occupancy).
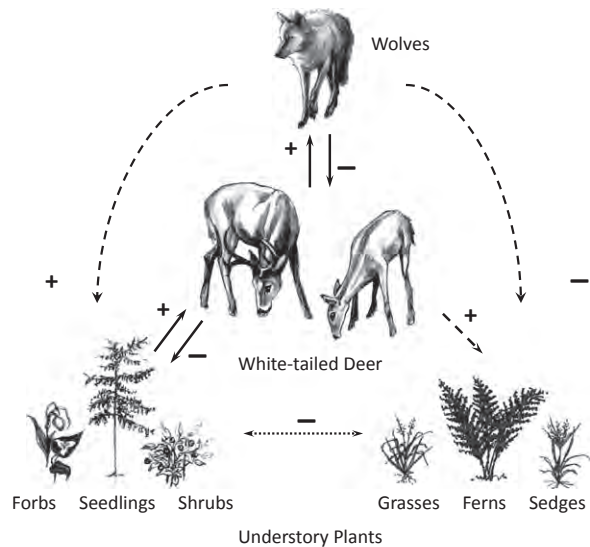
Fig. 1. Diagram of hypothesized tri-trophic interactions in northern Wisconsin forests. Solid arrows represent direct positive and negative interactions. Dashed arrows represent hypothesized indirect interactions. Dotted line represents competitive interactions.

We anticipated that understorey plants would vary in their response to release from browsing pressure dependent on the vegetation growth form in question. For example, tree seedlings, shrubs and forbs are highly preferred by white-tailed deer and collectively respond negatively to high browsing pressure. In contrast, ferns, grasses and sedges are generally avoided by white-tailed deer and thought to respond positively (though indirectly) to high browsing pressure, because they are released from competition with preferred species (Stromayer & Warren 1997; Cooke & Farrell 2001; Boucher, Crête & Ouellet 2004).

Based on previous studies of deer influence on terrestrial plant communities (Frelich & Lorimer 1985; Stromayer & Warren 1997; Cooke & Farrell 2001; Rooney & Waller 2003; Boucher, Crête & Ouellet 2004; Cote *et al.* 2004; Wiegmann & Waller 2006), we predicted that high wolf areas would be subject to reduced browse pressure and thus be characterized by an increased percentage cover of forbs, shrubs and seedlings. We further expected that ferns, grasses and sedges would demonstrate the opposite response to wolf recovery (decreased percentage cover in high wolf areas). The relationship between disturbance and species diversity described by Denslow (1985) predicts that species richness of seedling, shrub and forb species should be higher at high wolf areas (since browsing pressure should be lower and closer to historic levels).

As noted previously, the spatial scale at which species respond to ecological processes is determined by the life-history traits of each species and thus likely to vary significantly. To address this issue, we measured species richness across a range of spatial scales (0.01, 1.0, 10, 100, 400 and 1000 m²). In this manner, we sought to identify the appropriate scale of measurement for detecting responses to release from

herbivory (as measured by changes in species richness) for each vegetation growth form.

Materials and methods

STUDY SITE

Data were collected throughout the Chequamegon-Nicolet National Forest, as well as from various state and county forests spanning seven counties in north-central Wisconsin (Fig. 2). The forests of northern Wisconsin are transitional between deciduous forests to the south and boreal forests to the north (Pastor & Mladenoff 1992; Mladenoff *et al.* 1993). Northern white cedar wetlands occupy 5% of the forested landscape (WiDNR 1998). This community type develops on poorly drained sites with a slight through-flow of groundwater, producing elevated pH and nutrient richness of the soil (Black & Judziewicz 2008). Mature stands of white cedar are densely shaded with nearly closed canopies. The combination of these characteristics provides the unique light regimes and soil chemistry required by species restricted to this community type (see below).

Co-dominant trees in white cedar wetlands include balsam fir (*Abies balsamea*), yellow birch (*Betula alleghaniensis*) and black ash (*Fraxinus nigra*). Tag alder (*Alnus incana* subsp. *rugosa*), hollies (*Ilex mucronata* and *I. verticillata*), hazelnuts (*Corylus* spp.) and honeysuckles (*Lonicera* spp.) are common understorey shrubs. Cedar wetlands are rich in sedges (e.g. *Carex disperma*, *C. trisperma*), ferns (e.g. *Dryopteris* and *Gymnocarpium* spp.) and numerous wildflowers. Common wildflowers are goldthread (*Coptis trifolia*), starflower (*Trientalis borealis*), wild sarsaparilla (*Aralia nudicaulis*), naked miterwort (*Mitella nuda*), blue-bead lily (*Clintonia borealis*), bunchberry (*Cornus canadensis*), Canada mayflower (*Maianthemum canadense*) and trailing 'subshrubs' such as creeping snowberry (*Gaultheria hispidula*), dwarf red raspberry (*Rubus pubescens*) and twinflower (*Linnea borealis*). Orchids include yellow lady's slipper (*Cypripedium parviflorum*), heart-leaved twayblade (*Listera cordata*), lesser rattlesnake plantain (*Goodyera repens*) and blunt-leaved bog orchid (*Platanthera obtusata*).

RESEARCH DESIGN

Wolf packs establish and occupy territories that are patchily distributed across the landscape (Mladenoff, Sickley & Wydeven 1999). The effect of wolves on deer abundance and foraging behaviour is likely to be limited to locations continuously occupied by wolf packs. Presumably, the impact of wolves increases with the size of the pack and the number of years the territory has been consistently occupied. Since pack size and territory extent vary from year to year, this creates a mosaic of potential impact intensity across the landscape. WiDNR population estimates of wolves were ascertained by live-trapping and radiotracking, howl surveys and winter track surveys (Wydeven, Schultz & Thiel 1995). Territory extents were delineated using minimum convex polygons based on radiolocations of collared wolves and other wolf sign (Wiedenhoeft & Wydeven 2005).

Using ArcGIS, we overlaid current wolf territories with historic territory extents to delineate areas that have been continuously occupied for *c.* 10 years (high wolf areas) and areas that have essentially remained unoccupied since wolf recolonization of the region (low wolf areas). Only sites within the Chequamegon-Nicolet National Forest, state forest or county forest boundaries were selected. We used the Combined Data Systems (CDS) data for the Chequamegon-Nicolet National Forest (USDA 2001) and various state and county forest data sets to select stands characterized as northern white cedar wetlands. White cedar stands within consistently occupied wolf territories were then paired with the closest unoccupied white cedar stand of similar stand area and stand age. In this way, plots were assigned to either high wolf areas (8–10 years of recent wolf occupancy) or low wolf areas (0–3 years of recent wolf occupancy). To control for spatial autocorrelation and limit the potential for confounding variables to produce false associations, we paired high wolf sites with low wolf sites within a few kilometres (Fig. 3).

VEGETATION SURVEYS

We randomly placed 1 vegetation plot within each pre-selected white cedar stand and surveyed a total of 32 cedar stands (16 in low and 16 in high wolf areas). Fourteen plots were completed in 2008, and 18
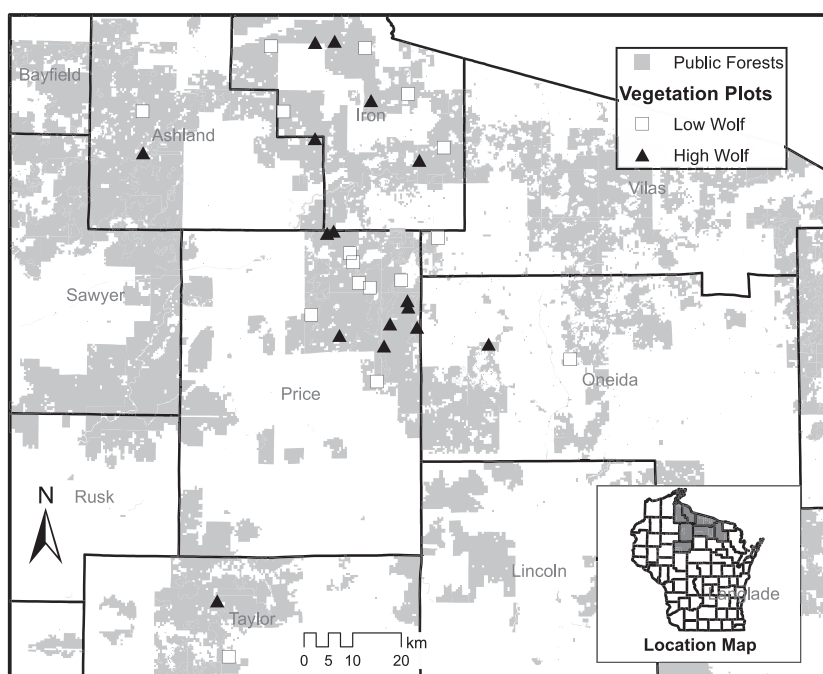
Fig. 2. Study areas in northern Wisconsin. Black triangles indicate vegetation plots located in high wolf areas. White triangles represent vegetation plots in low wolf areas.
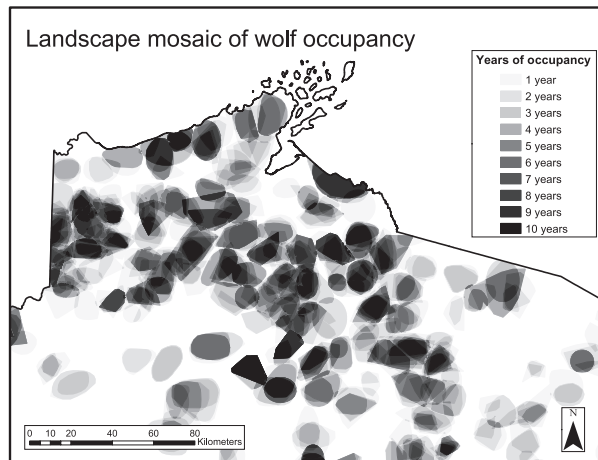
Fig. 3. Intensity of wolf impact based on 10 years (1998–2008) of wolf pack territory data (WiDNR). Years of occupancy represent the duration of wolf pack tenure. High wolf areas = 8–10 years of occupancy, low wolf areas = 0–3 years of occupancy.

plots were completed in 2009. Vegetation surveys followed the Carolina Vegetation Survey (CVS) protocol developed by Peet, Wentworth & White (1998). Plots consisted of 10 modules (10 × 10 m) in a 2 × 5 array (1000 m^2 in total). Four of the 10 modules were sampled intensively, while the remaining plots were surveyed for additional species occurrences only. Two corners in each of the intensive modules were sampled for the presence of vascular plant species (trees, shrubs, seedlings, ferns, forbs, grasses and sedges) using a series of nested quadrats (increasing incrementally in size from 0.01 to 10 m^2). Percentage cover data were estimated visually for each 100-m^2 module based on the following cover classes: 0–1%, 1–2%, 2–5%, 5–10%, 10–25%, 25–50%, 50–75%, 75–95%, 95–100%.

Identification of forbs conforms to Black & Judziewicz (2008). All other plant species names conform to Gleason & Cronquist (1991). Due to extensive time requirements, species identification of grasses and sedges was discontinued for the second field season.

DATA ANALYSIS

Percentage cover of all plant species in each growth form (tree, shrub, seedling, forb, fern, grass, sedge) was assigned the geometric mean of the cover class to which they were visually assigned. Geometric mean values for each of the four intensive modules were then averaged to provide one value for each plot. Student's t-tests were used to compare percentage plant cover between high and low wolf areas across all vegetation growth forms.

Species richness at each scale (0.01, 1.0, 10, 100, 400 and 1000 m^2) was calculated for each plot by averaging subsamples. The number of subsamples varied depending on the scale sampled (0.01–10 m^2, $n = 8$, 100 m^2, $n = 4$, and 400–1000 m^2, $n = 1$). Again, Student's t-tests were used to compare species richness between high and low wolf areas and across all vegetation growth forms and spatial scales. The multiscale nested structure of the CVS protocol also facilitates the construction of species–area curves. Species–area curves describe the rate at which species richness increases as the total area sampled increases (Rosenzweig 1995). We fit averaged species richness values to the power function to determine y-intercept and slope values (c and z values). We chose the power model because it was shown to outperform the exponential model when evaluated

using Akaike Information Criterion (AICc) (Barnett & Stohlgren 2003). The power model has an equation of the form:

$$S = cA^z \qquad \text{eqn 1}$$

where S represents the number of species, A represents the area, and c and z are constants.

For this type of analysis, the power function is often manipulated to log–log form:

$$\log(S) = z\log(A) + \log(c) \qquad \text{eqn 2}$$

Calculation of c and z values, where c = species richness at one unit of area (α-richness) and z = the rate at which species richness increases with area (β-richness), allows us to predict the direction and magnitude of differences in species richness. We grouped species–area curves for low and high wolf sites ($n = 16$) to compare α- and β-richness between these two treatments. Species–area curves were generated for all vegetation growth forms separately (note that grass and sedge species richness data are from the first year of the study only and are based on a reduced sample size, $n = 7$). T-tests and 95% confidence intervals were used to determine significant differences in c and z values as well as to indicate at which scales differences are most easily detected.

Results

PERCENTAGE COVER BY STRATA

We identified a total of 199 vascular plant species: 23 trees, 31 shrubs, 98 forbs, 12 ferns, 5 fern allies, 16 sedges, 7 grasses, 2 vines, 1 rush and 4 non-native species (see Callan 2010 for a complete list). In general, sites with high wolf occupancy had a diverse understorey community with complex vertical structure (Fig. 4a). In contrast, low wolf occupancy sites were characterized by a very limited herbaceous layer and almost no woody-browse (Fig. 4b). Some low wolf sites were characterized by an understorey dominated by ferns but still lacking in forbs, shrubs and tree seedlings.

Percentage cover of forbs was higher in high wolf areas (high wolf areas: 15.0 ± 4.4%, $N = 16$, low wolf areas: 8.8 ± 2.5%, $N = 16$, $P < 0.05$) as were shrub and tree seedling cover combined (high wolf areas: 11.2 ± 4.3%, $N = 16$, low wolf areas: 6.1 ± 2.1%, $N = 16$, $P < 0.05$), while cover of ferns was lower (high wolf areas: 6.2 ± 2.1%, $N = 16$, low wolf areas: 11.6 ± 5.3%, $N = 16$, $P < 0.05$) (Fig. 5). Percentage cover of grasses was equivalent in low and high wolf areas (high wolf areas: 0.50 ± 0.22%, $N = 16$, low wolf areas: 0.59 ± 0.50%, $N = 16$, $P = 0.32$), and sedge cover did not differ significantly (high wolf areas: 7.4 ± 4.0, $N = 16$, low wolf areas: 4.5 ± 1.8, $N = 16$, $P = 0.10$). Percentage tree cover was very similar between high and low wolf areas (high wolf areas: 69.9 ± 5.7%, $N = 16$, low wolf areas: 71.2 ± 7.4%, $N = 16$, $P = 0.39$).

SPECIES–AREA RELATIONSHIPS

When all species were included in the analysis, species–area curves in high wolf areas tended towards higher alpha richness (c) for all species combined (Table 1), but this difference was not significant ($P = 0.10$). Beta richness (z) ranged from 0.27–0.35 across all sites, but was similar between low

Fig. 4. Photo pair of understorey vegetation within the Chequamegon-Nicolet National Forest, WI. (a) Shows a high wolf area (within the Bootjack Lake pack territory) and (b) shows the paired low wolf area (in the buffer zone between the Bootjack Lake pack and the Miles Lake pack).
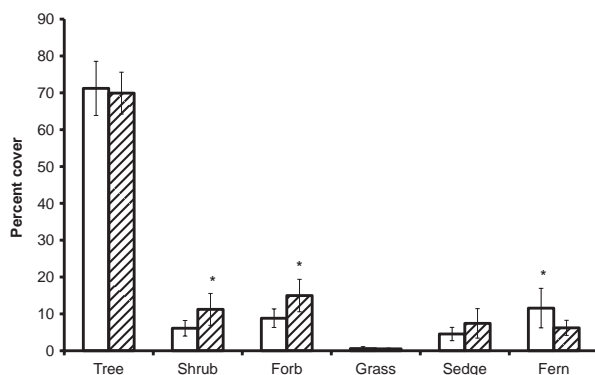
Fig. 5. Average percentage cover of high and low wolf area plots across 6 vegetation growth forms (forbs, shrubs, trees, ferns, grasses and sedges) with 95% confidence intervals. Values are averaged geometric means of cover classes (0–1%, 1–2%, 2–5%, 5–10%, 10–25%, 25–50%, 50–75%, 75–95%, 95–100%). Hatched bars represent high wolf areas. Asterisks indicate significant differences ($P < 0.05$).

and high wolf areas. When species richness of understorey plants was broken down into vegetation growth forms based on their hypothesized response to herbivory, differences between high and low wolf areas were more pronounced (Table 1). Alpha richness of forbs was much higher in high wolf areas ($P < 0.001$) as was alpha richness of shrubs ($P < 0.05$). Surprisingly, alpha richness of ferns was in fact higher in high wolf areas ($P < 0.05$), and alpha richness of sedges tended to be higher in high wolf areas, but this differ-

ence was not significant ($P < 0.10$). Again, beta richness was equivalent between high and low wolf areas across all vegetation growth forms.

As predicted for a trophic response, forb species richness at local scales (10 m^2) was significantly higher in high wolf areas (high wolf areas: 10.7 ± 0.9 N, low wolf areas: 7.5 ± 0.9, $N = 16$, $P < 0.0001$), as was shrub species richness [high wolf areas: 4.4 ± 0.4, low wolf areas: 3.2 ± 0.5, $N = 16$, $P < 0.001$(Fig. 6)]. Contrary to our expectations, species richness of ferns was higher at the 10-m^2 scale (high wolf areas: 2.99 ± 0.3, low wolf areas: 2.08 ± 0.47, $N = 16$, $P < 0.01$). Species richness of sedges was higher in high wolf areas at the smallest spatial scale measured, 0.01 m^2 (high wolf areas: 0.47 ± 0.16, low wolf areas: 0.23 ± 0.14 $N = 7$, $P < 0.05$), but this pattern was based on a limited sample size and was not observed at other spatial scales. Species richness of trees, seedlings and grasses was similar between low and high wolf areas across all scales.

Discussion

As predicted, percentage cover of forbs was 70% higher on average in high wolf areas, and species richness of forbs was 43% higher (at the 10-m^2 scale). Shrubs showed a similar pattern with 84% higher percentage cover for seedlings and shrubs grouped and 39% higher species richness for shrubs alone. Percentage cover of ferns was 47% lower in high wolf areas. Although we expected greater species richness of tree seedlings in high wolf/low deer impact sites (Tilghman 1989), this pattern was not observed. The presence of seedling species may be more related to proximity to seed sources (adults in the canopy) and less related to browsing pressure. The nearly equivalent percentage tree cover between high and low wolf areas eliminates the possibility that differences in light availability are responsible for the observed differences in percentage cover of the lower strata.

The similarity in percentage cover of grasses in high and low wolf areas was inconsistent with our predictions for a top-down trophic response since previous studies indicated an indirect positive relationship between deer browsing pressure and the percentage cover of grass species. Almost all visual estimates of grass cover fell in the same cover class: 0–1%. This area represents *c.* 1 m^2 of a 100-m^2 module. Percentage cover of grasses and sedges may need to be estimated at finer scales than at the 100-m^2 module. Evidence does suggest that sedges may actually be more abundant in high wolf areas. It is possible that sedge species in northern white cedar swamps respond negatively to white-tailed deer grazing even though *Carex* spp. collectively have been shown to respond positively in other vegetation types (Wiegmann & Waller 2006).

The similarity in *z* values (beta richness) between high and low wolf areas suggests that herbivory may have little or no impact on species turnover, habitat heterogeneity or mass effects. Although we observed consistent differences at broader scales, these may be due to local differences propagating up through higher scales of observation. Reduced browse intensity limits the ability of a few browse-resistant

Table 1. Slope (*z* or beta richness), intercept (*c* or alpha richness) and correlation coefficient (r^2) values by vegetation growth form for species–area curves of northern white cedar stands with low and high wolf occupancy. Values in parentheses represent 95% confidence intervals

	Low wolf areas			High wolf areas		
	z	*c*	r^2	*z*	*c*	r^2
All Species	0.32 (0.30–0.35)	8.98 (7.34–10.99)	0.94	0.32 (0.30–0.35)	10.82 (9.16–12.79)	0.96
Forbs	0.24 (0.22–0.26)	3.82 (3.33–4.39)	0.91	0.24 (0.22–0.26)	5.42 (4.84–6.05)	0.93
Shrubs	0.30 (0.29–0.31)	1.35 (1.20–1.51)	0.95	0.32 (0.31–0.33)	1.57 (1.40–1.76)	0.95
Seedlings	0.26 (0.25–0.27)	1.20 (1.04–1.37)	0.96	0.27 (0.25–0.29)	1.25 (1.00–1.54)	0.93
Trees	0.22 (0.21–0.23)	0.76 (0.60–0.93)	0.87	0.21 (0.19–0.23)	0.78 (0.63–0.95)	0.86
Ferns	0.22 (0.20–0.24)	0.94 (0.71–1.20)	0.81	0.24 (0.23–0.25)	1.24 (1.09–1.41)	0.94
Grasses	0.20 (0.16–0.24)	0.52 (0.42–0.62)	0.83	0.21 (0.18–0.24)	0.60 (0.36–0.92)	0.77
Sedges	0.23 (0.20–0.26)	1.37 (1.00–1.83)	0.86	0.21 (0.23–0.25)	1.80 (1.41–2.27)	0.91
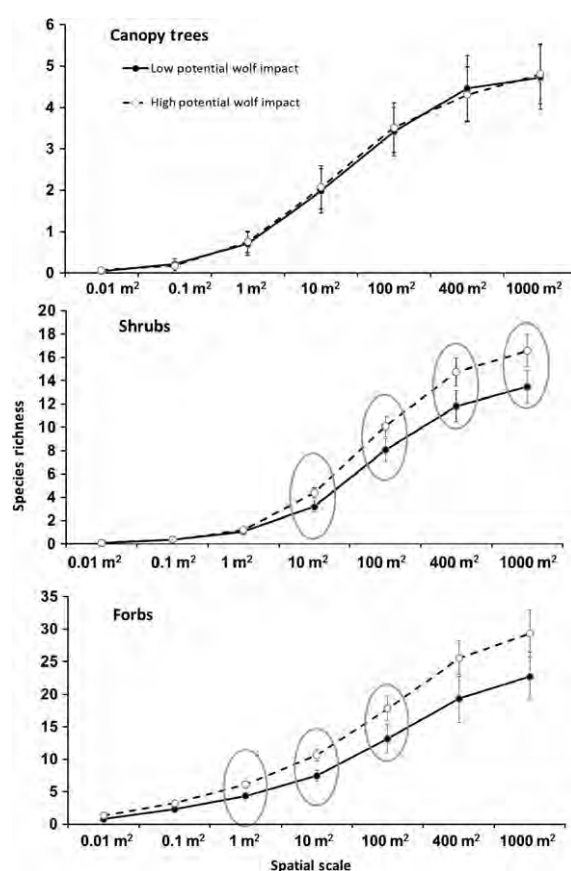
Fig. 6. Species–area curves for high and low wolf areas displayed across seven spatial scales for canopy trees, forbs and shrubs. High wolf area data points are represented by open circles and dashed lines. Data points are the mean number of species at each scale from each plot. Scales on the *y*-axis (number of plant species) vary depending on maximum species richness for each vegetation growth form. *X*-axis intervals are not to scale.

Plant species richness is determined by linked processes that act differentially across small, intermediate and large spatial scales (Schmida & Wilson 1985). Species richness at small scales (< 1 m²) is a consequence of direct competition and niche relations (variability in resource utilization and allocation). At intermediate scales (1–100 m²), species richness is more a consequence of microhabitat heterogeneity promoting the coexistence of species with different habitat requirements. At scales beyond 100 m², species richness is more likely determined by immigration of seeds from source habitats ('mass effect' dynamics, Schmida & Whitaker 1981). At this scale, the extent to which the plant community is linked to the regional species pool becomes the dominant process determining local recruitment and ultimately species richness (Rogers *et al.* 2009). Had we surveyed at scales < 1000 m², we might expect a point at which species richness between high and low wolf areas would converge. However, patch occupancy of cedar stands and metapopulation dynamics could become dominant processes at this scale, superseding species–area relationships and strengthening or weakening differences in species richness values between high and low wolf areas.

By sampling at multiple scales, we revealed that our ability to detect differences in species richness was not consistent among vegetation growth forms. Based on means and 95% confidence intervals, forbs show a stronger response at finer scales (1–100 m²), while shrubs show a response across broader scales (10–1000 m²). The design of future research should incorporate the proper scale in order to effectively detect top-down effects. Many vegetation studies survey at the scale of 1 m², which is likely to miss significant differences in shrub species richness. Whether these scales are appropriate for community types other than northern white cedar wetlands is unknown. However, it is likely that the relevant scales are determined by the process of deer herbivory itself and should be similar regardless of forest cover type.

Unfortunately, reciprocal relationships between trophic levels, like those found by McLaren & Peterson (1994) between wolves, moose and balsam fir on Isle Royale, are lacking in Wisconsin. At present, deer data are available for the past several decades, but only at the very coarse scale of deer management blocks (WiDNR 2010). Since most low and high wolf areas in our study were within the same deer man-

species to become locally dominant, thus increasing species richness at local scales. Additionally, increased species richness may be closely linked to increased density of individuals at local scales. This pattern has been observed in both temperate and tropical plant communities (Denslow 1995; Busing & White 1997; Hubbell 2001; Schnitzer & Carson 2001).

agement unit, we considered existing deer data to be unsuitable for the scale of this study. Future research should focus on monitoring deer abundance and/or foraging behaviour concurrent with wolf occupancy and vegetation response.

Several factors that benefit both plant diversity and wolf habitat quality, irrespective of deer density and any sort of trophic effects, could result in the pattern that we documented. In particular, road density has been shown to be negatively correlated with both plant diversity (Findlay & Houlahan 1997; Watkins *et al.* 2003) and wolf habitat selection (Mladenoff *et al.* 1995). In addition, understorey vegetation in white cedar stands may be more influenced by hydrology and edge effects than by trophic effects. Landscape-level connectivity between cedar stands is likely to influence mass effects. A bottom-up effect could also be responsible for observed patterns. Areas with high plant diversity may attract and maintain higher deer densities, which in turn support successful establishment by wolf packs. Continued research directed at ruling out confounding factors and differentiating between top-down and bottom-up effects is needed.

Our results provide compelling correlative evidence of top-down trophic effects generated by the recovery of Wisconsin's wolf population. By addressing wolf impact at the scale of wolf territory extents, instead of presence/absence of wolves for entire regions, we were able to have both replication of 'treatments' ($n = 16$) and comparable control sites ($n = 16$). We also identified species richness of forbs and shrubs in northern white cedar wetlands as ideal community-level responses for detecting trophic cascades involving wolves and white-tailed deer in the boreal forests of the Great Lakes region.

The spatially hierarchical sampling design we developed to analyse wildlife census data in conjunction with vegetation data provides a template for addressing other broad-scale ecological impacts. Regardless of the process in question, multi-scale approaches allow us to determine the scale at which a pattern becomes detectable. The ability to detect such signals above the ambient noise of ecological variation is essential to understanding the relationship between pattern and process.

If the methods employed here were applied across other forest types, we could predict long-term, region-wide effects of reintroducing top predators to this and other terrestrial systems. Our results indicate that wolf recovery in other regions of North America (such as the northeastern United States) could be vital to maintaining the ecological integrity of northern white cedar wetlands (and potentially other temperate and boreal forest systems as well). Whether efforts should be focused on reintroducing wolves or on increasing the connectivity between existing wolf populations and unoccupied wolf habitat should be carefully considered.

Acknowledgements

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The Cost Of Killing Washington's Wedge Wolves

by **Cassandra Profita** (/contributor/cassandra-profita/) Ecotrope | Nov. 14, 2012 6:50 a.m. | Updated: Feb. 19, 2013 1:28 p.m.

The Spokesman Review reports

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EarthFix is a public media partnership of Oregon Public Broadcasting, Idaho Public Television, KCTS9 Seattle, KUOW Puget Sound Public Radio, Northwest Public Radio and Television, Jefferson Public Radio, KLCC and the Corporation for Public Broadcasting.

In this map of Washington's wolf populations, the Wedge Pack in the northeast corner of the state is outlined as having been removed.

(http://www.spokesman.com/stories/2012/nov/14/repeat-of-wolf-kill-unlikely/) that the state of Washington spent an estimated $76,500 to kill a wolf pack blamed for killing or injuring 16 calves on a ranch in northeast Washington.

The Washington Department of Fish and Wildlife spent four days and about $22,000 killing six wolves in the pack using a helicopter and a marksman, the paper reports. That was after the agency spent 39 days and $54,500 killing one wolf.

Time and money weren't the only costs, though. It also cost the agency some public support, according to spokeswoman Madonna Luers.

"Our director (Phil Anderson) has said that he never wants to do this again," Luers said. "... The social acceptance is just not there."

The Wedge wolves were the first to be lethally removed by WDWF (http://ecotrope.opb.org/2012/08/washingtons-first-lethal-removal-of-wolves/). The agency sent the cost estimates to the senator who chairs a legislative committee overseeing the agency. He's planning a hearing to review the decision to kill the pack.

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California Department of Fish and Wildlife
Draft Wolf Plan

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Introduction/Overview

In reviewing the Draft Wolf Plan for the State of California, I operated under the assumption that wolves would be delisted in much of the conterminous US within the next 5 years and possibly before a wolf population is established in California (p. 10, lines 23-29). This means that state protection for wolves in California under the California Endangered Species Act (CESA) may be the only form of protection these wolves will receive as their population becomes established. I have summarized my assessments by topic below, and also have made notes throughout the text of the Draft Wolf Plan using TrackChanges.

The Draft Wolf Plan creates the framework for applying an adaptive management strategy to wolf conservation. This is a very wise approach. The plan reviews and does a thorough job of addressing most of the factors that can negatively impact wolves and their prey. Detail on how adaptive management would address those factors is fully described in Phase 2. However, information about how adaptive management would be applied is almost completely lacking from Phase 3.

My specific concerns the plan as a whole are: 1) the need for improvement of data gathering and analysis tools (monitoring, modeling) to apply best science; 2) the low wolf population thresholds in Phases 1 and 2 do not allow for environmental stochasticity or for development of a stable wolf population; and 3) the lack of measurable population objectives in Phase 3. A fourth topic of concern not discussed in the Draft Wolf Plan pertains to coyote management that allows hunting by humans. Recent events in other states (Utah, Iowa, the northeastern US) clearly demonstrate the propensity for coyote hunters to mistake wolves for coyotes. This is leading to frequent illegal lethal take of recolonizing wolves. I strongly recommend that coyote hunting be eliminated in California, in order to enable wolf conservation to proceed. Because coyotes will have a small but significant impact on elk, I further recommend an adaptive management strategy to manage these impacts.

Background

The background and literature review for the Draft Wolf Plan covers wolf ecology and ungulate ecology in depth. It clearly describes threats to wolves (with the exception of coyote hunting) and all threats to ungulate prey species typically recognized by science. It describes food web impacts, including reversal of mesopredator release, that could result from wolf recolonization, and strategies to address such impacts. The Plan also provides a thorough

analysis of the many uncertainties with regard to what we know about the past (e.g., distribution and population of wolves), current tools (e.g., models for wolf suitable habitat), and how these uncertainties make it difficult to predict the impacts of wolves on game populations and the ultimate carrying capacity for wolves in California. The Plan makes a solid case that California is very different ecologically than any of the other states in which wolves have become established. This means that wolf recolonization and management of California's wolf population may proceed in a very different manner in this state than elsewhere. One of the key points is that wolf carrying capacity, based on prey biomass, may be far lower in California than in places like Washington or Montana or Minnesota. The background section highlights the need for a more rigorous modeling approach to create models that will provide key tools in wolf (and ungulate) conservation decision making. Development of models developed specifically for California that utilize best science will be an important research priority (P. 14, lines 9-12).

Diseases

The Draft Wolf Plan provides a comprehensive assessment of diseases that may threaten wolves. These factors are not incorporated in the strategies for wolf conservation (Table 1-A). Lessons learned from Yellowstone, where the wolf population has declined severely due to disease (Smith et al. 2014), strongly suggest acknowledging the stochastic effects of disease in establishing the wolf population levels that define each wolf conservation phase in California.

Ungulate

Wolf recolonization and recovery in California will undeniably have impacts on ungulates. As the Draft Wolf Plan indicates, the strengths of these impacts are impossible to fully predict. It is expected that upon recolonization wolves will prey primarily on elk. However, given the low overall elk population in California (~11,000 individuals), and the fact that some of the individual herds are isolated and small (<500 individuals), elk may not be the primary prey of wolves initially or ever in California (pp. 106-114). Contrast this with an elk population of 150,000 in Montana, where wolves have become well established.

Wolves are opportunists that primarily prey on ungulates. They take the most vulnerable animals first. They also select elk over deer where elk are abundant, because it may be more energy-efficient for them to take down an animal that is far greater in biomass than deer (p. 134, lines 32-36). Given that the California deer population is over one order of magnitude greater than the elk population, and that deer are the dominant wild ungulate by biomass in every place that wolves are likely to recolonize, I do not expect that wolf predation on elk will be as much of an issue as is predicted in the Plan.

Recolonizing and established wolves have both compensatory and additive mortality effects on ungulate populations. Wolves will have additive mortality effects on prey populations that are below carrying capacity, as is the case in California. However, even in prey populations

that are above carrying capacity, wolves can have additive mortality effects (p. 138, lines 34-37; Eisenberg et al. 2014). Therefore, any wolf conservation plan in California must address the linked matter of conservation of wolf prey species, both for predation by wolves and for utilization by humans (e.g., hunting).

Without seeing the forthcoming California updated mule deer and elk management plans, I am unable to comment further on predator-prey interactions involving wolves and California's dominant (by biomass) ungulates.

Livestock

The Draft Wolf Plan does a thorough job of reviewing the history of livestock depredation in areas where wolves have become established (Washington, Oregon, the NRM). Depredation has been quite low in these areas (<1.4% of cattle and <4.2% of sheep depredation is attributable to wolves) and has been positively correlated to wolf population size. While wolf depredation on livestock will likely be similarly low in California, any depredation will create strong concern on the part of livestock producers and will need to be addressed.

The Draft Wolf Plan provides a sound strategy that focuses on non-lethal deterrents to prevent and address depredation. As is pointed out in the Plan (p. 157, lines 16-26), a significant percentage of wolf packs (~28%) depredate. When properly utilized, nonlethal deterrents reduce the potential for wolf depredation. However, none will completely eliminate the potential for depredation. Wolf removal is not the answer either, because when entire packs are removed, 60% of those territories are recolonized by new packs that eventually depredate (p. 157, lines 19-22).

Addressing wolf depredation on livestock involves an adaptive management strategy that will emphasize education about and implementation of a variety of nonlethal deterrents, with financial support to livestock producers to apply such deterrents. The Draft Wolf Plan outlines such as strategy. The guidelines for lethal removal of wolves specified in Table 1-Q, Phase 2 of (4 confirmed depredation incidents by the same individual) are reasonable; however they should be continued in Phase 3. The vagueness of the proposed actions for Phase 3 ("to be determined . . . based on wolf population and legal status") does not support wolf conservation in the long run. Lethal removal of wolves, while not a solution, may be the best approach in situations where all else has been tried.

Research/Information Management Needs

Research should prioritize development of models for assessing wolf habitat suitability, wolf carrying capacity, and wolf impacts on ungulates. These models will need to be created using best science. Modeling tools developed in 2003-2006, which have been used to create models for the Draft Wolf Plan, do not constitute best science, because these models are dated. The designation of jaguar critical habitat by the US Fish and Wildlife Services, which has been problematic, provides an example of the difficulties that can arise when applying models, how

models can be biased to produce results that reflect certain agendas, and how ineffective modeling can open the door to litigation (Menke and Hayes 2003; Hatten et al. 2005; Robinson 2005; USFWS 2013).

The California Department of Fish and Wildlife (CDFW) should focus on applying best science to develop tools to conserve wolves and manage ungulates in the state. Colorado Parks and Wildlife has long had an exemplary wildlife research program. Their use of rigorous science has supported conservation strategies for carnivores and ungulates in that state that have proven defensible. California needs defensible modeling, monitoring, and management methods in place that will help achieve wolf conservation and management and stand up to litigation challenges. Development of such tools needs to be a funding priority, as litigation can create expenses far in excess of what it would take to develop these tools properly.

Conservation

CESA mandates the CDFW to conserve wolves under Fish and Game Code (FGC) Section 2061. The factors that threaten wolf conservation presented in the Draft Wolf Plan, strategies that will ensure wolf conservation, and coordination with other state and federal agencies are very clearly and thoroughly described.

Description of wolf habitat suitability and characteristics of said habitat are appropriate, with the exception of roads. Wolves have demonstrated their propensity to cross busy travel corridors, such as Interstate highways. The model developed by Thiel (1985) for wolves in the Midwest has not been broadly applicable to recolonizing wolves in other areas and may not apply to California. However, the map provided of potential suitable wolf habitat in California, based on factors such prey abundance, public land ownership, forest cover, human influences, and domestic sheep presence (p. 191), represents a good, albeit conservative starting point for a discussion about wolf conservation. While it is impossible for wolves to reoccupy their historic range, it is likely that they will attempt to recolonize as much of that range as is currently suitable habitat. My ability to comment more fully on how predator-prey interactions between wolves and their primary ungulate prey (by biomass) in California (deer and elk) will influence wolf recolonization and habitat suitability is hampered by the fact that I have not yet seen the forthcoming updated mule deer and elk management plans. Finally, I agree that the greater density of humans in California is likely to impact California's potential wolf population size differently than in other regions where wolves have been assessed (p. 192, lines 36-39).

Trophic cascade effects driven by wolves (a keystone predator) in California will be insignificant unless a high wolf population develops. Scientists have found that without the strong bottom-up effect of fire in an area with a high wolf population, wolves alone were unable to drive a trophic cascade in an aspen-elk system (Eisenberg 2012; Eisenberg et al. 2013; Mech 2012). Given that wolves in California may never reach a high density, as a high density of wolves may not have been historically present, and given that the dominant habitat type for ungulates is oak, trophic cascades in California, if present, will be difficult to document. Similarly, while an ecologically sustainable wolf population will be relatively straightforward to

define, an ecologically effective one (e.g., one capable of driving a trophic cascade) will not be easily definable (Soulé et al. 2003). Thus, conserving this keystone predator as mandated by FGC section 1801, to perpetuate their intrinsic and ecological values (p. 7 lines 43-45), may be difficult to specify empirically.

 Nevertheless, as a keystone predator wolves are an essential component of a food web and help create greater biodiversity and ecological resiliency to climate change. Therefore, the precautionary principle indicates acknowledging the wolf's role as a keystone predator in California, and setting up monitoring strategies to measure any ecological effects of its presence across trophic levels. The Plan does a very good job of describing potential trophic relationships.

 The Plan notes that wolf mortality rates are context dependent, as is the case with any other species. The Plan also reviews the complex effects of wolf mortality on wolf pack status (Borg et al. 2014). While it is unclear what effects federal wolf delisting will have on wolves in California, it is likely that these effects will be negative, creating wolf population sinks outside of California in areas that have functioned as source populations. Therefore, delisting wolves outside of California will create instability of wolf populations in California.

Strategy Overview

 The California wolf conservation strategy is summarized in Table 1. Below are my comments on this table. If an element is not mentioned below, that means I have no concerns or comments about it.

Element A: Planning early for next steps in wolf recovery is wise. I suggest continuing this approach, but resetting the wolf number/temporal criteria to reflect changes made to Element B , as specified below.

Element B: Phase 1 should be 5 breeding pairs for 3 consecutive years. Phase 2 should be 9 breeding pairs for 3 consecutive years. Phase 3 should specify a minimum wolf population to maintain in the state. Population levels and time in years to move to the next phase are insufficient, as currently specified in the Draft Plan, to allow for environmental stochasticity, wolf poaching, and potential need for lethal removal of wolves due to depredation.

Element L: Relocation of wolves as specified in Phase 2.3, subsequent to a reduction of allocated big game tags is not based on science, it is based on natural resources management economics. It is inappropriate to apply such an economic approach to a wolf population that is in the early stages of becoming established. It risks scapegoating wolves further, and this could have negative impacts on human perception of wolves.

Element O: Given the negligible safety threat that wolves signify for humans, I suggest striking this element.

Element P: The allowed lethal control threshold specified in Phase 2 of total human-caused mortality not in excess of 10% is too high. Sustainable wolf take ranges widely (from 12% - 49%), as reported by various authors (Gude et al. 2001; Adams 2008; Creel and Rotella 2010). It is impossible to predict what sustainable wolf take may be in California. The precautionary principle suggests setting the threshold in Phase 2 for allowed lethal take based on human-caused mortality more conservatively—such as at 5%.

Element Q: As described for Phase 2, the approach/thresholds for lethal control of wolves CDFW proposes are sound. However, Phase 3 needs to be defined, otherwise this opens the door for lethal take without sideboards.

Element R: Lethal control of wolves to promote elk and other prey species population growth (Phases 2 and 3) is unacceptable. Other strategies need to be implemented, such as ungulate or wolf translocation. This opens the door for lethal take without sideboards and scapegoats the wolf in a system in which predator-prey relationships will be highly complex ecologically (Vucetich et al. 2004; Hebblewhite and Smith 2010).

Conclusion

  The Draft Wolf Plan states, "The best available scientific information is not, at this point, sufficient to predict with a high degree of confidence which habitat wolves will occupy in California, or how many wolves that habitat will support, over the long-term" (p. 7, lines 21-23). I agree with this assessment. Given the incomplete understanding of how wolf conservation may develop in California, the precautionary principle suggest a conservative approach to matters such as wolf take (e.g, avoiding take of wolves, setting robust wolf population thresholds between phases) and stopping and re-assessing the situation using best science and robust stakeholder feedback, as typified by an adaptive management strategy.

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Endangered Species Handbook

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Legislation

The Endangered Species Act

Legislation mandating a list of rare and endangered species was first enacted by Congress in 1966. The Endangered Species Act (ESA) was amended in 1969 when foreign species were added to the list. In 1973, a comprehensive model Act replaced the latter act, providing the most extensive safeguards of any legislation in the world to protect declining species.

The ESA prohibits harassing, harming, pursuing, hunting, shooting, wounding, killing, trapping, capturing and collecting listed species, unless specifically permitted, or attempting to engage in such activities within the United States or its territorial seas. Taking on the high seas is also prohibited, as are possessing, selling, delivering, carrying, transporting or shipping any species unlawfully taken within the United States, its territorial seas or on the high seas. It is also unlawful to deliver, receive, carry, transport or ship in interstate or foreign commerce in the course of commercial activity listed species, or to sell or offer listed species for sale in interstate or foreign commerce. The prohibitions apply to listed species, live and dead, their parts, and products made from their parts.

 Species are listed in two categories: Endangered and Threatened. Endangered is defined as any species which is in danger of extinction throughout all--or a significant portion--of its range. Prohibitions on activities that affect species may be less strict for animals listed in the Threatened category, but these are regulated by the U.S. Fish and Wildlife Service (USFWS) on a species-by-species basis. The ESA also allows listing species similar in appearance to those that are Endangered or Threatened, when doing so would provide additional protection for the listed species.

Stiff penalties may be imposed for violations of the Endangered Species Act. Criminal activities may be punished with fines up to $50,000 and/or one year imprisonment for crimes involving endangered species, and $25,000 and/or six months imprisonment for crimes involving threatened species. Misdemeanors or civil penalties are punishable by fines up to $25,000 for crimes involving endangered species and $12,000 for crimes involving threatened species. A maximum of $1,000 can be assessed for unintentional violations. Rewards of up to $2,500 are paid for information leading to convictions.

The ESA has been extremely effective in saving wildlife and plant species in danger of extinction. Contrary to some who have claimed that the Endangered Species Act has interfered with government and private projects, there have been very few conflicts, and on the whole, these have been resolved to the satisfaction of both parties. The Northern Spotted Owl controversy was resolved by government retraining of loggers and an increase in high technology jobs that more than compensated for jobs lost. Other arrangements have been made with paper companies to protect the endangered Red-cockaded
Woodpecker and, in southern California, with developers to protect the Coachella Fringe-toed Lizard. As of August 2001, the USFWS had issued 500 permits for 360 "Habitat Conservation Plans." Many involve financial benefit to landowners. If landowners donate land where endangered species are found to a nonprofit organization or the federal government, the transaction is tax-deductible. In spite of economic interests who wish to weaken the ESA, the majority of Americans support the law and protection of endangered species (see Vanishing Species chapter).

As of July 31, 2001, the Act listed 1,802 species of animals and plants as Endangered or Threatened. Of these, a total of 507 animal and plant species were native to the United States. The Act has been instrumental in saving native species, including endangered species such as the California condor, the Black-footed Ferret and the Bald Eagle, and Threatened species such as the Northern Spotted Owl. Programs of habitat protection, captive breeding, and other means of aiding in the recovery of listed species have prevented the extinction of hundreds of plant and animal species, many little known to the American public. The Hawaiian Islands have the largest number of listed species as a result of the destruction of native ecosystems and species by introduced animals and diseases, and clearing of forests for agriculture and ranching.

The Endangered Species Act has also been important in regulating the importation and exportation of exotic species listed. Foreign species listed totaled 555 animal and three plant species on July 31, 2001. These species include Leopards; Tigers; all species of rhinoceros; the great whales; the Andean Condor; Harpy Eagle; Imperial Parrot, among many other parrot species; Resplendent Quetzal; all sea turtles; numerous endangered tortoises; endangered caiman and crocodiles; iguanas; and fish, as well as seven endangered foreign invertebrates. Mammals comprise the majority of foreign species--251 Endangered and 17 Threatened (compared with only 63 Endangered and 9 Threatened U.S. species). These listings have prevented importation of many endangered species and their products. Prior to importation of any listed species, or part thereof, a permit must be obtained from the USFWS. Permits are not granted for commercial exploitation of non-captive-bred endangered species. Commercial importation of Leopard, Tiger or Ocelot skins, for example, is not allowed under the ESA. In spite of the severe penalties that can be exacted under the law, including jail sentences, illegal imports continue, and thousands are confiscated by USFWS agents each year. Many are tourist purchases, such as stuffed sea turtles, fur coats, and taxidermy specimens. Others are commercial items, such as reptile skins and, recently, products for the Asian medicine trade--Tiger bones and powdered rhinoceros horn.

For zoos, importation of live wild-caught specimens of endangered species requires ESA permits. If the species is listed on the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which lists many of the same species on Appendix I (the category for species threatened with extinction), both import permits from the U.S. CITES authorities and export permits from foreign CITES authorities are required. The USFWS has required rigid proof that importation of listed species would not result in declines in wild populations of that species, except for emergency situations where wild populations are under extreme threats such as uncontrolled poaching or habitat destruction. The combined burden of proof needed for ESA and CITES has been essential in preventing needless removal from the wild of endangered species. With the proliferation of wild animal parks, small zoos, and animals used in entertainment, the pressure to weaken the ESA to allow importation of endangered species has increased. One wildlife dealer wrote an editorial in a trade journal, *Pet Business* (March 1995), that encouraged weakening the ESA: "There is no logical reason for our government to pay hundreds of thousands of dollars, if not millions, a year to control non-indigenous endangered species." Without strict regulations under the ESA, however, the Act will lose its value in preventing commercialism of endangered species around the world.

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Trophic Downgrading of Planet Earth

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Until recently, large apex consumers were ubiquitous across the globe and had been for millions of years. The loss of these animals may be humankind's most pervasive influence on nature. Although such losses are widely viewed as an ethical and aesthetic problem, recent research reveals extensive cascading effects of their disappearance in marine, terrestrial, and freshwater ecosystems worldwide. This empirical work supports long-standing theory about the role of top-down forcing in ecosystems but also highlights the unanticipated impacts of trophic cascades on processes as diverse as the dynamics of disease, wildfire, carbon sequestration, invasive species, and biogeochemical cycles. These findings emphasize the urgent need for interdisciplinary research to forecast the effects of trophic downgrading on process, function, and resilience in global ecosystems.

The history of life on Earth is punctuated by several mass extinction events (2), during which global biological diversity was sharply reduced. These events were followed by novel changes in the evolution of surviving species and the structure and function of their ecosystems. Our planet is presently in the early to middle stages of a sixth mass extinction (3), which, like those before it, will separate evolutionary winners from losers. However, this event differs from those that preceded it in two fundamental ways: (i) Modern extinctions are largely being caused by a single species, *Homo sapiens*, and (ii) from its onset in the late Pleistocene, the sixth mass extinction has been characterized by the loss of larger-bodied animals in general and of apex consumers in particular (4, 5).

The loss of apex consumers is arguably humankind's most pervasive influence on the natural world. This is true in part because it has occurred globally and in part because extinctions are by their very nature perpetual, whereas most other environmental impacts are potentially reversible on decadal to millenial time scales. Recent research suggests that the disappearance of these animals reverberates further than previously anticipated (6–8), with far-reaching effects on processes as diverse as the dynamics of disease; fire; carbon sequestration; invasive species; and biogeochemical exchanges among Earth's soil, water, and atmosphere.

Here, we review contemporary findings on the consequences of removing large apex consumers from nature—a process we refer to as trophic downgrading. Specifically, we highlight the ecological theory that predicts trophic downgrading, consider why these effects have been difficult to observe, and summarize the key empirical evidence for trophic downgrading, much of which has appeared in the literature since the beginning of the 21st century. In

> "What escapes the eye ... is a much more insidious kind of extinction: the extinction of ecological interactions"
>
> Daniel H. Janzen (1)

so doing, we demonstrate the influence of predation and herbivory across global ecosystems and bring to light the far-reaching impacts of trophic downgrading on the structure and dynamics of these systems. These findings suggest that trophic downgrading acts additively and synergistically with other anthropogenic impacts on nature, such as climate and land use change, habitat loss, and pollution.

Foundations in Theory

Ecological theory has long predicted that major shifts in ecosystems can follow changes in the abundance and distribution of apex consumers (9, 10). Three key elements of that theory provide the foundation for interpreting recurrent patterns suggestive of trophic downgrading in more recent empirical work across ecosystems. First is the idea that an ecosystem may be shaped by apex consumers, which dates back more than a century but was popularized in the 1960s (9). This concept was later formalized as the dynamic notion of "trophic cascades," broadly defined as the propagation of impacts by consumers on their prey downward through food webs (11). Theoretical work on factors that control ecosystem state resulted in a second key advance, the recognition of "alternative stable states." The topology of ecosystem dynamics is now understood to be nonlinear and convoluted, resulting in distinct basins of attraction.

Alternative stable states occur when perturbations of sufficient magnitude and direction push ecosystems from one basin of attraction to another (12). Tipping points (also known as thresholds or breakpoints), around which abrupt changes in ecosystem structure and function (a.k.a. phase shifts) occur, often characterize transitions between alternative stable states. Ecosystem phase shifts can also display hysteresis, a phenomenon in which the locations of tipping points between states differ with the directionality of change (13). A third key concept, connectivity, holds that ecosystems are built around interaction webs within which every species potentially can influence many other species. Such interactions, which include both biological processes (e.g., predation, competition, and mutualism) and physicochemical processes (e.g., the nourishing or limiting influences of water, temperature, and nutrients), link species together at an array of spatial scales (from millimeters to thousands of kilometers) in a highly complex network.

Taken together, these relatively simple concepts set the stage for the idea of trophic downgrading.

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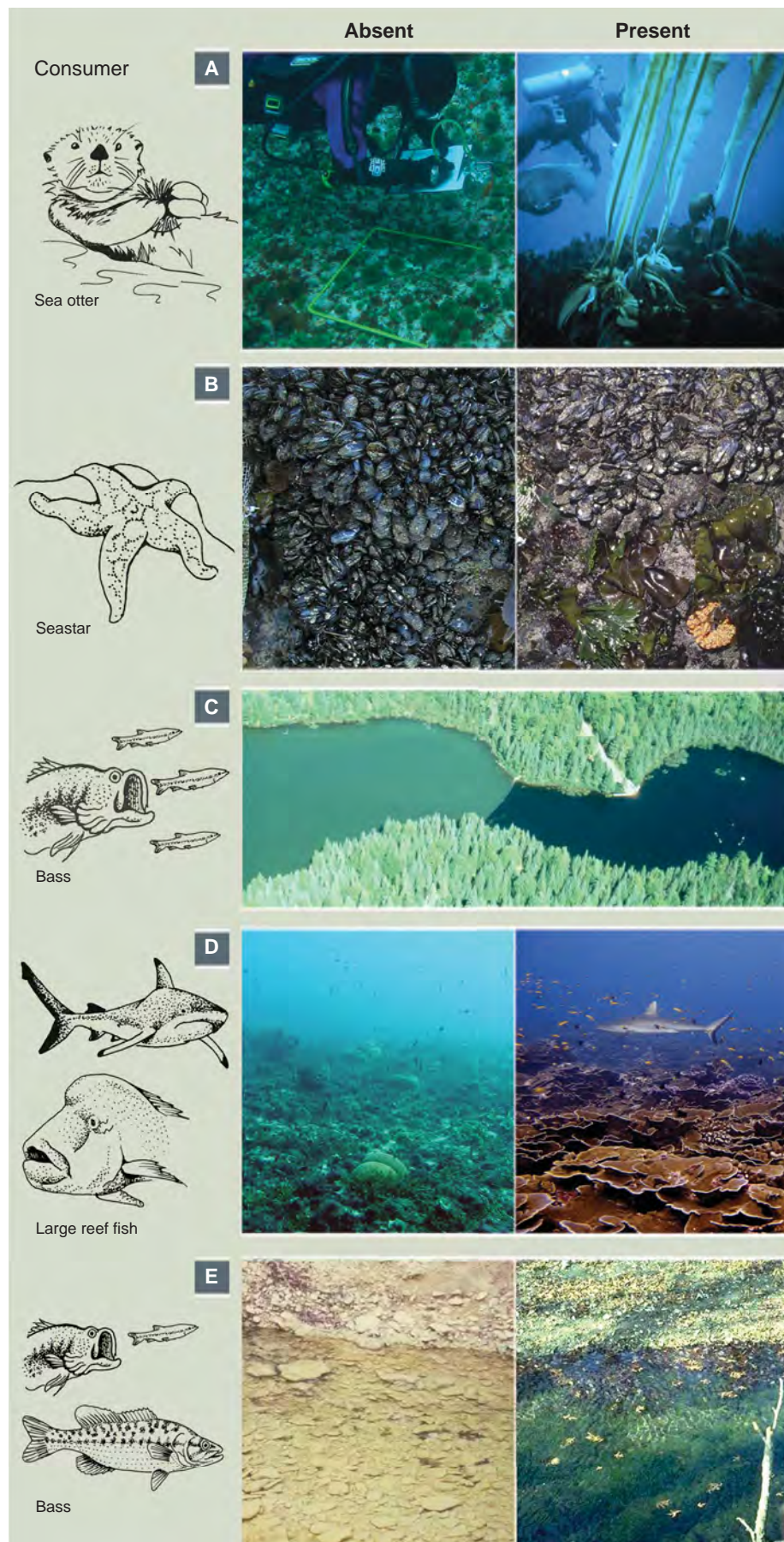
The loss of apex consumers reduces food chain length, thus altering the intensity of herbivory and the abundance and composition of plants in largely predictable ways (*10*). The transitions in ecosystems that characterize such changes are often abrupt, are sometimes difficult to reverse, and commonly lead to radically different patterns and pathways of energy and material flux and sequestration.

The Cryptic Nature of Trophic Downgrading

The omnipresence of top-down control in ecosystems is not widely appreciated because several of its key components are difficult to observe. The main reason for this is that species interactions, which are invisible under static or equilibrial conditions, must be perturbed if one is to witness and describe them. Even with such perturbations, responses to the loss or addition of a species may require years or decades to become evident because of the long generation times of some species. Adding to these difficulties is the fact that populations of large apex consumers have long been reduced or extirpated from much of the world. The irony of this latter situation is that we often cannot unequivocally see the effects of large apex consumers until after they have been lost from an ecosystem, at which point the capacity to restore top-down control has also been lost. Another difficulty is that many of the processes associated with trophic downgrading occur on scales of tens to thousands of square kilometers, whereas most empirical studies of species interactions have been done on small or weakly motile species

Fig. 1. Landscape-level effects of trophic cascades from five selected freshwater and marine ecosystems. (**A**) Shallow seafloor community at Amchitka Island (Aleutian archipelago) before (1971; photo credit: P. K. Dayton) and after (2009) the collapse of sea otter populations. Sea otters enhance kelp abundance (right) by limiting herbivorous sea urchins (left) (*20*). (**B**) A plot in the rocky intertidal zone of central California before (September 2001, right) and after (August 2003, left) seastar (*Pisaster ochraceus*) exclusion. *Pisaster* increases species diversity by preventing competitive dominance of mussels. [Photo credits: D. Hart] (**C**) Long Lake (Michigan) with largemouth bass present (right) and experimentally removed (left). Bass indirectly reduce phytoplankton (thereby increasing water clarity) by limiting smaller zooplanktivorous fishes, thus causing zooplankton to increase and phytoplankton to decline (*26*). (**D**) Coral reef ecosystems of uninhabited Jarvis Island (right, unfished) and neighboring Kiritimati Island (left, with an active reef fishery). Fishing alters the patterns of predation and herbivory, leading to shifted benthic dynamics, with the competitive advantage of reef-building corals and coralline algae diminished in concert with removal of large fish (*66*). (**E**) Pools in Brier Creek, a prairie margin stream in south-central Oklahoma with (right) and lacking (left) largemouth and spotted bass. The predatory bass extirpate herbivorous minnows, promoting the growth of benthic algae (*67*).

with short generation times that could be manipulated at small spatial scales. Although some influences of apex consumers (e.g., trophic cascades) seen in experiments scale up to systems with larger or more mobile species (*14*), others are harder to discern at small spatial and temporal scales (e.g., many of the indirect effects of trophic cascades on ecosystem processes described below). As a result, we have an incomplete and distorted picture of the influences of apex consumers across much of the natural world.

The Widespread Occurrence of Trophic Cascades

Despite these challenges, trophic cascades have now been documented in all of the world's major biomes—from the poles to the tropics and in terrestrial, freshwater, and marine systems (table S1). Top-down forcing and trophic cascades often have striking effects on the abundance and species composition of autotrophs, leading to regime shifts and alternative states of ecosystems (*15*). When the impacts of apex consumers are reduced or removed or when systems are examined over sufficiently large scales of space and time, their influences are often obvious (Figs. 1 and 2). Although purposeful manipulations have produced the most statistically robust evidence, "natural experiments" (i.e., perturbations caused by population declines, extinctions, reintroductions, invasions, and various forms of natural resource management) corroborate the essential role of top-down interactions in structuring ecosystems involving species such as killer whales (*Orcinus orca*) (*16*), lions (*Panthera leo*) (*17*), wolves (*Canis lupus*) and cougars (*Puma concolor*) (*18*), the great sharks (*19*), sea otters (*Enhydra lutris*) (*20*), diverse mesopredators (*21*), and megaherbivores (*22*). Although the extent and quality of evidence differs among species and systems, top-down effects over spatial scales that are amenable to experimentation have proven robust to alternative explanations (*23*).

The impacts of trophic cascades on communities are far-reaching, yet the strength of these impacts will likely differ among species and ecosystems. For example, empirical research in Serengeti, Tanzania, showed that the presence or absence of apex predators had little short-term effect on resident megaherbivores [elephant (*Loxodonta africana*), hippopotamus (*Hippopotamus amphibius*), and rhinoceros (*Diceros bicornis*)] because these herbivores were virtually invulnerable to predation (*24*). Conversely, predation accounted for nearly all mortality in smaller herbivores [oribi (*Ourebia ourebi*), Thompson's gazelle (*Eudorcas thomsonii*), and impala (*Aepyceros melampus*)], and these species showed dramatic increases in abundance and distribution after the local extinction of predators. Thus, top-down forcing in this system is more apparent in some species than others, at least when it is studied on relatively short time scales, although the aggregate ecological impact of apex consumers here, as elsewhere, remains great (*24*).

Other than the inclusion of top-down forcing, there is no rule of thumb on the interplay between apex consumers and autotrophs in intact ecosystems. This is largely a consequence of natural variation in food chain length (*10*). In some cases, the influence of apex consumers is to suppress herbivory and to increase the abundance and production of autotrophs. The sea otter/kelp forest system in the North Pacific Ocean (*20*) (Fig. 1A) and the wolf/ungulate/forest system in temperate and boreal North America (*25*) (Fig. 2C) function in this manner. Apex consumers in other systems reduce the abundance and production of autotrophs. The largemouth bass/planktivore/zooplankton/phytoplankton system in U.S. Midwestern lakes (*26*) (Fig. 1C) functions in such a manner.

Effects on Ecosystem Processes

Apart from small oceanic islands, all regions of our planet supported a megafauna before the
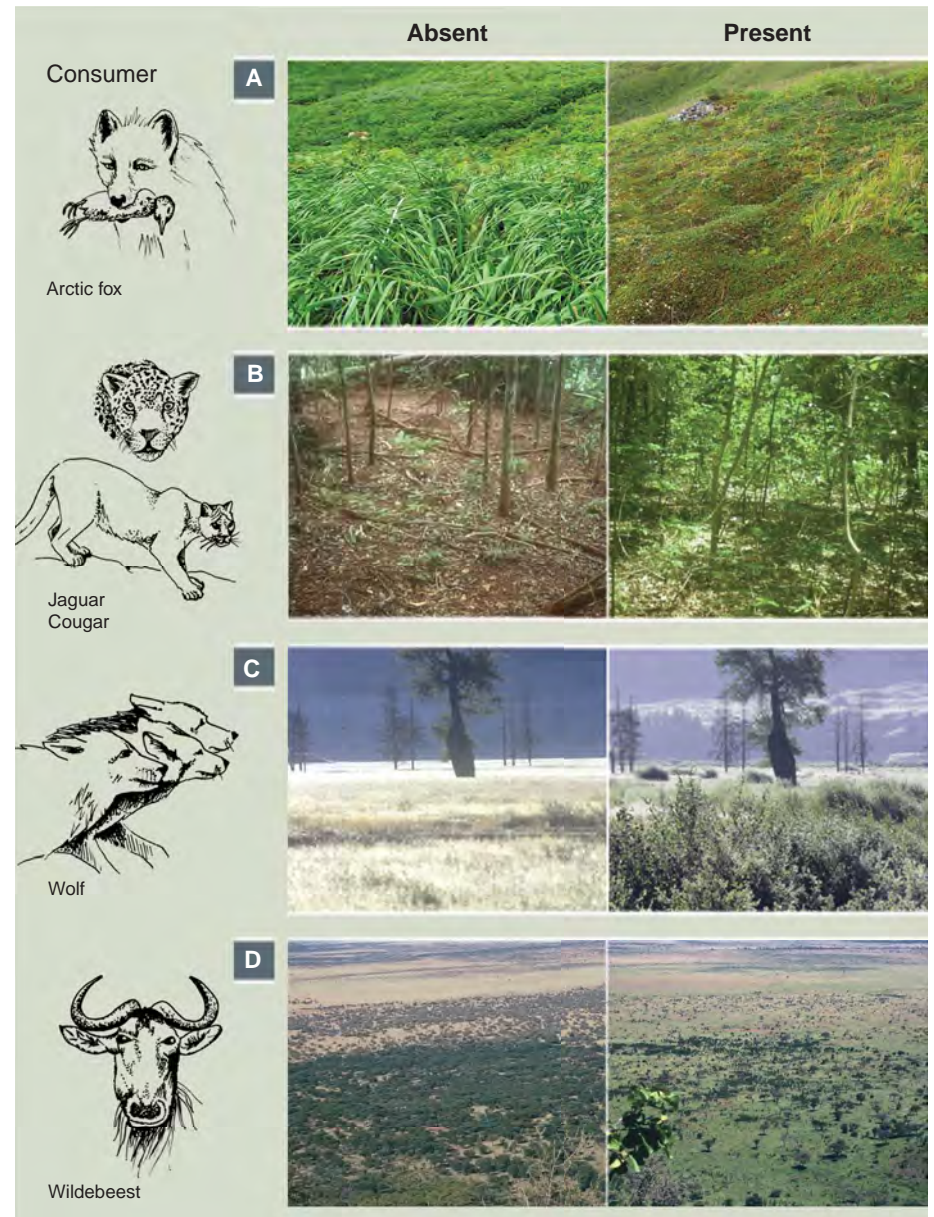
Fig. 2. Landscape-level effects of trophic cascades from four terrestrial ecosystems. (**A**) Upland habitat of islands with (right) and without (left) Arctic foxes in the Aleutian archipelago. Foxes drive terrestrial ecosystems from grasslands to tundra by limiting seabirds and thereby reducing nutrient inputs from sea to land (*47*). (**B**) Venezuelan forests on small islands of Lago Guri (left: jaguar, cougar, and harpy eagles absent) and mainland forest (right, predators present). A diverse herbivore guild erupted with the loss of predators from the island, thereby reducing plant recruitment and survival (*68*). (**C**) Riparian habitat near the confluence of Soda Butte Creek with the Lamar River (Yellowstone National Park) illustrating the stature of willow plants during suppression (left, 1997) from long-term elk browsing and their release from elk browsing (right, 2001) after wolf reintroductions of 1995 and 1996 (*25*). (**D**) Decline of woody vegetation in Serengeti after eradication of rinderpest (by early 1960s) and the recovery of native ungulates (by middle 1980s). Left, 1986; right, 2003 (*69*).

rise of *Homo sapiens* (*4*, *27*). The apex consumers influence their associated ecosystems through top-down forcing and trophic cascades, which in turn often lead to myriad effects on other species and ecosystem processes (Figs. 3 and 4). Here, we describe some of the known or suspected indirect effects of losing these apex consumers.

Herbivory and wildfire. Wildfires burn up to 500 million ha of the global landscape annually, consuming an estimated 8700 Tg of dry plant biomass, releasing roughly 4000 Tg of carbon to the atmosphere, and costing billions of dollars in fire suppression and property loss (*28*). The frequency and extent of wildfire have been largely attributed to a warming and drying climate and fuel accumulation from protective wildland management practices. However, the global distribution and biomass of vegetation are poorly predicted by temperature and rainfall (*29*), and recent analyses suggest that interdependencies among predation (including disease), herbivory, plant communities, and fire may better explain the dynamics of vegetation. Such interdependencies are well illustrated in East Africa, where the introduction of rinderpest in the late 1800s decimated many native ungulate populations, including wildebeest (*Connochaetes taurinus*) and buffalo (*Syncerus caffer*). Reductions of these large herbivores caused an increase in plant biomass, which fueled wildfires during the dry season. Rinderpest was eliminated from East Africa in the 1960s through an extensive vaccination and control program. Because of this, wildebeest and buffalo populations had recovered to what was thought to be historically high levels by the early 1980s. The resulting increase in herbivory drove these systems from shrublands to grasslands, thus decreasing the fuel loads and reducing the frequency and intensity of wildfires (*30*) (Fig. 4). Other examples of the interplay between megafauna and wildfire are the increase in fire frequency after the late Pleistocene/early Holocene decline of megaherbivores in Australia (*31*) and the northeastern United States (*32*).

Disease. The apparent rise of infectious diseases across much of the globe is commonly attributed to climate change, eutrophication, and habitat deterioration. Although these factors are undoubtedly important, links also exist between disease and predation (*33*). For example, the reduction of lions and leopards from parts of sub-Saharan Africa has led to population outbreaks and changes in behavior of olive baboons (*Papio anubis*). The baboons, in turn, have been drawn into increasing contact with people because of their attraction to crops and other human food resources. The increased baboon densities and their expanded interface with human populations have led to higher rates of intestinal parasites in baboons and the humans who live in close proximity to them (*17*). A similar result, involving different species and processes, occurred in India, where the decline of vultures also led to increased health risks from rabies and anthrax (*34*). Further examples of the interplay between predation and disease exist for
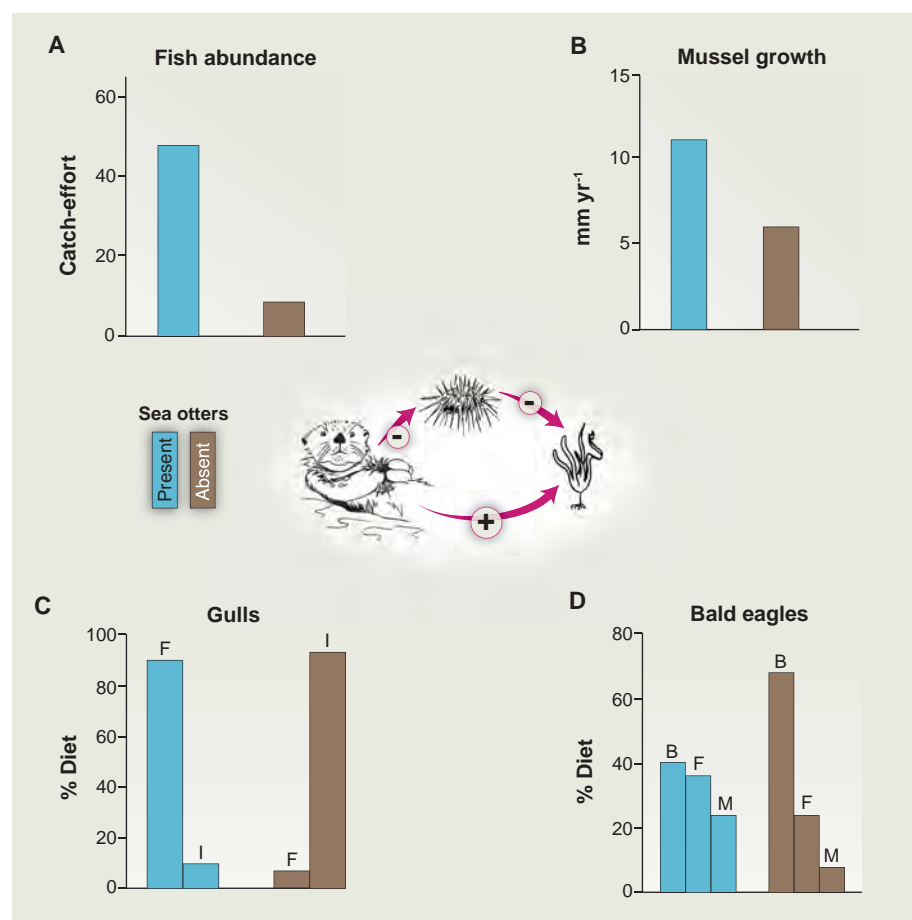
Fig. 3. Trophic cascade from sea otters to sea urchins to kelp (center) has myriad effects on other species and ecological processes. The increase in kelp enhances the abundance of kelp forest fish (**A**) (*70*). Enhanced kelp production increases the amount of particulate organic carbon in coastal ocean waters, thus increasing the growth rate of filter-feeding mussels (**B**) (*71*). The presence or absence of sea otters influences the diet of other consumers in the coastal ecosystems (**C** and **D**). In systems with abundant sea otters, Glaucous winged-gulls (*Larus glaucescens*) consume mostly fish (F), whereas in systems lacking sea otters, gulls consume mostly macroinvertebrates (I) (**C**) (*72*). When sea otters were abundant in the Aleutian archipelago, bald eagles (*Haliaeetus leucocephalus*) fed on fish (F), mammals (M), and birds (B) in roughly equal amounts. The loss of sea otters from this system led to a stronger reliance by the eagles on seabirds (**D**) (*73*). Blue bars from system with sea otters; brown bars from system without sea otters.

aquatic systems. The establishment of no-take marine reserves in the Channel Islands of southern California led to increases in the size and abundance of spiny lobsters (*Panulirus interruptus*) and declines in population densities of sea urchins, which are preyed on by the lobsters. The reduced urchin densities thwarted the spread of disease among individual sea urchins, which led to a lowered frequency of epidemics of sea urchin wasting disease within the reserves (*35*) (Fig. 4). In freshwater systems, the localized rise and fall of human malaria is associated with the impacts of predatory fishes on planktivores, which are in turn important consumers of mosquito larvae (*36*).

Physical and chemical influences. The influences of industrialization and agriculture on Earth's physical environments and geochemical processes are widely known. However, the contributing effects of changes in the distribution and abundance of apex consumers to the physical and chemical nature of our biosphere—the atmosphere,

soils, and water—are understudied and largely unappreciated. Even so, important connections between these entities have become apparent in the few instances where people have looked.

The atmosphere. Linkages between apex consumers and the atmosphere are known or suspected in freshwater, marine, and terrestrial ecosystems. Trophic cascades associated with the presence or absence of apex predatory fishes in lakes can affect phytoplankton density, in turn affecting the rate of primary production, the uptake rate of CO_2, and the direction of carbon flux between lakes and the atmosphere. Where apex predatory fishes are present in sufficient numbers, they reduce the abundance of smaller planktivorous minnows, thus releasing zooplankton from limitation by planktivores and increasing consumption rates of phytoplankton by zooplankton (Fig. 1B). This trophic cascade causes lakes to switch from net sinks for atmospheric CO_2 when predatory fishes are absent to net sources of atmospheric CO_2 when

these fishes are present (*37*) (Fig. 4). Similar processes occur in the oceans and on land. Industrial whaling during the 20th century transferred some 105 million tons of carbon from great whales to the atmosphere (*38*), and even today whale feces return various limiting nutrients from the aphotic to photic zones, thereby directly enhancing primary productivity (*39, 40*) and its influence on carbon flux and sequestration. From land, the demise of Pleistocene megaherbivores may have contributed to or even largely accounted for the reduced atmospheric methane concentration and the resulting abrupt 9°C temperature decline that defines the Younger-Dryas period (*41*).

Soils. Leaf-eating herbivores profoundly influence soils and their associated biota through altered plant allocation patterns of carbon and nutrients to the roots and rhizosphere, changing the quantity and quality of litter that plants return to the soil. Ungulate herbivores further influence soils through trampling, compaction, and the return of dung and urine. The collective influence of these processes is often an effect on species composition of the vegetation and altered successional pathways (*42, 43*). Predators of these herbivores and the trophic cascades they set in motion reverse these belowground effects (*44*). For example, the reintroduction of wolves to Yellowstone National Park has reduced the positive indirect effects of ungulates on soil nitrogen mineralization and potentially the nitrogen supply for plant growth (*45*). In contrast, introduced rats (*46*) and arctic foxes (Fig. 4) (*47*) have reduced soil fertility and plant nutrition on high-latitude islands by disrupting seabirds and their sea-to-land nutrient subsidies, with striking effects on plant community composition.

Water. Large consumers influence the composition and quality of both fresh and salt water through a variety of mechanisms. For example, the collapse of large demersal fish led to a 20% reduction in silica supply to pelagic diatoms in the Baltic Sea (*48*). In rivers, mass spawning by salmon suspends sediments, thus increasing downstream sediment transport (*49*) (Fig. 4). This flushing of stream bed sediments by the spawning fish and the increased circulation of fresh water through the gravel interstices of the stream bed have positive feedbacks on salmon populations by increasing oxygen for incubating eggs and fry and decreasing the frequency with which bed-mobilizing floods kill salmon in these early life stages (*50*). Similarly, in terrestrial systems wolves protect riparian trees and shrubs from over-browsing by large ungulates, in turn shading and cooling the adjacent streams, reducing stream bank erosion, and providing cover for fish and other aquatic life (*51, 52*).

Invasive species. A common feature of many successful invasive species is that they have left behind their natural predators and freed themselves from top-down control (*53*). Likewise, the loss of native predators leaves ecosystems more vulnerable to invasion by nonnative species (*54*). There are many examples of hypersuccessful invasions due to the absence or loss of top-down

control in aquatic and terrestrial systems. The experimental exclusion of native birds from small areas in Hawaii resulted in an up to 80-fold increase in nonnative spider density (*55*) (Fig. 4). Other examples include the spread of the invasive brown tree snake (*Boiga irregularis*) on the otherwise vertebrate predator–free island of Guam (*56*), the facilitating influence of reduced fish predation on the invasion of zebra mussels (*Dreissena polymorpha*) in the Mississippi River (*57*), and reduced abundance and spread of the introduced European green crab (*Carcinus maenas*) by predation from native blue crabs (*Callinectes sapidus*) in eastern North America (*58*).

Biodiversity. Earth's biodiversity (defined here as both species diversity and the associated functional diversity) is increasingly confined to formal protected areas. Although the establishment of protected areas mitigates certain threats to biodiversity—habitat loss and fragmentation, over-exploitation, and the spread of invasive species—when large apex consumers are missing, protected areas often fail to function as intended. The link between apex consumers and species diversity can occur via a number of interaction pathways, for example, by blocking competitive exclusion [predatory seastars in the rocky intertidal (*59*)], mesopredator release [coyotes (*Canis latrans*) maintaining small vertebrate species in chaparral habitats (Fig. 4) (*60*)], and indirect habitat effects [e.g., the loss of small vertebrates from over-grazed and degraded riparian habitats after the
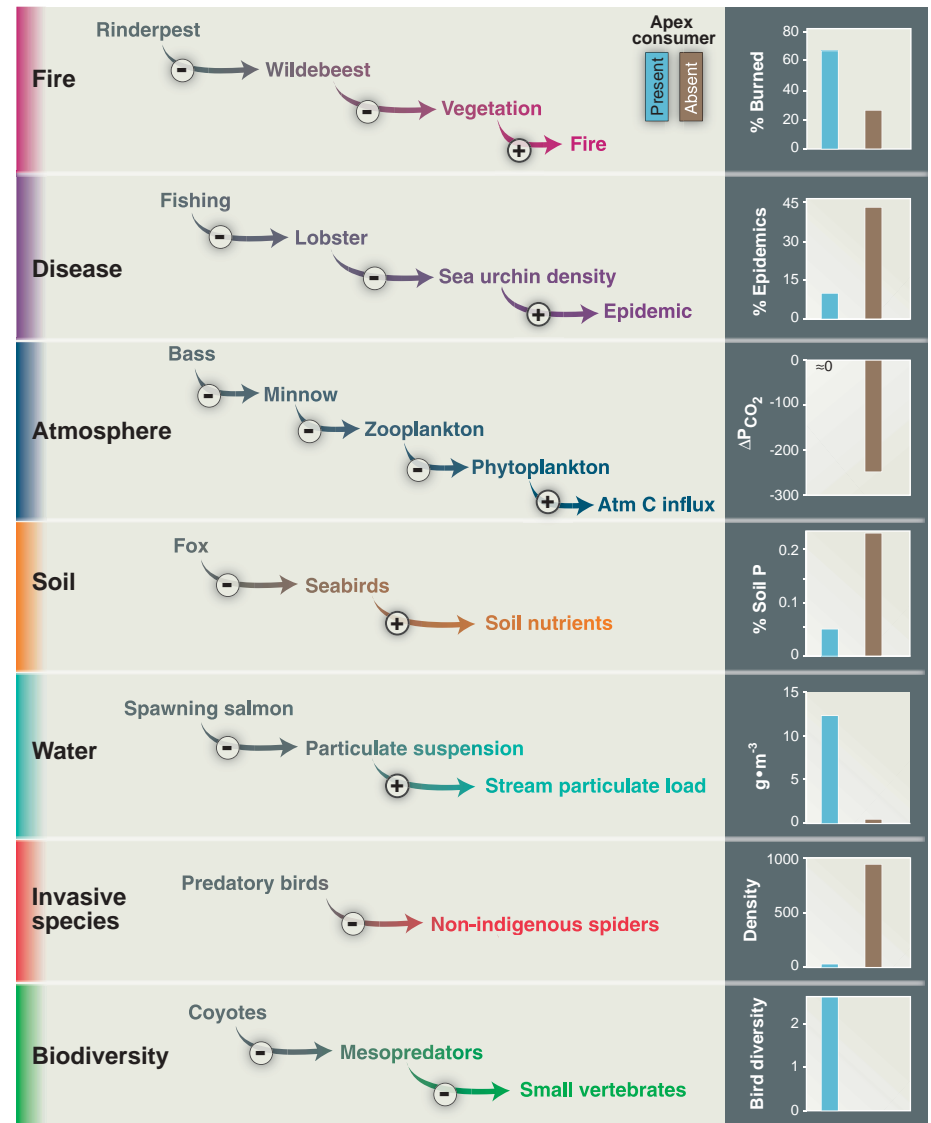
Fig. 4. Examples of the indirect effects of apex consumers and top-down forcing on diverse ecosystem processes, including wildfires (*30*); disease (*35*); composition of atmosphere (*37*), soil (*47*), and fresh water (*49*); invadability by exotic species (*55*); and species diversity (*60*). Interaction web linkages by which these processes are connected to apex consumers are shown in the center. Magnitude of effect is shown in graphs on right. Blue bars are data from systems containing the apex consumer; brown bars are data from systems lacking the apex consumer. Data replotted from original sources (cited above), except raw data on native bird diversity in chaparral habitats provided by K. Crooks.

loss of cougars (*61*) or wolves and grizzly bears (*Ursus arctos*) (*62*) from temperate and boreal forests of western North America].

Tree recruitment failure and the eventual transformation of forests to heaths and grasslands because of increased ungulate herbivory illustrates the influence of large apex consumers on functional diversity. This process is most clearly seen by contrasting areas where apex consumers have been absent for differing lengths of time. In North America, where wolves and other large carnivores were not extirpated until the early 20th century, the effects of their loss on plants is evident only as the recruitment failure of the younger trees. Because of the longevity of adult trees, the older individuals persist in what superficially appears to be a normally functioning forest ecosystem. These effects are best known from various U.S. National Parks, where the loss of large predators a few decades ago has left a characteristic signal of reduced tree growth rate (*63*) or recruitment failure (*64*) in the dominant tree species. A longer time horizon can be obtained from the Canadian island of Anticosti, where white-tailed deer (*Odocoileus virginianus*) have persisted in the absence of predators for more than a century, causing the successive elimination of saplings of less and less palatable trees and shrubs and increasing graminoid dominance in the understory (*65*). The Scottish island of Rùm, from which wolves have been absent for 250 to 500 years, provides a view of the likely final outcome of predator loss and elevated herbivory in many temperate forests. Rùm has transitioned over this same period from a forested environment to a treeless island.

These examples support the conclusion that disruptions of trophic cascades due to the decline of predation constitute a threat to biodiversity from within for which the best management solution is likely the restoration of effective predation regimes.

A Paradigm Shift in Ecology

The accumulation of theoretical and empirical evidence calls for an altered perspective on top-down forcing in ecosystem dynamics. Many practicing ecologists still view large animals in general, and apex consumers in particular, as ecological passengers riding atop the trophic pyramid but having little impact on the structure below. The influences of these animals, although acknowledged in particular cases, are generally regarded as anomalous, occurring in some systems but not in many others. This perception has generally led to the requirement of independent study and confirmation for each species and system before the null hypothesis that they serve no important ecological role can be rejected. We argue that the burden of proof be shifted to show, for any ecosystem, that consumers do (or did) not exert strong cascading effects.

Conclusions

Unanticipated changes in the distribution and abundance of key species have often been attributed in some unspecified manner to the "complexity of nature." We propose that many of the

ecological surprises that have confronted society over past centuries—pandemics, population collapses of species we value and eruptions of those we do not, major shifts in ecosystem states, and losses of diverse ecosystem services—were caused or facilitated by altered top-down forcing regimes associated with the loss of native apex consumers or the introduction of exotics. Our repeated failure to predict and moderate these events results not only from the complexity of nature but from fundamental misunderstandings of their root causes. Except for controlling predators to enhance fish, wild game, and livestock, resource managers commonly base their actions on the assumption that physical processes are the ultimate driver of ecological change. Bottom-up forces are ubiquitous and fundamental, and they are necessary to account for the responses of ecosystems to perturbations, but they are not sufficient. Top-down forcing must be included in conceptual overviews if there is to be any real hope of understanding and managing the workings of nature.

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COSTS AND CONSEQUENCES

The Real Price of Livestock Grazing on America's Public Lands

By Christine Glaser, Chuck Romaniello and Karyn Moskowitz   •   For the Center for Biological Diversity, January 2015

Executive Summary

Approximately 229 million acres of federal public lands in the western United States are used for livestock grazing for cattle and sheep. The Bureau of Land Management (BLM) and the United States Forest Service (USFS) are the two federal agencies with by far the largest grazing programs among federal agencies. These programs exist mostly on the grasslands, deserts, sagebrush steppe and national forests.

Each year in January, the federal government establishes the fee it charges livestock operators to use federal public lands for grazing privileges.

In advance of the release by the Bureau of Land Management of the 2015 federal grazing fee, we have prepared this report that focuses on the extent of the federal grazing program on BLM and USFS lands and associated appropriations and receipts from grazing fees, which are an indication of the cost to the taxpayer. This report is an update of an earlier 2002 study, *Assessing The Full Costs of the Federal Grazing Program*.

Key Findings

1. Receipts from grazing fees were $125 million less than federal appropriations in 2014. Total federal appropriations for the USFS and BLM grazing programs in fiscal year 2014 were $143.6 million, while grazing receipts were only $18.5 million.

Appropriations for the BLM and USFS grazing programs have exceeded grazing receipts by at least $120 million annually since 2002. Had the federal government charged the average private forage market rate for non-irrigated lands in the western states, grazing receipts would have been on average $261 million, greatly exceeding annual appropriations.

2. The gap between federal grazing fees and private land fees has widened considerably. The federal grazing fee in 2014 was set at the legal minimum of $1.35/AUM, or animal unit month, which is the amount of forage to feed a cow and calf for one month. The annual federal grazing fee has been set at the minimum required by law since 2007.

In 2013, the federal grazing fees of $1.35/AUM were just 6.72 percent of fees charged for non-irrigated private grazing lands in the West, which averaged $20.10 per AUM. The gap has widened considerably since 1981, when the federal fee was 23.79 percent of fees charged on private rangelands. The federal grazing fee is generally also considerably lower than fees charged on state-owned public lands.

3. The federal grazing subsidy is even larger when all costs to the taxpayer are accounted for. Indirect costs for livestock grazing include portions of different federal agencies budgets, such as the USDA Wildlife Services, which expends money to kill thousands of native carnivores each year that may threaten livestock; U.S. Fish and Wildlife Service, which expends part of its budget for listing species as threatened or endangered resulting from harm by livestock grazing; and other federal land management agencies that expend money on wildfire suppression caused by invasive cheat grass that is facilitated by livestock grazing. The full cost of the federal grazing program is long overdue for a complete analysis.

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Abbreviations

AUM	Animal Unit Month
BCPI	Beef Cattle Price Index
BLM	Bureau of Land Management
CF	Calculated Fee
CFR	Code of Federal Regulations
CRS	Congressional Research Service
DOD	Department of Defense
DOE	Department of Energy
DOI	Department of the Interior
FLPMA	Federal Land Policy and Management Act
FN	Footnote
FVI	Forage Value Index
FWS	U.S. Fish and Wildlife Service
FY	Fiscal Year
GAO	General Accounting Office
NASS	National Agricultural Statistics Service
NFS	National Forest System
NPS	National Park Service
PPI	Prices Paid Index
PRIA	Public Rangeland Improvement Act
RBF	Range Betterment Fund
USDA	United States Department of Agriculture
USDOI	United States Department of the Interior
USFS	United States Forest Service

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This report was prepared for the Center for Biological Diversity.

About the Authors

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Introduction

Several federal agencies permit livestock grazing on public lands in the United States, the largest being the U.S. Department of the Interior's Bureau of Land Management (BLM) and the Department of Agriculture's United States Forest Service (USFS). The vast majority of livestock grazing on BLM and USFS rangelands occurs in the 11 western states of Arizona, California, Colorado, Idaho, Oregon, Montana, New Mexico, Nevada, Utah, Washington and Wyoming. Rangelands are non-irrigated and generally have vegetation that consists mostly of grasses, herbs and/or shrubs. They are different from pastureland, which may periodically be planted, fertilized, mowed or irrigated.

In 2013, the BLM issued 15,739 permits to livestock operators and there were 5,711 livestock operators who had permits to graze in the national forest system. The numbers of USFS and BLM permits and livestock permittees are not directly additive, but due to a number of livestock operators who have permits from both agencies and/or more than one grazing permit per agency, the total number of livestock operators is likely to be fewer than 21,540. This compares to the approximately 800,000 ranchers and cattle producers in the United States. (Statistic Brain, 2012). The number of operators benefitting from the USFS and BLM grazing program in the West is therefore less than 2.7 percent of the nation's total livestock operators.

By statutory direction, BLM and USFS are supposed to manage their lands for multiple purposes. Some of the major extractive uses that these lands may be subject to are grazing, mining, logging, and energy (oil, gas, coal, geothermal, wind and solar) development. To repair past and current ongoing damage, the agencies have programs to restore ecosystems, protect wildlife and wildlife habitat, and water and soil resources. As one of the major multiple uses, grazing occurs on large expanses of BLM and USFS acreage in the West.

Other federal agencies with a land base, including the National Park Service, Fish and Wildlife Service, Department of Defense (Army, Army Corps of Engineers, Air Force and Navy), and Bureau of Reclamation, often permit some livestock grazing on their lands as well, but their landholdings are small in comparison. The Bureau of Indian Affairs tribal lands and state trust lands are the other major categories of non-public lands on which livestock grazing is permitted.

The focus of this report is on federal public lands managed by BLM and USFS, and the direct costs of these federal grazing programs to taxpayers. We examine the history of public lands ranching and how much grazing the BLM and USFS agencies have authorized between 2002 and 2013. A major portion of this report deals with BLM and USFS grazing fees. We explore in detail the fee formula that has been applied since the passage of the 1978 Public Rangelands Improvement Act (PRIA). We compare the PRIA fees to rates charged on private lands, state lands, and lands managed by other federal agencies.

Appendix A explores some of the indirect costs resulting from federal grazing programs.

1. Public Lands Ranching - A Brief History

After the U.S. Civil War, the western range livestock industry started to expand. Access to federal lands was not regulated or restricted. Nomadic herders drove large herds of livestock from place to place in search of forage, or herds were left roaming unattended and only rounded up for branding and marketing, or to move them between summer and winter ranges. However, some ranchers with homesteads let cattle roam only during the summer, and brought them close to the home ranch in the winter to feed them with hay. (BLM Utah)

Faced with overuse and land degradation – the classic tragedy of the commons — by the 1880s ranchers developed ways to protect what they considered their customary range by using barbed wire to fence in large areas of public land, or by finding ways to monopolize water sources, access to which is a necessity for maintaining livestock herds in the arid West. (BLM Utah)

During the 1890s, severe land degradation (from grazing as well as logging) led Congress to take steps to create "forest reserves." In 1905, the newly established Forest Service renamed these lands "National Forests," with the Forest Service being given authority to "permit, regulate, or prohibit grazing in the forest reserves." This did not immediately lead to a reduction of overuse. Full grazing privileges were given to livestock owners in the beginning, and stockmen were to be given "ample opportunity to adjust their business to the new conditions." (USDA 1905, 20) One immediate consequence of the regulations was the elimination of nomadic herders from the lands managed by the Forest Service. (International Society for the Protection of Mustangs and Burros)

In the western states outside of the national forests, access to vast areas of federal lands remained open, and they continued to deteriorate until passage of the Taylor Grazing Act of 1934. The Act directed the secretary of the Interior "to stop injury to the public grazing lands by preventing overgrazing." A newly established Division of Grazing (renamed the Grazing Service in 1939) delineated allotments, issued grazing permits and collected fees. After enactment of the Taylor Grazing Act, livestock numbers were significantly reduced and nomadic sheep and cattle herding was eliminated. (BLM Utah; BLM Wyoming)

During the Great Depression, under the authority of the Bankhead-Jones Farm Tenant Act of 1937, the federal government recovered millions of acres of failed western homesteads. Many of these lands in California, Montana, New Mexico and Texas were transferred to the Grazing Service or General Land Office. Other large parcels came under Forest Service management and were later named "national grasslands." (Olson 1997, 4-7)

In 1946, the Grazing Service and General Land Office were merged to form the Bureau of Land Management (BLM), giving the BLM jurisdiction not just over rangelands, but also over public land minerals and land transfers, among others. (Gorte 2012, 10)

In the 1960s and 1970s, federal laws were passed to protect the environment, among them the National Environmental Policy Act (NEPA) of 1969 and the Endangered Species Act (ESA) of 1973. These laws changed the expectation as to how public lands were to be managed, leading, among other things, to changes in the terms and conditions that applied to grazing leases and permits. (BLM 3/28/14)

In 1974, the Forest and Rangeland Renewable Resources Planning Act was passed—and later amended in 1976 as the National Forest Management Act. This act called for management of renewable resources on national forest lands through "analysis of environmental and economic impacts, coordination of multiple use and sustained yield opportunities as provided in the Multiple-Use Sustained-Yield Act of 1960." (74 Stat. 215; 16 U.S.C. 528–531) It also called for public participation in the development of the program." (USDA History of Forest Planning)

In 1976, the Federal Land Policy and Management Act (FLPMA) passed into law, giving the BLM the mission to manage public lands for multiple uses and "sustained yield." (USDOI, 2001, 1) FLPMA also established a Range Betterment Fund into which half of all BLM and USFS grazing fee receipts were to be directed for range improvements. (BLM WYOMING)

In 1978 the Public Rangelands Improvement Act (PRIA) was passed, which provided a formula for setting grazing fees on both Forest Service and BLM lands in 16 western states.[1] After a trial period of seven years, this formula was made permanent by Executive Order 12548 (Feb. 14, 1986). Executive Order 12548 established a fee minimum of $1.35 per Animal Unit Month (AUM)[2], and provided that annual fee adjustment could not exceed 25 percent of the previous year's fee. (Vincent 2012, 3)

The application of the PRIA fee formula has ultimately led to BLM and USFS grazing fees that increasingly diverge from rates charged by private landowners as well as other federal and state agencies.

Under PRIA, both the BLM and USFS divide their rangelands into allotments. Allotments can vary in size from a few acres to hundreds of thousands of acres of land, and may be intermingled with private lands. BLM uses a grazing permit system to "permit" grazing allotments within its grazing districts. Outside grazing districts, BLM leases its fragmentary lands to ranchers. The Forest Service does not have grazing districts, and uses permits to authorize grazing within its allotments. (GAO 2005, 12)

To be eligible for a permit or lease on one of BLM's allotments, livestock operators are required to own or control private "base property" that can serve to support the livestock with water, or necessary feed. Under USFS guidance, permits are issued to purchasers of permitted livestock or base property. (GAO 2005, 12)

Grazing is administered primarily through issuance of 10-year term permits for discrete grazing allotments. The 10-year permits can be renewed without competition. The current permittee or lessee has priority over others who may be interested in the permit or lease and thus has what is known as "preference." Permittees do not obtain title to federal lands through their grazing permits and leases. (GAO 2005, 16)

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[1] These 16 states are: Arizona, California, Colorado, Idaho, Kansas, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oklahoma, Oregon, South Dakota, Utah, Washington, and Wyoming. See Vincent 2012, 1, listing authorities that govern grazing on BLM and USFS lands in 16 contiguous Western states as P.L. 95-514, 92 Stat. 1803; 43 U.S.C. §§1901, 1905. Executive Order 12548, 51 Fed. Reg. 5985 (February 19, 1986).
[2] Animal Unit Month (AUM) is a "standardized unit of measurement of the amount of forage necessary for the complete sustenance of one animal unit for a period of 1 month." (BLM PLS 2012, 255). More precisely, it is "the use of public lands by one cow and her calf, one horse, or five sheep or goats for a month." (BLM 1/31/14)

2. Extent of the Federal Lands Livestock Grazing Program

a. Acres of BLM and USFS Western Lands

As reported by Gorte et al. (2012, 19) the BLM administers 174.5 million acres of federal lands outside of Alaska, and these are almost exclusively concentrated (99.78 percent) in 11 western states (Table 1). The 11 western states are Arizona, California, Colorado, Idaho, Oregon, Montana, New Mexico, Nevada, Utah, Washington and Wyoming. Gorte et al. also report that USFS administers 141.7 million acres in these 11 western states, or 82.94 percent of its total federal land holdings. (Table 2) The delineation of the "West" in Gorte et al. is different from the delineation of the "West" with regard to PRIA, which includes 16 western states. The additional states are Kansas, North Dakota, South Dakota, Oklahoma and Nebraska.

Table 1: BLM and USFS Total Acreage in 11 Western States, 2010

	Total Land Holdings 11 Western States (acres)	Total Land Holdings Other States (Outside Alaska)* (acres)	BLM and USFS Total (Outside Alaska) (acres)	% Holdings in Western States
USFS	141,762,880	29,161,710	170,924,590	82.94%
BLM	174,512,265	388,054	174,900,319	99.78%
Total BLM & USFS	316,275,145	29,549,764	345,824,909	91.46%
*BLM and USFS lands in Alaska are not subject to PRIA or the Taylor Grazing Act and are therefore not included in this analysis. (GAO 2005, 4, 15, 55; BLM Public Land Statistics 2013, 255; Vincent 2012, 1).				

Sources: Gorte et al. 2012, 19

b. Acres of BLM and USFS Western Grazing Lands

Western BLM Lands Grazed

Livestock grazing is the prevailing use of BLM lands, with 137.7 million acres, or 79 percent out of 174.5 million acres of BLM land in the West authorized for livestock grazing in 2004. (GAO 2005, 15) Acres grazed differ from year to year, and were especially low in 2004 because of the drought. (GAO 2015, 14)

Figure 1 (Table B1) shows acres authorized for grazing for each of the 11 western states where BLM holds land. The four states with the largest holdings of BLM grazing lands are Nevada, Utah, Wyoming and New Mexico.

Western USFS Acres Grazed

The USFS is organized by regions, not by states. The following map (Figure 2) delineates the USFS regions and Figure 3 (Table B2) shows how many acres of grazing land the USFS administers in each of its regions. Grazing lands administered by the USFS include national forest lands and national grasslands, combined they comprise the national forest system.

Figure 1
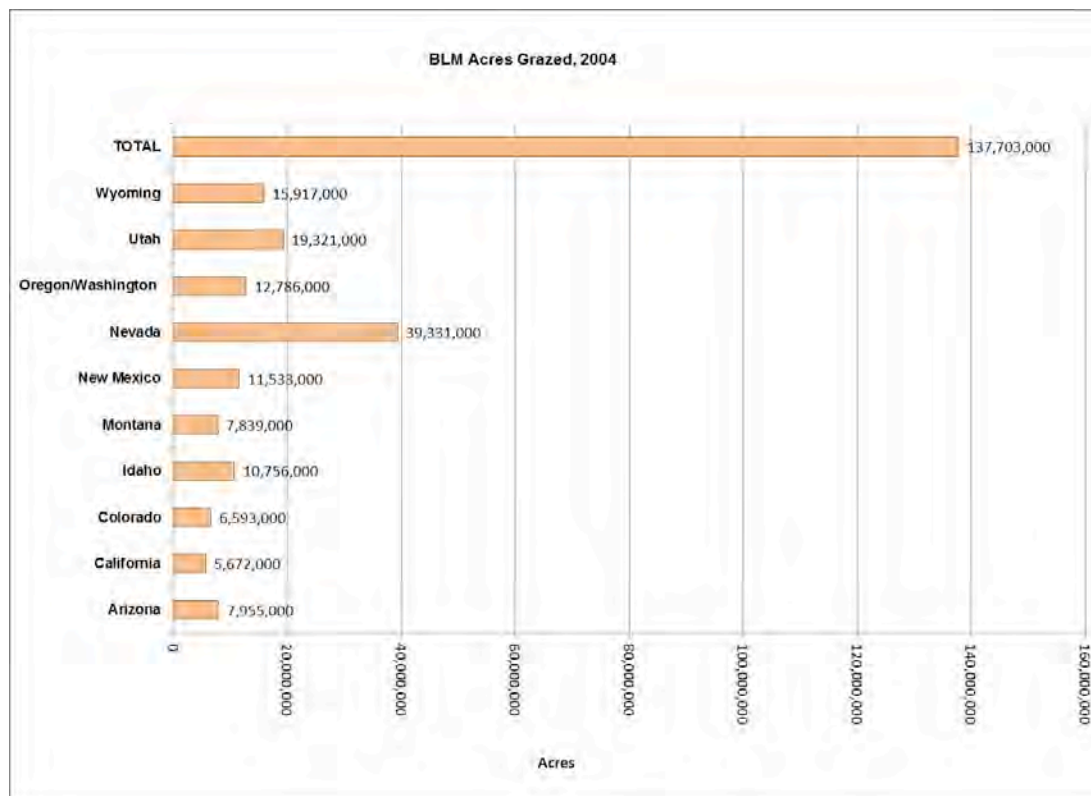
Ninety-nine percent (92.1 million out of 92.9 million acres) of all USFS grazing on national forest and grasslands are in the western Regions within 16 contiguous western states: Arizona, California, Colorado, Idaho, Kansas, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oklahoma, Oregon, South Dakota, Utah, Washington and Wyoming. (USDA Forest Service, Grazing Statistical Summary FY 2013, 96-97) The majority of national grasslands are located in the Great Plains states of Colorado, North Dakota, South Dakota and Wyoming. (Olson, 1997, 3)

The regions with the largest extent of USFS grazing lands are the Intermountain region (Nevada, Utah and Idaho), the Southwest region (Arizona and New Mexico), and the Rocky Mountain region (Colorado, South Dakota, Kansas, Nebraska and Wyoming).

Figure 2: Forest Service Regions

Source: USDA Grazing Statistical Summery 2013, 1.

Figure 3
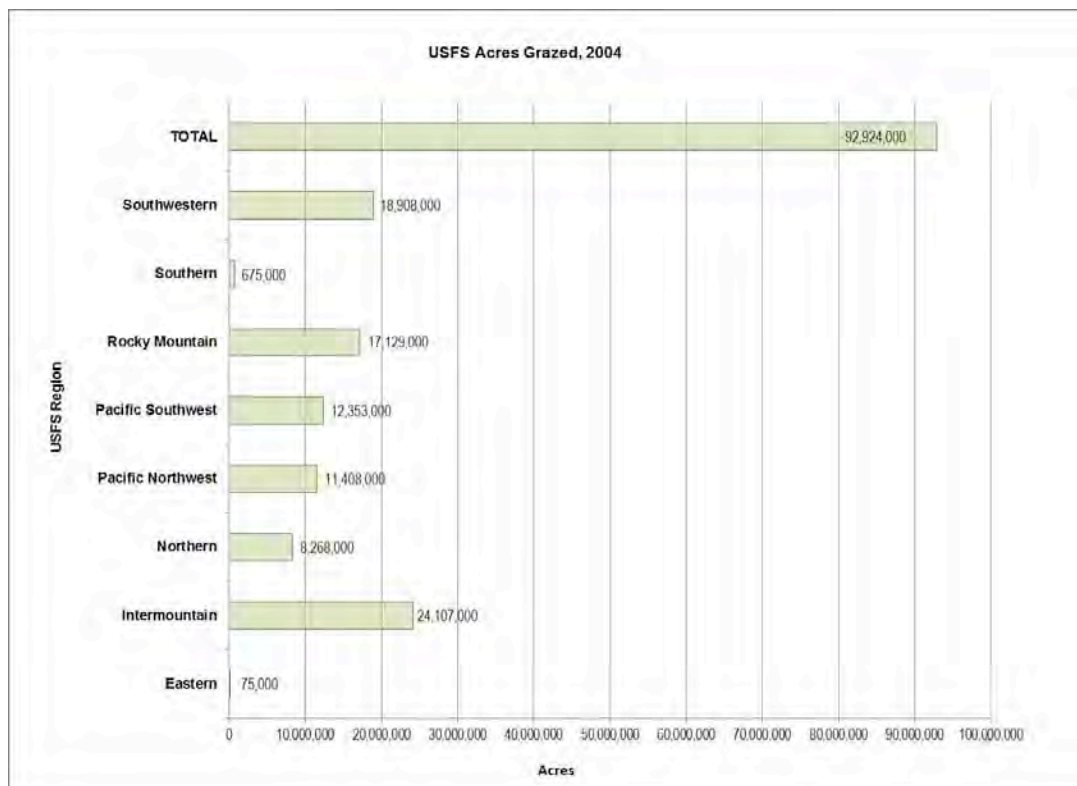
Other Federal Grazing Lands

In addition to BLM and USFS, other federal agencies allow grazing on their lands, including National Park Service, Bureau of Reclamation, U.S. Fish and Wildlife Service, Department of Energy, and Department of Defense. Together, they only manage a total of 4 million acres of grazing land nationwide. (GAO 2005, 17)

c. BLM and USFS—Animal Unit Months, Permits and Leases

The Animal Unit Month (AUM) is the measure of forage—plants that are eaten by livestock— used by federal land management agencies to allocate land for grazing. An AUM is defined as a "standardized unit of measurement of the amount of forage necessary for the complete sustenance of one animal unit for a period of 1 month." (BLM Public Land Statistics 2012, 255) More precisely, it is "the use of public lands by one cow and her calf, one horse, or five sheep or goats for a month." (BLM 1/31/14) The land area needed to produce an AUM will differ considerably depending on soil productivity and precipitation.

BLM Permits and Leases

BLM divides its rangelands into allotments. Allotments can vary in size from a few acres to thousands of acres of land, and may be intermingled with private lands. Grazing on BLM lands requires a Section 3 permit or a Section 15 lease. Section 3 permits are issued for allotments on public lands within the grazing districts. Fragmented BLM lands outside of grazing districts are known as Section 15 leases. (GAO 2005, 12) Permits and leases set out terms and conditions for grazing on BLM-managed lands and specify forage use (AUMs), season of use, and length of season. They generally cover a 10-year period and are renewable if the BLM determines that the terms and conditions of the expiring permit or lease have been met. (BLM 3/28/14) Both permits and leases specify the number of AUMs that a rancher may graze on a particular piece of land. Table 2 shows the number of BLM permit and lease authorizations issued from FY 2002 to FY 2013 as well as the associated authorized AUMs.

For FY 2013, BLM authorized 15,739 permits and leases, with a total of 8,513,271 AUMs. Table 2 shows that between FY 2002 and 2013, BLM authorized an average of 15,870 permits and leases annually, and an average of 8,359,496 AUMs. The lowest number of AUMs was 7,493,419 in 2003 and the highest was 8,985,228 in 2011.

USFS Permits

There are two notable differences between BLM and USFS reporting. Where BLM reports the "number of permits," USFS reports the "number of permittees." A permittee can hold multiple permits**.**

Further, USFS reports grazing use for the grazing season, and not for the fiscal year. BLM reports both, but did not have numbers for the 2013 grazing season. Therefore, above, we used the BLM fiscal year data, for USFS, we will use grazing season data.

Table 2: BLM Authorizations of Permits/ Leases and AUMs, 2002-2013

Fiscal Year	Total Number of Section 3 Permits and Section 15 Leases Authorized	Total AUMs Authorized (Section 3 and Section 15)
2002	15,851	8,287,394
2003	15,472	7,493,419
2004	15,544	7,574,004
2005	15,462	7,816,949
2006	16,416	8,515,292
2007	15,587	8,546,253
2008	17,292	8,531,813
2009	15,612	8,594,912
2010	15,751	8,673,822
2011	15,897	8,985,228
2012	15,815	8,781,600
2013	15,739	8,513,271
Average	*15,870*	*8,359,496*

Source: BLM Public Land Statistics from FY 2003 to FY 2013, Tables 3-7a and b, and 3-8a and b.

There were a total of 5,711 livestock operators who received permits on national forest service land during the 2013 grazing season, for 6,388,964 AUMs. Table 3 shows that between 2002 and 2013 USFS authorized permits for an average of 5,940 permittees, and an average of 6,335,542 million AUMs. The lowest number of AUMs authorized was 5,288,091 in 2004, the highest was 7,056,298 in 2010.

BLM and USFS Combined Totals

Table 4 shows the number of BLM permits, USFS permittees, and associated total AUMs for the grazing season. BLM numbers differ somewhat from Table 2 because they are reported by grazing season rather than for the fiscal year, to match the USFS's reporting. Because BLM's Public Lands Statistics did not report 2013 grazing season numbers, there are no entries for BLM for 2013.

Total authorized AUMs for BLM and USFS between 2002 and 2012 averaged 14,639,848, with a range of between 12,656,540 in 2004 and 15,819,413 in 2010. The number of total AUMs was reduced due to drought in 2003 and 2004. (GAO 2005, 14)

Table 3: USFS Authorized Number of Permittees and AUMs, 2002-2013

Grazing Season	Total Authorized Number of Permittees	Total Authorized AUMs
2002	6,830	6,402,125
2003	5,638	5,725,785
2004	5,791	5,288,091
2005	6,457	6,569,171
2006	5,305	5,675,098
2007	5,344	5,920,850
2008	5,931	6,621,931
2009	6,141	6,673,526
2010	6,206	7,056,298
2011	6,014	6,799,016
2012	5,906	6,905,657
2013	5,711	6,388,964
Average	*5,940*	*6,335,542*

Sources: USDA Grazing Statistical Summaries FY 2002 to 2013 (categories of "paid permits" or "commercial livestock").

Table 4: USFS and BLM – Permits, Leases and Permittees by Grazing Seasons, 2002-2013

Number of Permittees, Permits and Leases			AUMs		
Grazing Season	National Forest System Authorized Number of Permittees	BLM Authorized Permits and Leases	National Forest System Authorized AUMs	BLM Authorized AUMs	BLM & NFS Total Authorized AUMs
2002	6,830	15,072	6,402,125	7,670,129	**14,072,254**
2003	5,638	14,880	5,725,785	7,253,613	**12,979,398**
2004	5,791	14,867	5,288,091	7,368,449	**12,656,540**
2005	6,457	15,998	6,569,171	8,518,458	**15,087,629**
2006	5,305	15,943	5,675,098	8,558,443	**14,233,541**
2007	5,344	15,935	5,920,850	8,476,842	**14,397,692**
2008	5,931	15,935	6,621,931	8,590,864	**15,212,795**
2009	6,141	17,654	6,673,526	8,608,534	**15,282,060**
2010	6,206	16,070	7,056,298	8,763,115	**15,819,413**
2011	6,014	16,117	6,799,016	8,997,890	**15,796,906**
2012	5,906	16,044	6,905,657	8,594,442	**15,500,099**
2013	5,711	n/a	6,388,964	n/a	**n/a**
Average	*5,940*	*15,865*	*6,335,543*	*8,309,162*	*14,639,848*

Sources: USDA Grazing Statistical Summaries, FY 2002 to 2013 (category of "paid permits" or "commercial livestock"); BLM Public Land Statistics from 2004 to 2013, Tables 3.10a and b.

Other Federal Agencies' AUMs

BLM and USFS are indeed the significant players in the federal grazing arena. For the purpose of comparison, all other federal agencies approved 794,000 AUMs in 2004 (GAO 2005, 17).

3. Cost of the Federal Livestock Grazing Program

a. Grazing Receipts and their Distribution

USFS and BLM combined inflation-adjusted receipts from grazing fees have declined between 2002 and 2014. As Table 5 below shows, this decline was greater for the BLM than for the USFS. Combined BLM and USFS receipts were $27.6 million in 2002; they dipped in 2004 because of the drought, rose again slightly above the 2002 level in 2006, and from there decreased to $18.5 million in 2014.

Not all of the grazing fees that are collected get returned to the U.S. Treasury. Federal law requires that 50 percent of all grazing revenue, for both BLM and USFS, goes into range rehabilitation and improvement funds. Activities that can be funded include, but are not limited to, constructing fences to contain livestock, installing water tanks, building impoundments to improve access to water for livestock, and seeding to improve vegetation and forage. Half of these funds are designated for use in the district, region or national forest from which they were generated. The remaining half is designated for use as directed by the secretary. (GAO 2005, 31) Counties receive between 12.5 percent and 50 percent and the balance, between 25 percent and 37.5 percent gets returned to the U.S. Treasury. (Table 6)

Table 5: USFS and BLM Grazing Receipts 2002-2014, in 2014

	Receipts*		
Fiscal Year	**USFS Grazing (2014 Dollars)**	**BLM Grazing Receipts (2014 Dollars)**	**USFS and BLM Total (2014 Dollars)**
2002	$7,889,000	$19,733,000	**$27,622,000**
2003	$6,169,000	$15,985,000	**$22,154,000**
2004	$7,010,000	$8,191,000	**$15,201,000**
2005	$8,397,000	$11,787,000	**$20,184,000**
2006	$7,620,000	$20,321,000	**$27,941,000**
2007	$6,514,000	$18,006,000	**$24,520,000**
2008	$6,247,000	$17,538,000	**$23,785,000**
2009	$6,148,000	$19,284,000	**$25,432,000**
2010	$6,005,000	$16,189,000	**$22,195,000**
2011	$5,974,000	$15,624,000	**$21,598,000**
2012	$5,689,000	$15,352,000	**$21,041,000**
2014	$5,300,000	$13,217,000	**$18,517,000**
2013	$5,027,000	$14,585,000	**$19,612,000**
*The numbers are gross receipts, i.e. payments to counties have not been subtracted.			

Sources: USDA Forest Service, Budget Overviews for Fiscal Years 2004, 2006, 2007, 2008, 2010-2015, Budget Justification Fiscal Years 2005, 2009 (2012 and 2013 numbers are "Enacted"; 2014 numbers are "Estimated."); BLM Fiscal Years 2004 to 2015 Bureau Highlights - Appendices (Receipts by Source Category). BLM grazing receipts for 2014 "Estimated." All other receipts are "Actual."

Table 6: Distribution of Fee Receipts by Agency and Land Classification

	Payments to Counties	Range Betterment/Improvement Fund	US Treasury
USFS	25%	50%	25%
BLM Section 3 (permits)	12.50%	50%	37.50%
BLM Section 15 (leases)	50%	50%	
BLM Bankhead-Jones (grasslands)	25%	50%	25%

Sources: GAO 2005, 31-32; BLM 2012.

b. Grazing Appropriations

Direct grazing appropriations, funds designated for use for BLM or USFS rangeland/grazing management programs and range improvement/betterment funds, are shown in Table 7. USFS inflation-adjusted appropriations have increased, whereas BLM appropriations have decreased. BLM and USFS combined inflation-adjusted appropriations have decreased somewhat since 2003, with the exception of the year 2012, when they increased to almost their 2004 level.

Table 7: USFS and BLM Direct Grazing Appropriations 2002-2014, in 2014 Dollars

Appropriations			
Fiscal Year	USFS (2014 Dollars)	BLM (2014 Dollars)	USFS and BLM (2014 Dollars)
2002	$50,040,000	$105,948,000	**$155,988,000**
2003	$55,998,000	$104,771,000	**$160,768,000**
2004	$59,012,000	$101,369,000	**$160,381,000**
2005	$59,950,000	$93,989,000	**$153,940,000**
2006	$58,831,000	$92,214,000	**$151,045,000**
2007	$56,877,000	$87,794,000	**$144,671,000**
2008	$55,480,000	$90,830,000	**$146,310,000**
2009	$57,126,000	$88,213,000	**$145,340,000**
2010	$56,190,000	$88,751,000	**$144,941,000**
2011	$53,751,000	$89,343,000	**$143,094,000**
2012	$59,248,000	$99,616,000	**$158,864,000**
2013	$54,245,000	$86,495,000	**$140,740,000**
2014	$58,356,000	$85,280,000	**$143,636,000**

Sources: USDA Budget Overview 2004, 2006-2008, 2010-2015; USDA Budget Justification 2005, 2009; BLM Bureau Highlights 2004-2015. NOTE: USFS numbers were reported as "Enacted" for the years 2004 and 2007-2014, and for other years as "Final Appropriations." BLM 2012 and 2014 numbers were reported as "Enacted"; in 2013, the number for range improvement, which is part of the total, was reported as "Requested." For other years, BLM numbers were reported as "Actual."

c. Difference Between Appropriations and Receipts

In FY 2014, the total inflation-adjusted appropriations for BLM and USFS were $143.6 million; grazing receipts amounted to $18.5 million, or 13 percent of the appropriations (Table 8 and Figure 4).

The difference between appropriations and receipts was $128.4 million in 2002, and reached its highest level of $145.2 million in 2004. Its lowest level of $120.2 million was reached in 2007. The percent of receipts to appropriations was 18 percent in 2002, dipped to 9 percent in 2004, rose again to 18 percent in 2006, and decreased to 13 percent in 2013.

The difference between appropriations and receipts is a measure of the cost to taxpayers of the grazing program. The direct federal subsidy of the BLM and USFS livestock grazing programs exceeded $120 million every year for the past 12 years.[3]

Table 8: Total BLM and USFS Direct Grazing Appropriations vs. Receipts 2002-2014

Year	Total Appropriations (2014 Dollars)	Total Receipts (2014 Dollars)	Appropriations Minus Receipts (2014 Dollars)	Percent Receipts to Appropriations Percent of Receipts to Appropriations
2002	$155,988,000	$27,622,000	$128,365,000	18%
2003	$160,768,000	$22,154,000	$138,614,000	14%
2004	$160,381,000	$15,201,000	$145,181,000	9%
2005	$153,940,000	$20,184,000	$133,756,000	13%
2006	$151,045,000	$27,941,000	$123,104,000	18%
2007	$144,671,000	$24,520,000	$120,151,000	17%
2008	$146,310,000	$23,785,000	$122,525,000	16%
2009	$145,340,000	$25,432,000	$119,907,000	17%
2010	$144,941,000	$22,195,000	$122,746,000	15%
2011	$143,094,000	$21,598,000	$121,496,000	15%
2012	158,864,000	$21,041,000	$137,824,000	13%
2013	140,740,000	$19,612,000	$121,127,000	14%
2014	143,636,000	$18,517,000	$125,119,000	13%

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[3] Federal receipts are gross numbers, before distribution to counties, for this comparison.

Figure 4

Annual Federal Grazing Appropriations, Receipts, and Taxpayer Costs: 2002 - 2014
(Millions of 2014 Inflation-Adjusted Dollars)
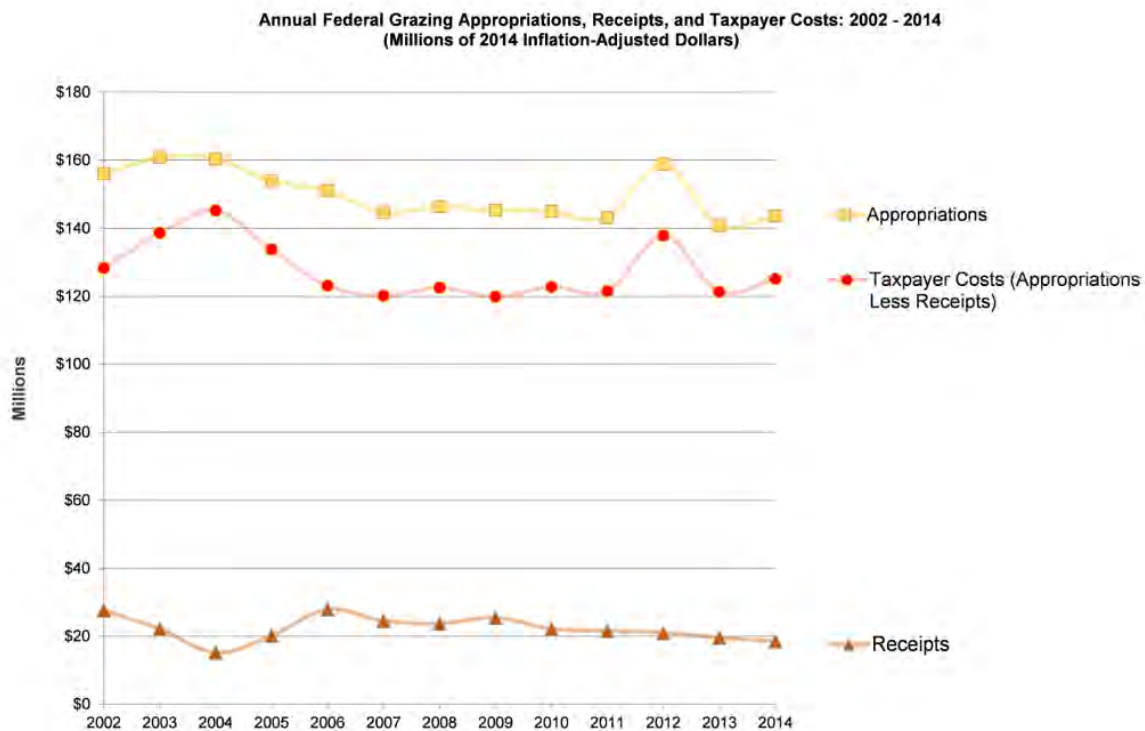
As shown, inflation adjusted grazing appropriations for USFS have increased, whereas they have decreased for BLM (Table 7). However when comparing grazing receipts as a percent of appropriations separately for BLM and USFS (Tables B3 and B4), different trends emerge.

The percentage of receipts to appropriations declined markedly for the Forest Service, from 16 percent in 2002 to 9 percent in 2014. (Table B3)

The changes in the percentage of receipts to appropriations are less pronounced for BLM, because appropriations have fallen as well as receipts. The percentage of receipts to appropriations for BLM was 19 percent in 2002 and is down to 15 percent in 2014, but fluctuated a lot in-between and rose to 22 percent in both 2006 and 2009. (Table B4)

d. PRIA Fee Impacts on Receipts and Scenarios for Reducing Taxpayer Costs

As demonstrated above, BLM and USFS grazing receipts have declined in real, or inflation adjusted dollars, since 2002. The decline in grazing receipts over these years is mostly attributable to the decline in grazing fees rather than a decline in the number of AUMs. The grazing fee is based on a specific formula called PRIA and explained in the next chapter.

Specifically, the inflation-adjusted PRIA fee was $1.88 in 2002, and $1.36 in 2013 (Table B6), a decline of 28 percent. Grazing receipts in 2002 were $27.6 million and in 2013 they were $19.6 million (Table 7), a decline of 29 percent. Receipts decline when either the numbers of AUMs

fall in any given year, or fees decline. As Tables 2 and 3 show, AUMs have been fairly stable over the years, except for the drought period around 2004.

Before the PRIA formula came into effect, BLM and USFS charged fees that were designed to cover agency costs or were market-based.

In order to cover direct appropriation costs for the BLM and USFS programs, the grazing fee would have had to be set at $10.25 per AUM based on 2012 figures. This calculation is based on using the 2012 inflation-adjusted appropriations for BLM and USFS of $158.9 million (Table 7), and total AUMs of 15.5 million (Table 4). [4]

Other federal agencies as well as state agencies administering grazing programs in the West sometimes charge rates that are considerably higher than the $10.25 per AUM.

If the BLM and USFS had charged private markets rates, on average between 2002 and 2012, grazing receipts would have amounted to $261 million annually. This is based on applying private grazing fee rates to non-irrigated land to the corresponding number of AUMs for each of those years. (Table B5)

Specifically, applying the inflation-adjusted 2012 private grazing fee of $19.23 per AUM, grazing fees would have been $298 million, way above the appropriations of $158.9 million for that year. (Table B5)

4. BLM and USFS Grazing Fees

a. History of Fee Setting Approaches

Charging fees for grazing livestock has been Forest Service policy since 1906. The BLM and its predecessors have charged fees since 1936, after enactment of the Taylor Grazing Act in 1934. (GAO 2005, 84)

The USFS and BLM have used a number of different concepts at different points in time to establish how much the federal government should charge livestock operators for grazing their animals on federal lands:

- Fair market value: The fee is determined by the interaction of willing buyers and sellers that are knowledgeable about the value of what they are transacting, behave in their own best interest, and are free of undue pressure to conduct the transaction. A knowledgeable buyer and seller would be aware of the quality and productivity of the land and of market prices for leases or permits on other comparable lands, and the seller would expect to derive some profit from the transaction.

- Costs to the government: The fee is determined with the goal of covering the costs to the government of providing land for grazing.

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[4] 2012 is the most recent year where combined USFS and BLM AUMs data are available (Table 6).

- Fees based on the development of livestock prices: Fees increase or decrease depending on livestock prices.

- PRIA Fees: Fees are set to achieve a policy objective of supporting the livestock industry ("prevent economic disruption to the Western livestock industry" (43 U.S.C. 37, §1901(5)), taking into account the price for beef and lamb and the costs of production for the livestock industry. Costs of the public agency for providing grazing land are not included in this fee structure.

In the early 1900s, the Forest Service assessed fees by comparing those of similar privately owned rangeland, so as to approximate fair market value. From the early 1920s to 1968, the USFS based its fees on beef and lamb prices. BLM and its predecessors started out basing their fees on agency expenses, but changed this approach in 1958 to basing fees on livestock prices, similar to the USFS fee structure. (GAO 2005, 84) In the 1960s, the Bureau of the Budget (predecessor of Office of Management and Budget) set a fee schedule for these two agencies that had the goal of achieving fair market value. (GAO 2005, 84) This was based on an Office of Management and Budget circular of 1959, which directed that "fair market value" be obtained (36 C.F.R. §222.50 (b)).

> 36 CFR §222.50 General procedures.
>
> (b) Guiding establishment of fees are the law and general governmental policy as established by Bureau of the Budget Circular A-25 of September 23, 1959, which directs that: A fair market value be obtained for all services and resources provided the public through establishment of a system of reasonable fee charges, and that the users be afforded equitable treatment. This policy precludes a monetary consideration in the fee structure for any permit value that may be capitalized into the permit holder's private ranching operation.

The Public Rangeland Improvement Act (PRIA) of 1978 acknowledged that the public rangelands were in unsatisfactory condition with regard to productive potential for livestock, wildlife and wildlife habitat, recreation, forage and soil conservation, and might decline further under prevailing management. It acknowledged the need for intensive programs for maintaining, managing and improving these lands. (43 U.S.C. 37, §1901(1)-(4) In further elaborating the policy objectives, it stated that "to prevent economic disruption and harm to the Western livestock industry, it is in the public interest to charge a fee for livestock grazing permits and leases on the public lands which is based on a formula reflecting annual changes in the costs of production."(43 U.S.C. 37, §1901(5))

The Public Rangeland Improvements Act (PRIA) established a fee formula on an experimental basis (to be applied for the grazing years 1979 through 1985), explained in 43 U.S.C. 37 §1905:

> For the grazing years 1979 through 1985, the Secretaries of Agriculture and Interior shall charge the fee for domestic livestock grazing on the public rangelands which Congress finds represents the economic value of the use of

the land to the user, and under which Congress finds fair market value for public grazing equals the $1.23 base established by the 1966 Western Livestock Grazing Survey multiplied by the result of the Forage Value Index (computed annually from data supplied by the Economic Research Service) added to the Combined Index (Beef Cattle Price Index minus the Price Paid Index) and divided by 100: Provided, That the annual increase or decrease in such fee for any given year shall be limited to not more than plus or minus 25 per centum of the previous year's fee.

In 1981, USFS and BLM began charging the same fees based on this fee formula. After the seven-year trial period, President Reagan issued Executive Order 12548 (Feb. 14, 1986) to continue the PRIA fee formula indefinitely, and established a minimum fee of $1.35 per AUM. (Vincent 2012, 3)

The PRIA fee formula is applied only for grazing on western USFS forestlands and permits and leases on BLM lands. Detailed regulations for western states can be found in 36 CFR 222.51, and in 43 CFR 4130.8-1.

Fees for grazing on USFS Grasslands are regulated by 36 CFR 222.52, which states that: "Grazing fees for National Grasslands will be established under concepts and principles similar to those in §222.51." These fees are usually slightly higher than the fees based on the PRIA formula. (GAO 2005, 39)

Grazing on USFS lands in non-western states is regulated either by 36 CFR 222.53, setting out non-competitive procedures based on fair market value, or they are regulated by 36 CFR 222.54, which provides for determining fees by competitive procedures. Other federal agencies base their grazing fees mostly on market value. (GAO 2005, 41-44)

Table 9: PRIA-Based Grazing Fees from 1981 to 2014

Dollars per AUM		
1981....................$2.31	1993....................$1.86	2005....................$1.79
1982....................$1.86	1994....................$1.98	2006....................$1.56
1983....................$1.40	1995....................$1.61	2007....................$1.35
1984....................$1.37	1996....................$1.35	2008....................$1.35
1985....................$1.35	1997....................$1.35	2009....................$1.35
1986....................$1.35	1998....................$1.35	2010....................$1.35
1987....................$1.35	1999....................$1.35	2011....................$1.35
1988....................$1.54	2000....................$1.35	2012....................$1.35
1989....................$1.86	2001....................$1.35	2013....................$1.35
1990....................$1.81	2002....................$1.43	2014....................$1.35
1991....................$1.97	2003....................$1.35	
1992....................$1.92	2004....................$1.43	

Sources: Vincent 2012, 3; BLM 1/31//14; BLM 2013

Actual grazing fees charged since 1981 based on the PRIA formula for USFS and BLM permits and leases are shown in the table below. Several attempts at legislative reform have been made since 1986 with the goal of changing the PRIA formula to bring grazing fees charged on federal lands closer to rates charged for private and state grazing lands in the western states. None of these attempts were successful. (Vincent 2012, 5-6)

For the years 2002 to 2014, Table 9 shows that the PRIA fee was $1.43 in 2002, rose to its highest level of $1.79 in 2005, and then fell to the its $1.35 legal minimum level for the years 2007 to 2014.

When adjusted for inflation, PRIA fees have declined from $1.88 in 2002 to $1.35 in 2014, with a high of $2.20 in 2005 (in 2014 dollars). (Table B6)

b. PRIA Formula Explained

A 2012 report by Vincent explains that the PRIA formula is to represent the fair market value of grazing, beginning with a 1966 base value of $1.23 per AUM. This value is adjusted for three factors: (1) the rental charge for pasturing cattle on private rangelands (FVI), (2) the sales price of beef cattle (BCPI), and (3) the cost of livestock production (PPI). (Vincent 2012, 3) The values for FVI, BCPI and PPI that were used to calculate PRIA fees from 1981 to 2014 are shown in Table 12 below.

The following formula is used to determine the grazing fee for any given grazing season:

$$CF = \$1.23 \times \frac{FVI + BCPI - PPI}{100}$$

The example below describes the application of the PRIA formula.

Applying index numbers for data year 2013 (Table 12) to calculate the PRIA fee for 2014 would result in a calculated fee (CF) of $0.75.

$$2014\ CF = \$1.23 \times (507+548-994)/100 = \$0.75$$

Since $1.35 has been set as a minimum value, the actual grazing fee was $1.35 for 2014.

CF = Calculated Fee is calculated fee (CF) is the value resulting from the application of the above formula and is based on prior year values for the formula components (FVI, BCPI, PPI). The actual fee may differ from the calculated fee. If the calculated fee is below the minimum of $1.35 per AUM, then the actual fee will be set at $1.35. Or, if the fee adjustment would exceed 25 percent of the previous year's fee, then the fee would be constrained within the 25 percent limit.

$1.23 was the base year fee for forage for the year 1966. The base year fee of $1.23 was calculated as the difference between the costs of conducting ranching business on private lands, including any grazing rates charged, and the costs of ranching on public lands, <u>not</u> including

grazing fees. The costs were computed in a 1966 study that included 10,000 ranching businesses in the western states. (GAO 2005, 40, FN 27)

FVI = Forage Value Index is based on grazing rates charged per head month on privately owned, non-irrigated land in eleven western states.[5] Private grazing rates – for the prior year – are published by USDA's National Agricultural Statistics Service (NASS) in the January Agricultural Prices report. They are divided by the base year rate ($ 3.65) times 100, to arrive at the Index Value.

BCPI = Beef Cattle Price Index is based on weighted average annual selling price for beef cattle in 11 western states of the prior year. It is published by USDA's NASS in the December Agricultural Prices report. The beef cattle price is divided by the base year price ($22.04) times 100 to arrive at the index.

PPI = Prices Paid Index is based on several categories of livestock production costs and is published by USDA's NASS in the December Agricultural Prices report. (43 CFR 4130 .8–1)

As explained above, based on a 1966 study, it was determined that a public lands grazing fee of $1.23 would make total grazing costs on public land (non-fee costs + fee of 1.23) equal to total costs on private land (including lease rates for private grazing land). This $1.23 fee was at the time 33.69 percent of the private grazing fee, which amounted to $3.65.

The PRIA formula has been used to adjust federal grazing fees yearly, and has resulted in an ever-widening gap between private rates and PRIA fees, as will be shown in more detail below. PRIA fees have declined since 1981 in both nominal terms and adjusted for inflation, whereas private fees have increased nominally and changed little in real terms. (Table B6)

This development is the result of the construction of the PRIA formula. In the nominator it adds the difference between the BCPI (Beef Cattle Price Index) and PPI (Prices Paid Index) to FVI (Forage Value Index). PPI has mostly been larger than the BCPI, as can be seen in Table 10. This results in a negative BCPI-PPI number, which reduces the nominator below the level of FVI, and therefore reduces the factor by which the base fee is multiplied. With FVI thus being systematically reduced, it is not possible for the PRIA fee to increase in sync with private rates. The calculated fee can even drop below the 1.23 base fee or become negative (Table 10). Only the legally established minimum floor of $1.35 prevents that.

If the fee formula had been CF = 1.23 X FVI/100, public grazing fees would have increased about five-fold since 1966, from $1.23 to about $6.15. This can be seen in Table 10, where FVI starts at a level of 100 in 1966 and reaches a level of 507 in 2013, resulting in a five-fold increase in private forage rates. The public grazing fee would still be about 1/3 of the private grazing fee, just as it was in 1966, when the base fee of $1.23 was established.

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[5] Montana, Idaho, Wyoming, Colorado, New Mexico, Arizona, Utah, Nevada, Washington, Oregon, and California

5. PRIA Fees Compared To Private, State and Other Federal Grazing Fees

Several grazing fee studies and surveys have been conducted over the years, demonstrating that rates for private grazing lands in the western states are generally higher, and sometimes considerably higher, than fees based on the PRIA formula. Fees charged for state grazing lands also tend to be higher than PRIA rates, though they generally are lower than private rates. Livestock operators also generally pay rates that are higher than PRIA rates on federal lands administered by other federal agencies, including National Park Service or U.S. Fish and Wildlife Service.[6]

Tables 10 to 13 show how PRIA fees are different from rates charged by private, state and other federal landowners. One of the differences, besides PRIA being generally lower, is that PRIA fees are uniformly applied across the western states, while it is obvious when looking at non-PRIA rates (i.e. rates charged by private, state and other federal land-owners) that they can vary considerably within and across states. This is to be expected if supply and demand conditions are not uniform, and market-based fee setting approaches are used. Supply conditions include such factors as quality of the forage, access to water, grazing infrastructure, and services offered (or not offered) by private or public landowners. Differences in supply conditions can lead to differences in livestock management costs, and in turn affect how much a rancher is willing to pay for a lease or permit. Livestock operator costs are also not uniform on BLM and USFS land. A 1992 study for the states of Idaho, New Mexico and Wyoming showed that total non-fee costs for livestock operators (excluding the federal grazing fee) on BLM land on average were $15.41 per AUM and on USFS land were $21.89 per AUM. (VanTassel, 2012)

a. PRIA Fees Compared to Private Fees

Table 10 includes a column shaded in light grey, which shows the average private grazing fees (for non-irrigated land in the 16 western states) from 1981 to 2013. The column on the right calculates PRIA fees as a percent of private land grazing fees. Going back to the PRIA base year 1966, the calculated fee would have been 33.69 percent of the private fee.

Starting in 1981, when PRIA fees were first charged by both BLM and USFS, the PRIA fee was down to 23.79 percent of the private fee, the highest it has been since then. By 1984 the percentage had gone down to 14.33 percent, but it rose sporadically for a few years after that. Since 1991 it has trended downward, reaching a low of 6.72 percent in 2013.

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[6] Van Tassell et al. 1997; Torell et al. 1993; Torell et al. 2003; Van Tassel 2012; Bioeconomics 2011, GAO 2005.

Table 10: PRIA Fee Calculation 1980 through 2014 and Comparison to Private Rates

Data Year	FVI	BCPI	PPI	PRIA Fee Year	Calculated Fee (CF)	PRIA Fee	Private Rates	% PRIA Fee of Private Rates
1966	*100*	*100*	*100*		*$1.23*		*$3.65*	*33.69%*
1980	216	291	319	1981	$2.31	$2.31	$9.71	23.79%
1981	242	268	359	1982	$1.89	$1.86	$9.75	19.08%
1982	229	262	378	1983	$1.39	$1.39	$9.59	14.49%
1983	242	256	387	1984	$1.37	$1.37	$9.56	14.33%
1984	243	262	395	1985	$1.35	$1.35	$9.06	14.90%
1985	251	243	397	1986	$0.93	$1.35	$8.33	16.21%
1986	233	235	388	1987	$0.98	$1.35	$8.09	16.69%
1987	234	272	381	1988	$1.54	$1.54	$8.98	17.15%
1988	240	297	386	1989	$1.86	$1.86	$10.06	18.49%
1989	243	306	402	1990	$1.81	$1.81	$10.86	16.67%
1990	253	326	419	1991	$1.97	$1.97	$9.78	20.14%
1991	265	327	436	1992	$1.92	$1.92	$10.46	18.36%
1992	275	316	440	1993	$1.86	$1.86	$10.60	17.55%
1993	279	333	451	1994	$1.98	$1.98	$11.30	17.52%
1994	282	304	455	1995	$1.61	$1.61	$11.20	14.38%
1995	301	277	473	1996	$1.29	$1.35	$11.40	11.84%
1996	293	252	499	1997	$0.57	$1.35	$11.70	11.54%
1997	310	281	512	1998	$0.97	$1.35	$12.30	10.98%
1998	323	272	514	1999	$1.00	$1.35	$12.30	10.98%
1999	326	281	516	2000	$1.12	$1.35	$12.60	10.71%
2000	329	313	554	2001	$1.08	$1.35	$13.10	10.31%
2001	345	330	559	2002	$1.43	$1.43	$13.50	10.59%
2002	356	303	559	2003	$1.23	$1.35	$13.80	9.78%
2003	367	342	593	2004	$1.43	$1.43	$14.30	10.00%
2004	378	402	618	2005	$1.99	$1.79	$14.60	12.26%
2005	400	413	686	2006	$1.56	$1.56	$15.20	10.26%
2006	414	418	724	2007	$1.32	$1.35	$15.90	8.49%
2007	427	394	762	2008	$0.73	$1.35	$16.20	8.33%
2008	444	394	891	2009	$-0.65	$1.35	$16.10	8.39%
2009	433	355	806	2010	$-0.22	$1.35	$16.70	8.08%
2010	441	398	866	2011	$-0.33	$1.35	$17.90	7.54%
2011	460	509	946	2012	$0.28	$1.35	$18.80	7.18%
2012	490	556	980	2013	$0.81	$1.35	$20.10	6.72%
2013	507	548	994	2014	$0.75	$1.35	n/a*	n/a

Source: USDA National Agricultural Statistics Service (NASS) Quickstats; USDA NASS Agricultural Prices (January and December Surveys); GAO 2005, 83; correspondence with BLM rangeland specialist; USDA NASS 2007.

Figure 5

Annual Grazing Fees for BLM and USFS and Private Land: 1981-2013

Figure 6

PRIA Fee As a Percentage of Private Rates: 1980 - 2012
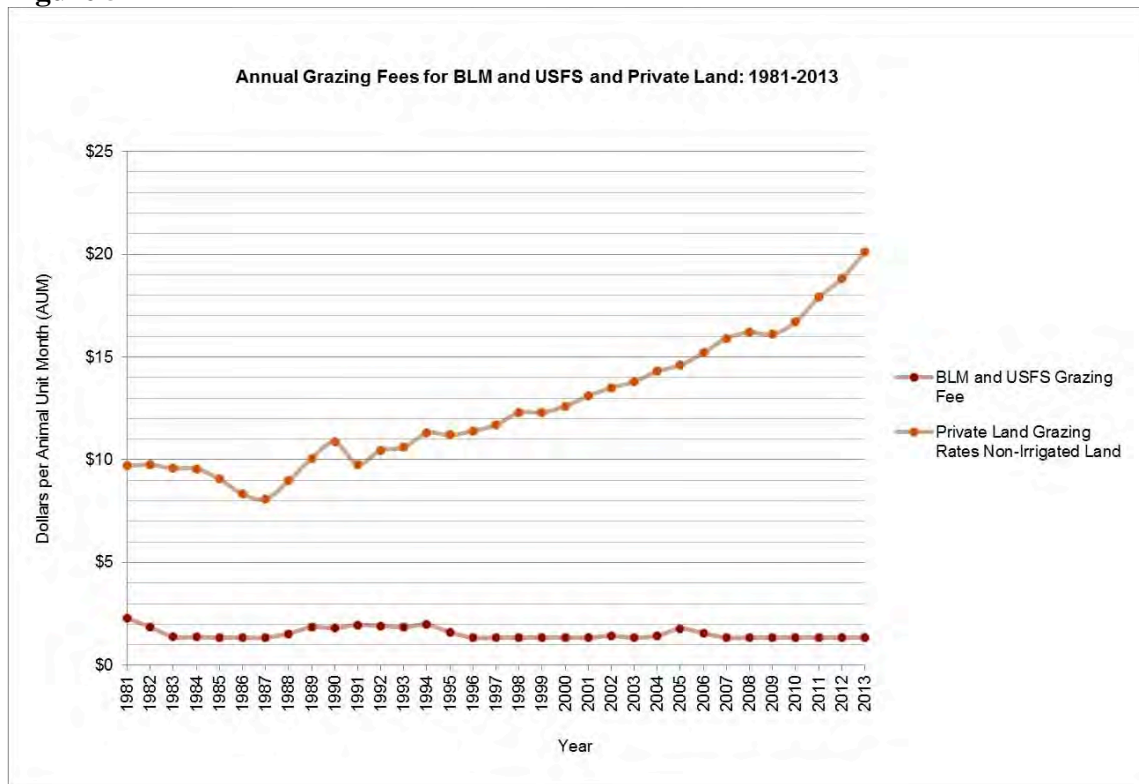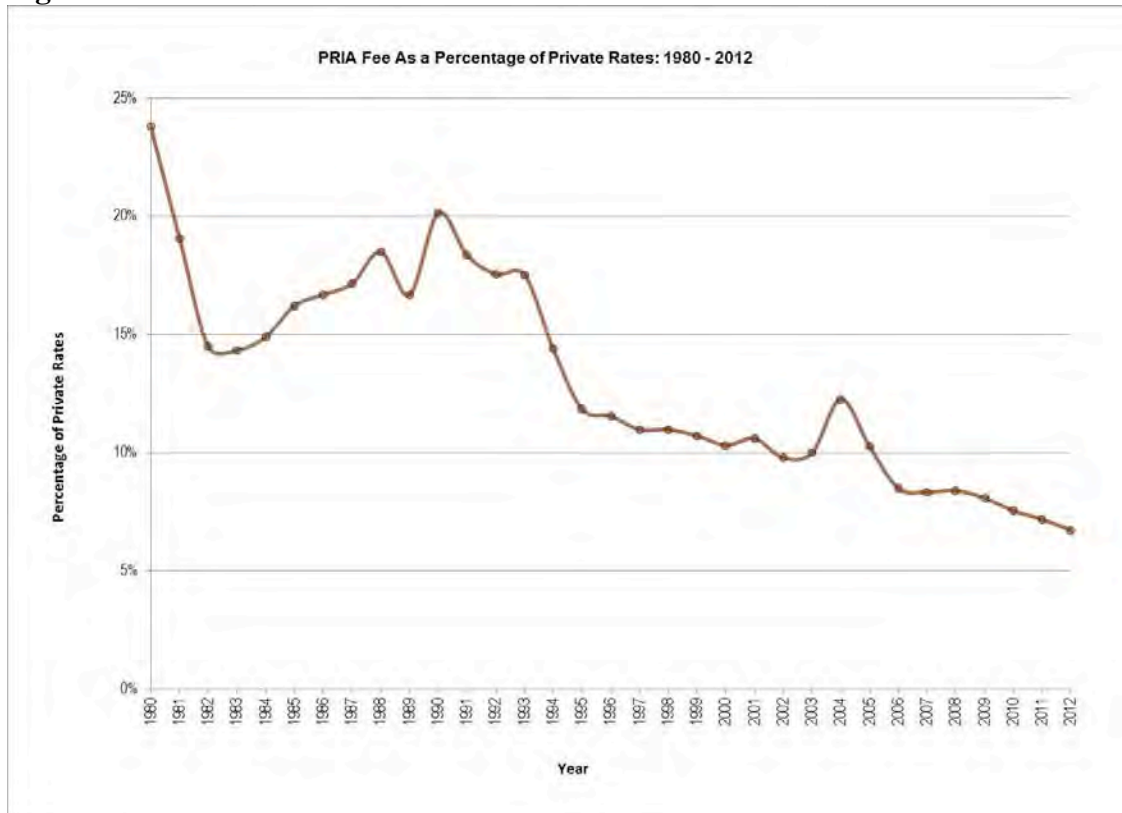
Table 11 compares PRIA fees to average private grazing fees per AUM in 16 western states for the years 2002 and 2013. The state averages for private grazing fees varied considerably among the 16 states. In 2002, rates ranged from $7.30 to $20.9. In 2013, fees varied between $9 and $33.50 per AUM.

How much private rates can vary even *within* one state is exemplified by a 2013 Colorado State University Extension survey. Rates for privately owned, non-irrigated pasture leases for Colorado averaged $16.49 per AUM, and ranged from $3.72 and $38 per AUM. [7]

**Table 11: Private Rates and PRIA Fees per AUM for Non-Irrigated Land
In 16 Western States, 2002 and 2013**

	PRIA Fee 2002	PRIA Fee 2013
	$1.35	$1.35
State	**Average Private Fee 2002**	**Average Private Fee 2013**
Arizona	$7.30	$9.00
California	$12.80	$19.50
Colorado	$12.60	$17.50
Idaho	$11.70	$15.50
Kansas	$13.00	$17.00
Montana	$15.10	$21.00
Nebraska	$20.90	$33.50
Nevada	$10.50	N/A
New Mexico	$8.80	$13.00
North Dakota	$12.50	$18.00
Oklahoma	$7.50	N/A
Oregon	$11.80	$15.00
South Dakota	$16.90	$27.90
Utah	$11.60	$14.50
Washington	$9.60	$13.50
Wyoming	$13.50	$18.70

Sources: Private rates provided by National Agricultural Statistics Quickstats

b. Fees Charged by other Federal Agencies

In 2005, the Government Accountability Office (GAO) undertook an extensive survey of grazing rates. Included in the survey were the PRIA based rates charged by BLM and USFS and the rates charged in western states by other federal agencies that are not subject to the PRIA formula. The lowest rate charged by other federal agencies in 2004 was $0.29 per AUM, charged by the U.S. Fish and Wildlife Service, the highest was $112.50 charged by the U.S. Corps of Engineers. (GAO 2005, 39)

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[7] Tranel et al. 2013,Table 7, 9.

A number of federal agencies including the National Park Service, U.S. Fish and Wildlife Service, Bureau of Reclamation, and Department of Defense set fees that reflect, or come close to, market value.

Some of the agencies, such as the Air Force and National Park Service, charge per acre; and others, such as the Corps of Engineers, receive a total bid price for an allotment. To achieve a fair market value, some agencies use a competitive bidding process that can involve notifying the public of the opportunity to permit or lease a grazing allotment, the acceptance of sealed bids, and the selection of the highest bid. Other agencies conduct a market appraisal of a grazing property, or use an average prevailing rate for the local area, and set a fee based on those values. (GAO 2005, 41-42) USFS applies market-based methods for determining fees in the eastern national forest lands. (36 CFR 222.53, 36 CFR 222.54)

Table 12: Fees Charged by Other Federal Agencies in 2004

Agency	Range of fees charged Per AUM	Average Fee Charged
DOI		
National Park Service	$1.35 to $7.00 ($1.50 to $25.00 per acre)	$4.30
Bureau of Reclamation	$1.27 to $56.46	$10.93
U.S. Fish and Wildlife Service	$0.29 to $34.44	$11.24
DOE		$1.43
DOD		
Air Force	$1.35 to $26.67	$15.49
Army	$0.99 to $66.09	$19.10
Corps	$0.82 to $112.50	$6.22
Navy	$10.42 to $97.49	$32.60
PRIA Fee 2004	**$1.43**	

Source: GAO 2005, 39.

c. Fees Charged by State Agencies

There is also considerable variation in fees charged and fee setting approaches used by state agencies that manage public grazing lands in 17 western states.[8] Table 13 shows averages and ranges of fees charged for the years 2004 and 2010. As the 2005 GAO study reports, six states (Montana, Nebraska, New Mexico, North Dakota, Oklahoma, and South Dakota) offer their leases to the highest bidder through a competitive process. Six states (Arizona, California, Colorado, Texas, Washington and Wyoming) use market-based approaches. These rely on regional market rates, land appraisals, or formulas that adjust the market price and account for differences between state and private lands and livestock market conditions. Three states (Idaho, Oregon and Utah) use formulas that apply either a base fee, adjusted for local livestock market conditions, or a fixed percentage of livestock production value." (GAO 2005, 93-94)

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[8] GAO included 17 western states, including the 16 states in which the PRIA fees apply, plus Texas.

Table 13: Grazing Fees Charged by State Land Agencies in Western States in 2004 and 2010

State	2004 State Land Agencies Fees	2010 State Land Agencies Fees
Arizona	$2.23	$2.28
California	$1.35 to $12.50	No set fee
Colorado	$6.65 to $8.91	35% less than private
Idaho	$5.15	$5.12
Kansas	*	*
Montana	$5.48 to $80.00	Minimum of $6.12
Nebraska	$16.00 to $28.00	$22.50 to $38.00
Nevada	*	*
New Mexico	$0.71 to $10.15 per acre	$3.19
North Dakota	$1.73 to $19.69 per acre	Set by auction
Oklahoma	$7.00 to $16.00	$8.34 to $20.83
Oregon	$4.32	$5.30
South Dakota	$3.00 to $56.00 per acre	$10.82
Texas	$4.16 to $12.50	$65.00 to $150.00
Utah	$1.43 or $2.35	3.92 to $7.00
Washington	$5.41 or $7.76	$8.78
Wyoming	$4.13	$4.64
PRIA Rate	**$1.43**	**$1.35**
Kansas and Nevada do not have grazing on state trust lands.		

Sources: GAO 2005, 45-46 (2004 fees); Bioeconomics 2011, 9 (2010 fees)

As part of the 2005 GAO study, state officials were interviewed and maintained that their state trust lands, received from the federal government to generate revenue for public education, are often comparable in range condition, productivity and land value to federal lands. For example, in Wyoming and Oklahoma, state lands are intermingled with or adjacent to federal lands and have similar characteristics. (GAO 2005, 93)

6. Indirect Costs Of Federal Public Lands Grazing

The direct budgeted BLM and USFS costs as shown in the body of this paper are not the only costs of the federal grazing program. They are however the clearly measurable ones.

The USFS and BLM administer many other programs and projects not budgeted under grazing or range management budget line items that nevertheless may benefit public lands livestock operators or compensate for the negative impacts of livestock grazing. The funds spent on these activities are indirect costs of the BLM and USFS grazing programs. An example of a BLM program that benefits livestock operators is the Wild Horse and Burro Management Program that removes competitors from the range; USFS has a vegetation and

watershed management program that deals, for example, with soil erosion, stream degradation and weed infestations resulting from livestock grazing. For more examples of USFS and BLM programs supporting livestock grazing or compensating for its impacts see Tables A1 and A2.

In addition, there are other federal agencies that have programs benefitting grazing or attempting to compensate for its impacts. The U.S. Fish and Wildlife Service, for example, conducts consultations with USFS and BLM regarding impacts of grazing on threatened or endangered species, and for recovery plans developed for such species. For more examples see Table A3. Examples for how potential livestock grazing impacts on the state and local level see Table A4.

Indirect costs may be divided into tangible and intangible. Tangible costs are easily expressed in monetary terms, such as federal funding for fire suppression necessitated by grazing impacts. (Table A2)

Intangible costs, such as the loss of an endangered species due to public lands grazing, damage to ecosystems, or the destruction of archeological, historical and cultural resources of the indigenous people of the West, are not readily expressed in monetary terms. [9] The costs of such damage or are often "externalized," that is, paid by communities or individuals that would otherwise benefit from the goods and services that flow from unimpaired forests, grasslands, deserts and rivers, or from the preservation of their heritage.

In this report, we do not attempt a comprehensive review of the subject or provide an estimate of the dollar value of indirect costs of the federal livestock program. A comprehensive analysis of the indirect costs of the federal grazing program is long overdue.

Conclusions

Since 2002, on average, 14.6 million AUMs have been authorized annually for grazing on USFS and BLM lands in the West. Inflation-adjusted federal appropriations for the management of the livestock grazing programs have decreased over this time period. Grazing receipts have also decreased—but at a steeper rate than the decline in appropriations. This is reflected in the percentage of receipts to appropriations, which has decreased from 18 percent in 2002 to 13 percent in 2014.

Grazing receipts have decreased mainly because the PRIA fee has decreased by 28 percent between 2002 and 2014 in inflation-adjusted dollars.

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[9] Economists have developed a variety of methods for estimating the monetary value of or damage to ecosystems, as well as other intangible costs. See the website http://www.ecosystemvaluation.org/dollar_based.htm for an overview of such approaches. One method is to use monetary costs resulting from damage to ecosystems as a proxy for estimating externalized, intangible, ecological and social costs. For example, the costs of eradicating invasive species and recreating conditions favorable for native re-vegetation can be used as an estimate of the value of these native plant communities.

There is also a growing disparity between BLM and USFS grazing fees and the rates charged for grazing on private non-irrigated land in the West. The percentage of federal fees to private rates has decreased to 6.72 percent in 2013. This decline is the continuation of a long-term decline that started right after PRIA fees were first applied by both BLM and USFS in 1981. The PRIA fee then was 23.79 percent of the private rate.

The result of this growing gap between public land fees and private rates is that livestock operators on BLM and USFS lands pay significantly less than operators on non-irrigated private rangeland, indicating a deepening of federal support for the livestock operators who have permits and leases for grazing on USFS and BLM lands.

Additionally, the PRIA fee is uniformly applied to BLM (11 western states) and USFS (16 western states) grazing leases and permits. This is a markedly different approach from fees charged by other federal agencies, and fees charged on state trust lands and private lands. Many federal agencies and state agencies use market-based fee-setting approaches that lead to considerable variations in fees within and between states, besides being generally higher than PRIA fees. Given that grazing fees are offsetting smaller and smaller portions of the appropriations, and the disparity between private rates for non-irrigated lands and the federal fee have increased considerably, the fee-setting approach for BLM and USFS lands requires a reevaluation.

Appendix A

Table A1: BLM Budget Items Potentially Containing Indirect Costs of Grazing BLM

Budget Item*	Explanation
Soil, Water, and Air Management	Livestock are the principal cause of soil erosion and stream degradation. (Jones 2000; Belsky et al, 1999)
Riparian Management	Livestock are the most pervasive cause of riparian damage. Up to 80% of Western streams have been damaged by livestock. (Belsky, et al. 1990)
Cultural Resources Management	Most harm to archeological resources is from livestock and from ranch access roads, fences, tanks and other ground disturbing range developments. (Osborn et al. 1987; Broadhead 1999)
Wild Horse and Burro Management	Removes wild competitors for forage. **
Wildlife and Fisheries Management	Considerable harm to wildlife results from the pervasive competition for forage and removal of cover by livestock (Fleischner 1994)
Threatened and Endangered Species Management	Considerable harm to threatened and endangered species results from the pervasive competition for forage and removal of cover by livestock (Fleischner 1994, Flather et al. 1994;Czech and Kraussman 1997)
Resource Management Planning	Grazing is a major element of planning. It covers a larger area than all other uses.**
Hazardous Materials Management	Herbicides are the main tool used to control weeds that are spread by livestock operations. Many noxious weeds are spread by livestock operations. (Belsky and Gelbard 2000, Reisner, 2013)
Transportation and Facilities Management	Field offices and additions are necessitated in part by the range program. Frequent monitoring and inspections related to grazing permits require transportation.**
Workforce and Organizational Support	Out of a workforce of 5994 full time equivalents (FTE), 670 worked directly for range management. (BLM Budget Justification FY 2015, VII-25,26) That amounts to 13.4% of BLM's workforce, not counting anyone working indirectly to support livestock grazing in the administration of other programs.

*Budget Categories are from BLM Bureau Highlights 2015; ** Moskowitz and Romaniello 2002, Table A-2

Table A2: USFS Budget Items Potentially Containing Indirect Costs of Grazing Program

Budget Item*	Explanation
Land Management Planning Inventory and Monitoring	Every 10-15 years land management plans must be revised, they must include suitability analysis for grazing, and an Environmental Impact Statement. Inventory and monitoring are required of forage use and range condition as part of the permitting process, as well as for Forest Plans and Biological Opinions.**
Recreation, Heritage and Wilderness	Fencing off campgrounds and archeological sites may be necessitated largely due to livestock. (Osborn et al. 1987; Broadhead 1999)
Wildlife and Fisheries Habitat Management	Grazing is often the land use most in conflict with wildlife habitat needs and necessitates fencing. (Fleischner 1994)
Vegetation & Watershed Management	Grazing is often the land use most damaging to soils and vegetation, causing widespread soil erosion and infestations of grasslands with weeds, shrubs and conifers.(Belsky and Blumenthal 1995, Reisner 2013)
Wildland Fire Management	Grazing is the principle cause of the growth of highly flammable thickets in western ponderosa pine forests, and for invasion of rangelands by pinion, juniper and other woody shrubs. Wildland fire management includes thinning of thickest and prescribed fires to reduce fuel loads. (Belsky and Blumenthal 1995)
Forest and Rangeland Research	Research stations spend some of their efforts studying the impacts of grazing on native species and ecosystems. **
*Budget Categories are from USDA 2015 Budget Overview, 2015; **Explanations based on Moskowitz and Romaniello, 2002, Appendix A-1	

Table A3: Other Federal Agencies' Indirect Costs of Grazing on Federal Lands

Federal Agency	Explanation
USDA Wildlife Services	Kills thousands of native carnivores each year to protect livestock in the West from predators. (Moskowitz and Romaniello 2002, 24)
US Fish and Wildlife Service	Expends part of its budget for listing native species impacted by grazing as threatened or endangered, for consultations with USFS and BLM over impacts of grazing on listed species, and for recovery plans for such species. (Moskowitz and Romaniello 2002, 24)
USDA's livestock assistance program	Payments to ranchers in the event of livestock loss due to natural disasters, like droughts. Moskowitz and Romaniello (2002, 25) report that on average public lands ranchers qualify for this subsidy four out of 10 years.
Department of Commerce National Marine Fisheries Service	Performs the functions of the Fish and Wildlife Service for anadromous fish like salmon that can be impacted by livestock grazing. (Moskowitz and Romaniello 2002, 25)
USDA's Natural Resources Conservation Service	Addresses watershed damage caused by livestock. (Belsky et al. 1999)
Bureau of Reclamation	Increased soil erosion from grazing (Jones 2000; Belsky et al, 1999) can lead to increased sedimentation of waterways and reservoirs, shortening the useful life of reservoirs and causing higher peak flows, which affect the design of dams. (Moskowitz and Romaniello 2002, 25)
US Army Corps of Engineers	Costs of flood control related to increased peak flows and higher erosion due to compaction of soils and removal of vegetation by livestock grazing. (Belsky et al. 1999)
Environmental Protection Agency	Monitoring and addressing grazing impacts on water quality due to erosion. (Moskowitz and Romaniello 2002, 25)
Department of Justice	Costs of defending federal land agencies in lawsuits brought by grazing industry and environmental groups. (Moskowitz and Romaniello 2002, 26)
USDA - Cooperative State Research, Education and Extension Service	Supports USFS, BLM in the management of their range resources. (GA0 2005, 27)
USDA Office of General Counsel	Provides legal advice and support to USFS in managing grazing lands and permits. (GAO 2005, 27)
United States Geological Survey	Conducts research on the effects of grazing on plant communities, including invasive species; on runoff and erosion, on select species or groups of species, and on ecosystem health including riparian areas. GAO 2005, 28)

Table A4: Indirect Costs on State and Local Level

Affected Entities	Explanation
Recreation-related industries	Recreation and the industries associated with it are negatively affected from impacts of livestock on riparian habitats, trampling of vegetation and fecal matter on the ground, waterways impacted by erosion, impacts on cultural resources, and diminished opportunities for wildlife viewing. (Moskowitz and Romaniello 2002, 29)
States and Communities	States and communities are impacted by increased grazing-related fire risks. (Belsky and Blumenthal 1995; Swetnam and Baisan 1994)
State and Local Governments	Livestock grazing assists weed invasions. (Belsky and Gelbard 2000, Reisner 2013) Weed populations on federal lands can become source populations for invasions on other lands and thus require increased weed control expenses of state and local governments. (Moskowitz and Romaniello 2002, 31)
State Historic Preservation Offices Indigenous Peoples	Studies have shown that livestock grazing can have a destructive impact on archeological and historical sites. (Osborne et. al 1987; Broadhead 1999) Cultural artifacts of indigenous people (an intangible cost) are destroyed as the result of cattle trampling, soil erosion, and range development measures such as bulldozing and plowing. The (tangible) costs of consultations over impacts of public lands grazing on archeological resources are borne at least in part by states through their State Historic Preservation Offices. (Moskowitz and Romaniello 2002, 32)
Water Utilities	Livestock borne pathogens cause illness and increase water treatment costs in the West, because of the need of monitoring and control of these pathogens by water utilities throughout the West. (Moskowitz and Romaniello 2002, 32)

Appendix B

Table B1: BLM Acres Grazed by State, 2004

	BLM Grazing Lands (acres)
Arizona	7,955,000
California	5,672,000
Colorado	6,593,000
Idaho	10,756,000
Montana	7,839,000
New Mexico	11,533,000
Nevada	39,331,000
Oregon/Washington	12,786,000
Utah	19,321,000
Wyoming	15,917,000
TOTAL	**137,703,000**

Sources: GAO 2005, 15

Table B2: USFS Acres Grazed by Region, 2004

Forest Service Regions	Acres Grazed
Eastern	75,000
Intermountain	24,107,000
Northern	8,268,000
Pacific Northwest	11,408,000
Pacific Southwest	12,353,000
Rocky Mountain	17,129,000
Southern	675,000
Southwestern	18,908,000
Total Acres of Grazed Land in All Regions	**92,924,000**
Total Acres of Grazed Land in Western Regions*	**92,173,000**
Percent of USFS Grazed Lands in the West	**99.19%**
*All regions other than Eastern and Southern.	

Source: GAO 2005, 15

Table B3: USFS Grazing Receipts and Appropriations 2002-2014 in 2014 dollars*

Fiscal Year	USFS Grazing Appropriations in 2014 dollars	USFS Total Receipts in 2014 dollars	Appropriations minus Receipts in 2014 dollars	Percentage Of USFS Receipts to Appropriations
2002	**50,040**	7,889	42,151	16%
2003	**55,998**	6,169	49,829	11%
2004	**59,012**	7,010	52,003	12%
2005	**59,950**	8,397	51,553	14%
2006	**58,831**	7,620	51,211	13%
2007	**56,877**	6,514	50,363	11%
2008	**55,480**	6,247	49,233	11%
2009	**57,126**	6,148	50,978	11%
2010	**56,190**	6,005	50,184	11%
2011	**53,751**	5,974	47,777	11%
2012	**59,248**	5,689	53,559	10%
2013	**54,245**	5,027	49,217	9%
2014	**58,356**	5,300	53,056	9%

Table B4: BLM Grazing Receipts and Appropriations 2002-2014, in 2014 Dollars

Fiscal Year	BLM Appropriations in 2014 dollars	BLM Receipts in 2014 dollars	BLM Appropriations minus Receipts in 2014 Dollars	Percent Receipts to Appropriations
2002	105,948	19,733	86,215	19%
2003	104,771	15,985	88,786	15%
2004	101,369	8,191	93,178	8%
2005	93,989	11,787	82,203	13%
2006	92,214	20,321	71,892	22%
2007	87,794	18,006	69,789	21%
2008	90,830	17,538	73,292	19%
2009	88,213	19,284	68,929	22%
2010	88,751	16,189	72,562	18%
2011	89,343	15,624	73,720	17%
2012	99,616	15,352	84,265	15%
2013	85,982	14,585	71,397	17%
2014	85,280	13,217	72,063	15%

*Table B4 is derived from Tables 5 and 7

Table B5: Scenario of USFS and BLM Grazing Revenues with Application of Private Grazing Rates

Year	Private Grazing Rates (in 2014 dollars)	BLM and USFS AUMs (grazing season)	Grazing Revenue ($)
2002	$17.75	14,072,254	249,782,509
2003	$17.58	12,979,398	228,177,817
2004	$17.58	12,656,540	222,501,973
2005	$17.33	15,087,629	261,468,611
2006	$17.55	14,233,541	249,798,645
2007	$17.84	14,397,692	256,854,825
2008	$17.72	15,212,795	269,570,727
2009	17.49	15,282,060	267,283,229
2010	$17.60	15,819,413	278,421,669
2001	$18.40	15,796,906	290,663,070
2012	$19.23	15,500,099	298,066,904
Averages	***$17.82***	***14,639,848***	***261,144,544***

Table B6: PRIA Fees and Private Fees 1981 to 2014 (Nominal and Adjusted for Inflation)

Year	PRIA Fee	PRIA FEE in 2014	Private Rates	Private Fee in 2014 dollars
1966	$1.23	$7.43	$3.65	$18.39
1981	2.31	$5.43	$9.71	$22.84
1982	1.86	$4.12	$9.75	$21.61
1983	1.39	$2.99	$9.59	$20.65
1984	1.37	$2.86	$9.56	$19.93
1985	1.35	$2.72	$9.06	$18.28
1986	1.35	$2.68	$8.33	$16.55
1987	1.35	$2.67	$8.09	$15.97
1988	1.54	$2.93	$8.98	$17.11
1989	1.86	$3.44	$10.06	$18.60
1990	1.81	$3.26	$10.86	$19.55
1991	1.97	$3.39	$9.78	$16.80
1992	1.92	$3.24	$10.46	$17.66
1993	1.86	$3.03	$10.60	$17.28
1994	1.98	$3.13	$11.30	$17.89
1995	1.61	$2.46	$11.20	$17.12
1996	1.35	$2.03	$11.40	$17.14
1997	1.35	$1.99	$11.70	$17.28
1998	1.35	$1.97	$12.30	$17.94
1999	1.35	$1.92	$12.30	$17.52
2000	1.35	$1.86	$12.60	$17.37
2001	1.35	$1.83	$13.10	$17.74
2002	1.43	$1.88	$13.50	$17.75
2003	1.35	$1.72	$13.80	$17.58
2004	1.43	$1.76	$14.30	$17.58
2005	1.79	$2.12	$14.60	$17.33
2006	1.56	$1.80	$15.20	$17.55
2007	1.35	$1.51	$15.90	$17.84
2008	1.35	$1.48	$16.20	$17.72
2009	1.35	$1.47	$16.10	$17.49
2010	1.35	$1.42	$16.70	$17.60
2011	1.35	$1.39	$17.90	$18.40
2012	1.35	$1.38	$18.80	$19.23
2013	1.35	$1.36	$20.10	$20.23
2014	1.35	$1.35	n/a	n/a

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Why do wolves eat livestock?
Factors influencing wolf diet in northern Italy

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ABSTRACT

Thanks to protection by law and increasing habitat restoration, wolves (*Canis lupus*) are currently re-colonizing Europe from the surviving populations of Russia, the Balkan countries, Spain and Italy, raising the need to update conservation strategies. A major conservation issue is to restore connections and gene flow among fragmented populations, thus contrasting the deleterious consequences of isolation. Wolves in Italy are expanding from the Apennines towards the Alps, crossing the Ligurian Mountains (northern Italy) and establishing connections with the Dinaric populations. Wolf expansion is threatened by poaching and incidental killings, mainly due to livestock depredations and conflicts with shepherds, which could limit the establishment of stable populations. Aiming to find out the factors affecting the use of livestock by wolves, in this study we determined the composition of wolf diet in Liguria. We examined 1457 scats collected from 2008 to 2013. Individual scats were geno-typed using a non-invasive genetic procedure, and their content was determined using microscopical analyses. Wolves in Liguria consumed mainly wild ungulates (64.4%; in particular wild boar *Sus scrofa* and roe deer *Capreolus capreolus*) and, to a lesser extent, livestock (26.3%; in particular goats *Capra hircus*). We modeled the consumption of livestock using environmental features, wild ungulate community diversity, husbandry characteristics and wolf social organization (stable packs or dispersing individuals). Wolf diet varied according to years and seasons with an overall decrease of livestock and an increase of wild ungulate consumption, but also between packs and dispersing individuals with greater livestock consumption for the latter. The presence of stable packs, instead of dispersing wolves, the adoption of prevention measures on pastures, roe deer abundance, and the percentage of deciduous woods, reduced predation on livestock. Thus, we suggest promoting wild ungulate expansion, the use of prevention tools in pastures, and supporting wolf pack establishment, avoiding lethal control and poaching, to mitigate conflicts between wolf conservation and husbandry.

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1. Introduction

The wolf (*Canis lupus*), because of its adaptability to different environments and its ability to re-colonize territories when no persecution occurs, has in just a few decades expanded its range in Europe (Balciauskas, 2008; Breitenmoser, 1998; Chapron et al., 2003, 2014). The Russian wolf population is the largest in Europe, supporting those of Baltic and North-European countries, and it is contiguous with the populations of Eastern Europe from which wolves began the re-colonization of Central Europe (Ansorge et al., 2006; Linnell et al., 2005). The Spanish wolf *Canis lupus signatus* (2200–2300 individuals) is slowly extending its distribution (Mech and Boitani, 2003).

Wolves greatly declined in Italy, surviving in two small isolated sub-populations confined to the southern and central part of the Apennines. At their nadir in the early seventies of the last century, wolves in Italy numbered about 100 individuals (Zimen and Boitani, 1975). Since the late eighties, wolves have shown a spontaneous rapid recovery, re-colonizing all the Apennines and reaching the western Italian and French Alps (Boitani, 2000; Breitenmoser, 1998; Fabbri et al., 2007; Marucco and McIntire, 2010; Valière et al., 2003).

The re-colonization of the Alps would be a fundamental step for wolf conservation in Italy and Central Europe as well (Genovesi, 2002). Moreover, the early and ongoing wolf expansion from the eastern

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Alps will predictably increase chances to originate mixed packs and increase the local genetic diversity as has been already described (Fabbri et al., 2014; Randi, 2011).

The sub-population of wolves inhabiting the Liguria region thus plays a crucial role in assuring the linkage between the wolves of central Italy and those of the Western Alps (Fabbri et al., 2007). If this link should break, the wolf population of the Western Alps would be isolated, perhaps failing to recolonize the remaining part of the Alps.

The distribution of wolves is usually determined by the abundance of its preys, environmental characteristics, and the risk associated with the presence of humans (Eggermann et al., 2011; Jędrzejewski et al., 2004; Massolo and Meriggi, 1998). This last point is the key problem of wolf conservation because wolves can have a dramatic impact on livestock breeding, affecting human attitudes that can lead to illegal killing, increasing the risk of extinction (Behdarvand et al., 2014; Kovařík et al., 2014).

The impact of wolves on livestock is different according to geographical region. In regions with a very low abundance of wild ungulates, as in Portugal and Greece, wolves feed mainly on livestock (Migli et al., 2005; Papageorgiou et al., 1994; Vos, 2000). On the other hand, in Germany attacks on livestock are rare because shepherds equip the pastures with electric fences to protect their herds and because the wild ungulate availability is high (Ansorge et al., 2006).

In other new-recolonizing areas such as France or North Italy, wild ungulates are the main prey of wolves, but the use of livestock is still noticeable (MEEDDAT–MAP, 2008; Meriggi et al., 2011; Milanesi et al., 2012).

Systematic research on wolf feeding ecology has been carried out since 1987 in the Ligurian Apennines. These studies showed an increasing use of wild ungulates in the time but also a medium–high use of livestock species as prey (Meriggi et al., 1991, 1996, 2011; Schenone et al., 2004). Consequently, wolf presence in Liguria, as well as in other areas of natural re-colonization, causes a conflict with human populations that perceive predator presence as a negative element that can compromise a poor rural economy. Thus, wolves suffer a high mortality mainly due to illegal killing and accidents. This situation makes the population vulnerable and actions aimed at a greater protection of the species are required.

Usually wolf populations are structured in stable packs and lone wolves; packs are formed by a pair of adults, by their offspring and other related individuals (i.e. the offspring of previous years), and sometime by adopted individuals, whereas lone wolves are erratic individuals that can temporarily establish in an area without packs. In general lone wolves are young dispersing from packs but they can also be adults moving far from their original pack because of pack disruption or break off for several causes (killing by humans, low prey availability and related increasing aggressiveness, natural death of the dominant pair) (Mech and Boitani, 2003). Packs are established in areas with high prey availability, because only a high availability of preferred prey can dampen the aggressiveness of the pack members and avoid pack disruption (Thurber and Peterson, 1993). Dispersing and erratic individuals use the areas without wolf packs that can be considered suboptimal habitats because of the low prey availability, high human disturbance, and possibly potential problems with local people (Fritts and Mech, 1981). Illegal killing can break the packs, increasing erratic wolves and reproductive pairs that can have a greater impact in particular on livestock rearing (Wielgus and Peebles, 2014).

The objective of the present study was to determine which factors influence wolf diet, in particular, the choice of livestock as prey, which is the first step to find solutions for wolf conservation. With this aim, we determined wolf diet, by analyses of scats collected in the whole Liguria region from 2008 to 2013. We highlighted the factors influencing it, i.e. years, seasons, ungulate abundance, and social structure of wolves (packs or dispersing individuals). Then we related livestock consumption to environmental features, wild ungulate abundance and

diversity, husbandry characteristics, wolf grouping and habitat occupancy behavior (stable packs or dispersing individuals).

2. Material and methods

2.1. Study area

This research was carried out in the Liguria region, north Italy (44°30′16″, 8°24′10″). The study area spreads over 5343 km² including a part of the Northern Apennines and of the Western Italian Alps, until the border with France. The region is divided in four provinces, Imperia, Savona, Genoa and La Spezia, respectively from the western to the eastern part (Fig. 1). Altitude ranges from 0 to 2153 m a.s.l.; 36% of the area is between 0 and 400 m a.s.l., 35% between 400 and 800 m, 21% between 800 and 1200 m, and 8.5% more than 1200 m a.s.l. Forests cover 63.8% of the region (deciduous woods: 28.8%; conifer woods: 7.1%; mixed woods: 27.9%), pastures 6.2%, agricultural areas 17.1%, and urbanized areas 3.9%. Towns and villages, as well as farmlands, are concentrated on flat terrains, close to the coasts. The climate extends from Mediterranean on the coast to sub-oceanic in the mountains. The temperature extends from −2 °C in winter to 35 °C during summer. Mean annual precipitation ranges from 750 to 1250 mm in the west to 1350–1850 in the central and eastern part of the region. On the ridge of the mountains and in the upper part of the valleys, snow cover can reach more than one meter from November to April.

The wild ungulate community includes wild boar (*Sus scrofa*), widely distributed with high densities (21,500 individuals shot per year in Liguria, on average from 2007 to 2012), roe deer (*Capreolus capreolus*), abundant in particular in the central provinces (30.9 individuals per km² on average from 2009 to 2012). Fallow deer (*Dama dama*), introduced for hunting, is present in the provinces of Genoa and Savona (10.7 and 5.8 individuals per km² respectively). Chamois (*Rupicapra rupicapra*) is present only in the Maritime Alps (927 individuals counted on average from 2007 to 2012), while red deer (*Cervus elaphus*) and mouflon (*Ovis aries musimon*) are very rare in the study area (data from Wildlife Services of Imperia, Savona, Genoa and La Spezia).

This high availability of wild prey promoted a natural re-colonization of the region by wolves in the late eighties, starting from the provinces of Genoa and La Spezia (Meriggi et al., 1991, 1996, 2011; Schenone et al., 2004). Now the wolf is present in the four provinces with a minimum population of 58 individuals of which 21 distributed in 5 packs and 37 lone wolves, estimated by genetic analyses (see Results).

Livestock (15,000 cows and 33,900 sheep and goats) are free-grazing on pastures from April to October but the grazing period can be expanded or reduced depending on the weather. Pastures are often partly composed of shrubs and woodlots. Only few shepherds adopt prevention methods (i.e. nocturnal recovery, guardian dogs, and electric fences) to deter wolf attacks.

2.2. Data collection

We divided the study area in 64 isometric cells of 10 × 10 km, as a trade-off between the average territory size of the wolf in Italy (Ciucci et al., 1997; Corsi et al., 1999; Apollonio et al., 2004; Caniglia et al., 2014) and sampling feasibility. In each cell, we randomly chose an itinerary among the existing footpaths according to the Tessellation Stratified Sampling (TSS) method that permits a better distribution and representativeness of the random samples than a simple random design (Barabesi and Fattorini, 2013; Barabesi and Franceschi, 2011). We traced a total of 64 itineraries in the study area (total length = 287.6 km, mean ± SD = 4.5 ± 1.59 km, min. = 2.3, max. = 10.4) that were covered once a season (spring: March to May; summer: June to August; autumn: September to November; winter: December to February), from January 2008 to August 2013 searching for wolf scats and signs of wild ungulate presence (tracks, sightings, rooting,

Fig. 1. Provinces of Liguria region and wolf pack territories.

rubbing, wallowing, resting sites, feeding and territorial marks). We identified wolf scats by the size, texture, shape, and their characteristic odor. All signs of presence were mapped and georeferred by a Garmin GPS.

We assessed wild ungulate abundance at transect level by computing an Index of Kilometric Abundance (IKA) for each species (number of found signs divided by the transect length, Meriggi et al., 1991, 1996, 2015; Milanesi et al., 2012). We estimated the abundance of livestock (cattle, sheep, goats, and horses) on pastures and defined the husbandry practices by direct interviews with shepherds and by the official data of Veterinary services of the four provinces.

Around each transect we defined a buffer zone corresponding to the potential hunting area of wolves. We used a width of 13 km, corresponding to the average travel distance of wolves during the night to go from dens or resting sites to hunting sites in Italy (Ciucci et al., 1997).

In each buffer, we measured from the Corine Land Cover III level and the Digital Elevation Models (DEM) 12 environmental variables concerning the land use, altitude, aspect, and slope using Arc GIS 9.0 software (Appendix A). Moreover, in each buffer we defined the husbandry variables: number of livestock heads, reared species, presence or absence of prevention methods, number of used pastures, average time past on pastures and the presence of the production "Cow-Calf line" consisting in cows giving birth alone, in the pasture and involving a great risk of predation by wolves on newborn calves (Dondina et al., 2014; Meriggi et al., 1991, 1996).

We also collected all claimed and verified cases of predation upon livestock during the study period, recording the preyed species and the exact location of the events.

2.3. Genetic analyses

From 2007 to 2013 we collected a total of 403 presumed wolf biological samples for genetic analyses. The genetic samples included 6 tissue and blood samples obtained from wolves found dead in the study area, 5 of urine, 2 hairs and 389 fresh scats containing cells of intestine epithelium. Small external portions of scats and clean tissue fragments were individually stored at −20 °C in 10 vials of 95% ethanol. Blood samples were stored at −20 °C in 2 vials of a Tris–sodium dodecyl sulfate buffer. DNA was automatically extracted using a MULTIPROBE IIEX Robotic Liquid Handling System (Perkin Elmer, Weiterstadt, Germany) and QIAGEN QIAmp DNA stool or DNeasy tissue extraction kits (Qiagen Inc., Hilden, Germany).

We identified individual genotypes for samples at 12 unlinked autosomal canine microsatellites (short tandem repeats [STR]): 7 dinucleotides (CPH2, CPH4, CPH5, CPH8, CPH12, C09.250, and C20.253) and 5 tetranucleotides (FH2004, FH2079, FH2088, FH2096, and FH2137), selected for their high polymorphism and reliable scorability for wolves and dogs (Caniglia et al., 2014).

We determined sex of samples using a polymerase chain reaction (PCR)–restriction fragment length polymorphism assay of diagnostic ZFX/ZFY gene sequences (Caniglia et al., 2012, 2013, 2014). We used a first panel of 6 STR to identify the genotypes with Hardy–Weinberg probability-of-identity (PID) among unrelated individuals, PID = 8.2×10^6, and expected full-siblings, $PID_{sibs} = 7.3 \times 10^3$ (Mills et al., 2000; Waits et al., 2001) in the reference Italian wolves. We then used another panel of 6 STR, also selected for their polymorphism and reliable scorability, to increase the power of admixture and kinship analyses, decreasing the PID values to PID = 7.7×10^9 and $PID_{sibs} = 3.1 \times 10^4$ (Caniglia et al., 2014). We identified maternal haplotypes by sequencing 350 base pairs of the mitochondrial DNA (mtDNA) control region, diagnostic for the haplotype W14, which is unique to the Italian wolf population, using primers L-Pro and H350 (Randi et al., 2000; Caniglia et al., 2014). We identified paternal haplotypes by typing 4 Y-linked microsatellites (Y-STR), MS34A, MS34B, MSY41A, and MS41B (Sundqvist et al., 2001), characterized by distinct allele frequencies in

dogs and wolves (Iacolina et al., 2010). We amplified autosomal and Y-linked STR loci in 7 multiplexed primer mixes using the QIAGEN Multiplex PCR Kit (Qiagen Inc.), a GeneAmp PCR System 9700 Thermal Cycler (Applied Biosystems, Foster City, California), and the following thermal profile: 94 °C for 15 min, 94 °C for 30 s, 57 °C for 90 s, 72 °C for 60 s (40 cycles for scat, urine, and hair samples, and 35 cycles for muscle and blood samples), followed by a final extension step of 72 °C for 10 min. We carried out amplifications in 10-μl volumes including 2 μl of DNA extraction solutions from scat, urine, and hair samples, 1 μl from muscle or blood samples (corresponding to approximately 20–40 ng of DNA), 5 μl of QIAGEN Multiplex PCR Kit, 1 μl of QIAGEN Q solution (Qiagen Inc.), 0.4 μM deoxynucleotide triphosphates, from 0.1 to 0.4 μl of 10 μM primer mix (forward and reverse), and RNase-free water up to the final volume. We amplified the mtDNA control region in a 10-μl PCR, including 1 or 2 μl of DNA solution, 0.3 pmol of the primers L-Pro and H350, using the following thermal profile: 94 °C for 2 min, 94 °C for 15 s, 55 °C for 15 s, 72 °C for 30 s (40 cycles), followed by a final extension of 72 °C for 5 min. PCR products were purified using exonuclease/shrimp alkaline phosphatase (Exo-Sap; Amersham, Freiburg, Germany) and sequenced in both directions using the Applied Biosystems Big Dye Terminator kit (Applied Biosystems, Foster City, California) with the following steps: 96 °C for 10 s, 55 °C for 5 s, and 60 °C for 4 min of final extension (25 cycles).

DNA from scat, urine, and hair samples was extracted, amplified, and genotyped in separate chambers reserved for low-template DNA samples, under sterile ultraviolet laminar flow hoods, following a multiple-tube protocol (Caniglia et al., 2012, 2013), including both negative and positive controls. We obtained genotypes from scat, urine, and hair samples replicating the analyses from 4 to 8 times, and from blood and muscle DNA replicating the analyses twice. DNA sequences and microsatellites were analyzed in a 3130XL ABI automated sequencer (Applied Biosystems), using the ABI software SEQSCAPE 2.5 for sequences, GENEMAPPER 4.0 for microsatellites (Applied Biosystems) (Caniglia et al., 2014) and GIMLET to control the good attribution of several samples to the same individual.

We assigned individual genotypes to their population of origin (wolves or dogs) using the Bayesian software STRUCTURE 2.3 (Falush et al., 2003). According to previous studies (Caniglia et al., 2014), the optimal number of populations was set at K = 2, the value that maximized the posterior probability of the data. At K = 2, we assessed the average proportion of membership (qi) of the sampled populations to the inferred clusters. Then we assigned genotypes to the Italian wolf or dog clusters at threshold $qi = 95$ (individual proportion of membership; Randi, 2008), or identified them as admixed if their qi values were intermediate.

We identified familiar relationships i.e. packs, using a maximum-likelihood approach (Caniglia et al., 2014) implemented in the software COLONY 2.0 (Wang and Santure, 2009). We selected all the genotypes that were sampled in restricted ranges (<100 km²) at least 4 times and for periods longer than 24 months. We determined their spatial distributions by 95% kernel analysis, choosing band width using the least-squares cross-validation method (Kernohan et al., 2001; Seaman et al., 1999), using the ADEHABITATHR package for R (Calenge, 2006) and mapped them using ARCGIS 10.0. According to spatial overlaps, we split individuals into distinct groups that might correspond to packs, for which we performed parentage analyses. We considered as candidate parents of each group all the individuals sampled in the 1st year of sampling and more than 4 times in the same area and as candidate offspring all the individuals collected within the 95% kernel spatial distribution of each pack and in a surrounding buffer area of approximately 17-km radius from the kernel (see Caniglia et al., 2014). We ran COLONY with allele frequencies and PCR error rates as estimated from all the genotypes, assuming a 0.5 probability of including fathers and mothers in the candidate parental pairs.

2.4. Diet analysis

All the scats found on itineraries were preserved in PVC bags at −20 °C for 1 month, and then washed in water over two sieves with decreasing meshes (0.5–0.1 mm). We identified prey species from undigested remains: hair, bone, hoof, and claw (medium and large-sized mammals), hair and mandible (small mammals), seeds and leaves (fruits and plants). Moreover, hairs were washed in alcohol and observed with an optical microscope (Leica DM750) to identify the species from the characteristics of cortical scales, medulla, and root (Brunner and Coman, 1974; Debrot et al., 1982; De Marinis and Asprea, 2006; Teerink, 1991). We estimated the proportion of prey for each scat as they were eaten (Kruuk and Parish, 1981; Meriggi et al., 1991, 1996, 2015; Milanesi et al., 2012) and each prey species was assigned to a percent volumetric class: <1%; 1–5%; 6–25%; 26–50%; 51–75%; 76–95%; >95% that was converted in a final percent volume: 0.5%; 2.5%; 15.5%; 38%; 63%; 85.6% and 98% respectively. Prey species were grouped in six food categories (wild ungulates, livestock, small mammals, medium-sized mammals, fruits, grasses). We calculated the mean percent volume (MV%) and the percent frequency of occurrence (FO%) for each food category and species of wild and domestic ungulates. We determined the diet composition for two main seasons (grazing season: from April to October when livestock is on the pastures, and non-grazing season: from November to March), for each year of study, and for each itinerary (pooling the study years), for each pack, for pooled packs and for dispersing individuals.

2.5. Data analysis

We adapted the index provided by Massolo and Meriggi (1998) as a measure of the diversity of wild ungulate community; we used the IKA as a measure of abundance and 5 identical classes for all wild ungulate species. We divided the range of the IKA values for all species pooled to determine the class intervals for each season because the probability of detecting a track depends on the weather, mainly the presence of snow, mud, or leaves:

$$DI = \frac{\Sigma A_i * N}{\Sigma A_{i\,max} * K}$$

where A_i is the class of abundance of ith species, A_{imax} the class of maximum abundance of the ith species, N the number of species present for a transect, and K the maximum number of species. The index was calculated for each transect.

We defined pack territories by Kernel Analyses at 95% on GPS coordinates of genetic samples of wolves with parental ties. Scats within territories were considered to belong to the relative pack, and those outside the territories were assumed to belong to dispersing individuals. The scats localized on the overlap of two territories were not included in the analysis, because their origin was not identifiable with certainty.

To estimate the minimum number of scats necessary to assess the diet of wolves we used the Brillouin index (1956) (Hass, 2009; Milanesi et al., 2012; Meriggi et al., 2015):

$$H_b = \frac{\ln N! - \Sigma \ln n_i!}{N}$$

where H_b is the diversity of prey in the sample, N is the total number of single prey taxa in all samples, and n_i is the number of single prey taxa of the ith category. For each sample, a value of H_b was calculated and then re-sampled 1000 times by the bootstrap method to obtain the average values and 95% confidence intervals. We determined the adequacy of sample size by whether an asymptote was reached in the diversity curve and in the curve obtained from the incremental change in each H_b with the addition of two more samples.

We evaluated the significance of the differences in the diet between years and seasons by two-way non-parametric multivariate analysis of variance (NPMANOVA), and between packs and dispersing individuals by one-way NPMANOVA with permutation (10,000 replicates), using the Bonferroni correction of the p-value for pair-wise comparisons (Anderson, 2000, 2001). Annual, seasonal and pack-dispersing wolf variations of mean percent volumes of all categories and all ungulate species were verified by Kruskall–Wallis test with permutation (10,000 replicates).

Moreover we compared the observed and expected use of livestock species for each pack and for dispersing wolves by the Chi-square goodness-of-fit (Exact test) and Bonferroni's confidence interval analyses, testing the null hypothesis (H_0) of a use proportional to the availability (Manly et al., 2002). In this analysis we considered predation cases as use; in particular we calculated the expected frequencies from the availability of livestock (number of heads) in each pack territory and outside pack areas.

To identify the main factors affecting livestock consumption by wolves we carried out Multiple Regression Analyses (MRA) of MV% of domestic ungulates recorded for each transect vs. the variables measured in the buffers around the transects; only transects (N = 34) with at least 10 scats which corresponds, according to the Brillouin diversity index, to an incremental change of 5% for grazing season and 3% for non-grazing one, were included in the analyses. We identified all the possible subsets of uncorrelated (P > 0.05) predictor variables by calculating the correlation matrix (Pearson product moment coefficient) among habitat variables. For each subset, we performed MRA between MV% of livestock and transect variables. We obtained a number of models that were ranked by the information theoretic approach (Akaike, 1973). We computed the corrected value of Akaike information criterion (AICc) because the ratio sample/parameters was small (Burnham and Anderson, 2002), selecting the model with the lowest AICc as the best model and ranking the following ones by their differences from the lowest AICc (Δ_i). For the following analysis, we considered only models with $\Delta_i \leq 2$ (Best and Rayner, 2007; Burnham and Anderson, 2002). Furthermore, we measured the relative importance of models by their Akaike weights (w_i; Anderson et al., 2000, 2001). We followed the AIC statistical approach because it allows the comparison of all the models, as many as the uncorrelated subsets, and the selection of the ones that best explain the effect of transect variables on livestock consumption. Moreover, the AIC tool allowed us to conduct an explanatory analysis taking into account all possible predictor combinations. For each model, we calculated the Variance Inflation Factor (VIF) in order to detect collinearity among predictor variables (Zuur et al., 2010). To validate the final model, we tested for deviation from normality of the residual distribution by the Shapiro–Wilk normality test, for homoscedasticity by the Breush–Pagan test (Breusch and Pagan, 1979), and for residual autocorrelation by the Durbin–Watson test (Pires and Rodrigues, 2007).

3. Results

3.1. Genetic analysis

Genetic identifications of the 403 samples yield 205 (50.8%) reliable multilocus genotypes, corresponding to 58 wolves (31 males M and 27 females F), 5 dogs (4 M, 1 F), 9 wolf × dog hybrid individuals (8 M, 1 F). Wolf individuals were sampled from a minimum of 1 to a maximum of 10 times. The hybrids were sampled from 1 to 3 times while the 5 dogs once each.

Parentage analyses led to the assigning of 20–21 wolves to five distinct packs (Fig. 1, Table 1), respectively named: Imperia pack, Savona pack (on the border between Savona and Imperia), Beigua pack (in the Mount Beigua Regional Park, on the border between Savona and Genoa), Antola pack (in the Mount Antola Regional Park, in the province of Genoa) and Spezia pack. The minimum estimated territory sizes were

Table 1
Composition of the five packs detected in Liguria region by genetic analyses from 2008 to 2013.

Pack	Males	Females	Offspring of alpha pair	Adopted	Immigrants	Migration distance
Imperia	1	3	2	0	0	–
Savona	2–3	2	1–2	1	0	–
Beigua	3	2	1	2	2	97 and 75 km
Antola	3	2	1	2	1	122
Spezia	2	1	1	0	0	–

533 km² for Imperia pack, 779 km² for Savona pack, 144 km² for Antola pack, 83 km² for Beigua pack, and 101 km² for La Spezia pack. The remaining 37 wolves apparently were not related to any pack and were considered as floating or dispersing individuals (Caniglia et al., 2014). Thirteen dispersing wolves were resampled from one to nine times showing an average distance from the first to the last sampling of 19.9 km (SE = 5.19) with a maximum distance of 60.4 km.

3.2. Wolf diet

We analyzed a total of 1457 scats (year 1: 128; year 2: 276; year 3: 242; year 4: 350; year 5: 318; year 6:143) of which 863 were attributed to grazing season and 593 to the non-grazing one. Sample size was sufficient for each year and season according to the Brillouin index (minimum sample sizes: pooled years: 23 scats; year 1: 16; year 2: 19; year 3: 23; year 4: 19; year 5: 15; year 6: 15; grazing season: 17; non-grazing season: 19).

In view of the low proportion of scats attributed to dogs by genetic analyses (16 out of 389 fresh scats; 3.97%) we considered that errors did not influence the results. By scat analyses we detected 21 kinds of prey, pooled into eight categories (Table 2). Pooling the study years and the provinces, wild ungulates were the main food of wolves, followed by domestic ungulates. Other food categories showed a mean percent volume less than 3 for small mammals, medium sized mammals and grasses, and less than 1% for invertebrates, fruits, and garbage (Fig. 2). Among wild ungulates, the most consumed were wild boar and roe deer; the others species were less used (Fig. 3A). Among livestock species, wolves chiefly consumed goats, followed by cattle (mainly calves) and sheep; horse consumption was negligible (Fig. 3B).

3.3. Temporal variations of wolf diet

Two-way NPMANOVA showed significant changes in wolf diet according to years (F = 13.31; P < 0.0001) but not according to seasons (F = 1.51; P = 0.153), and a significant interaction between the two factors (F = 43.56; P < 0.0001). Significant differences resulted for all pairwise comparisons with exception of year 1 versus years 2, 3, 4, and 6, between years 2 and 3, and between years 5 and 6 (Table 2).

Livestock consumption increased significantly until year 3 and then decreased. Wild ungulates increased in the diet from the first to the last study year. Small mammals showed significant variation between years with a peak in the second one and the same was for the medium-sized mammals. Also for fruits, grasses, and garbage significant but moderate annual variations resulted (Table 2). The frequencies of occurrence of livestock and wild ungulates were negatively correlated (Spearman rank correlation: $r_s = -0.886$; n = 6; P = 0.019) and those of medium-sized and small mammals positively ($r_s = 0.941$; n = 6; P = 0.005).

Among livestock species, sheep consumption significantly decreased in the study period, while goat and cattle increased until the third year and then decreased (Table 2). Goats strongly contributed to the overall livestock consumption ($r_s = 0.943$; n = 6; P = 0.005). Concerning wild ungulate species, wild boar increased in the wolf diet until the fifth study year and then decreased, roe deer increased during the study

Table 2
Yearly variations of mean percent volume (MV%) and frequency of occurrence (FO%) of categories and prey species in wolf diet (Liguria region, N-Italy, 2008–2013).

Categories and species	Year 1		Year 2		Year 3		Year 4		Year 5		Year 6	
	n = 128		n = 276		n = 242		n = 350		n = 318		n = 143	
	MV%	FO%	MV%	FO%	MV%	FO%	MV%	FO%	MV%	FO%	MV%	FO%
Livestock	26.7	32.0	32.1	35.9	40.2	47.5	27.9	34.3	14.9	18.6	19.5	21.0
Ovisaries	5.5	19.5	4.4	13.1	4.6	15.7	3.1	12.5	2.3	13.6	0.1	3.3
Capra hircus	16.0	61.0	22.9	72.7	24.0	57.4	15.4	55.8	7.3	49.2	11.0	53.3
Bos taurus	5.3	19.5	4.4	13.1	11.7	27.0	9.1	30.8	5.3	37.3	8.4	43.3
Equus caballus	0.0	0.0	0.4	1.0	0.0	0.0	0.3	0.8	0.0	0.0	0.0	0.0
Wild ungulates	60.1	71.1	48.5	55.1	51.5	56.7	66.8	72.6	79.4	83.6	76.6	79.7
Sus scrofa	36.0	61.5	29.3	61.2	23.9	50.4	41.8	63.4	45.2	59.0	25.0	36.0
Capreolus capreolus	14.3	25.3	13.3	28.3	20.3	42.3	13.7	23.2	31.5	44.0	42.2	57.0
Cervus elaphus	4.0	7.7	1.8	3.3	4.5	8.0	5.2	7.9	0.2	0.4	0.6	0.9
Dama dama	5.9	11.0	3.8	12.5	2.9	5.1	4.4	7.5	1.2	1.5	8.1	11.4
Ovis aries musimons	0.0	0.0	0.4	0.7	0.0	0.0	0.3	0.4	0.0	0.0	0.0	0.0
Rupicapra rupicapra	0.0	0.0	0.0	0.0	0.0	0.0	1.4	2.0	1.4	1.9	0.7	0.9
Medium-sized mammals	4.4	7.0	8.0	12.7	4.4	5.4	4.0	0.9	0.6	0.9	0.7	1.4
Small mammals	2.1	2.3	5.9	7.6	1.9	5.0	0.4	0.9	0.5	0.9	1.4	1.4
Invertebrates	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Fruits	0.1	0.8	1.5	7.6	0.8	1.7	0.9	1.1	0.9	1.6	0.0	0.0
Grasses	4.9	17.2	3.5	19.6	1.1	5.4	1.9	7.1	2.5	4.1	0.0	0.0
Garbage	0.0	0.0	0.0	0.0	0.0	0.0	0.1	1.1	0.0	0.0	0.0	0.0

NPMANOVA pairwise comparisons between years: 1–5 P = 0.003; 2–4 P = 0.002; 2–5 P = 0.002; 2–6 P = 0.002; 3–4 P = 0.005; 3–5 P = 0.002; 3–6 P = 0.002; 4–5 P = 0.005.
Livestock: H = 60.26; df = 5; P < 0.0001; wild ungulates: H = 108.55; df = 5; P < 0.0001; small mammals: H = 34.77; df = 5; P < 0.0001.
Medium-sized mammals: H = 68.66; df = 5, P < 0.0001; fruits: H = 40.07; df = 5, P < 0.0001; grasses: H = 77.07; df = 5, P < 0.0001.
Garbage: H = 12.67; df = 5; P = 0.027.
Ovis aries: H = 13.71; df = 5; P = 0.018; *Capra hircus*: H = 46.36; df = 5; P < 0.0001; *Bos taurus*: H = 14.63; df = 5; P < 0.012.
Sus scrofa: H = 49.56; df = 5; P < 0.0001; *Capreolus capreolus*: H = 90.20; df = 5; P < 0.0001; *Cervus elaphus*: H = 24.59; df = 5; P < 0.0001.
Dama dama: H = 20.95; df = 5; P = 0.001.

period, while red and fallow deer showed significant annual variations but without an evident trend (Table 2).

For livestock species we did not find significant seasonal changes, whereas among wild ungulate species significant differences resulted for wild boar (H = 34.37; df = 1; P < 0.0001) and for roe deer (H = 25.50; df = 1; P < 0.0001); in particular wild boar was more consumed in non-grazing season and, on the contrary, roe deer was more used in the grazing one (Table 3).

3.4. Variations in wolf diet between packs and dispersing wolves

Considering the five packs separately, we found overall significant differences in the use of food categories (NPMANOVA: F = 9.85; P = 0.0001); in particular the diet of Spezia pack was different from all the others. Moreover, we found significant differences comparing the diet of Beigua pack with those of Imperia and Antola. La Spezia pack consumed more livestock and medium-sized mammals and less wild ungulates and grasses than all the other packs (Table 4).

Among livestock species, we detected significant differences for goats and cattle, the first species being more used by Spezia pack, and the second by Imperia and Spezia ones. Also the use of wild ungulate
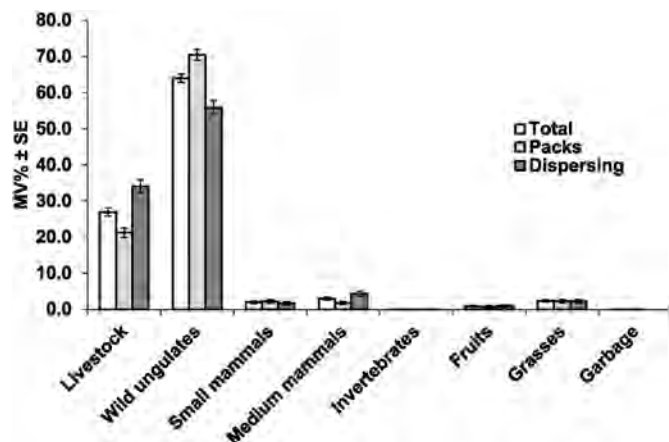
Fig. 2. Mean percent volume ± SE of prey categories in wolf diet in Liguria from 2008 to 2013.
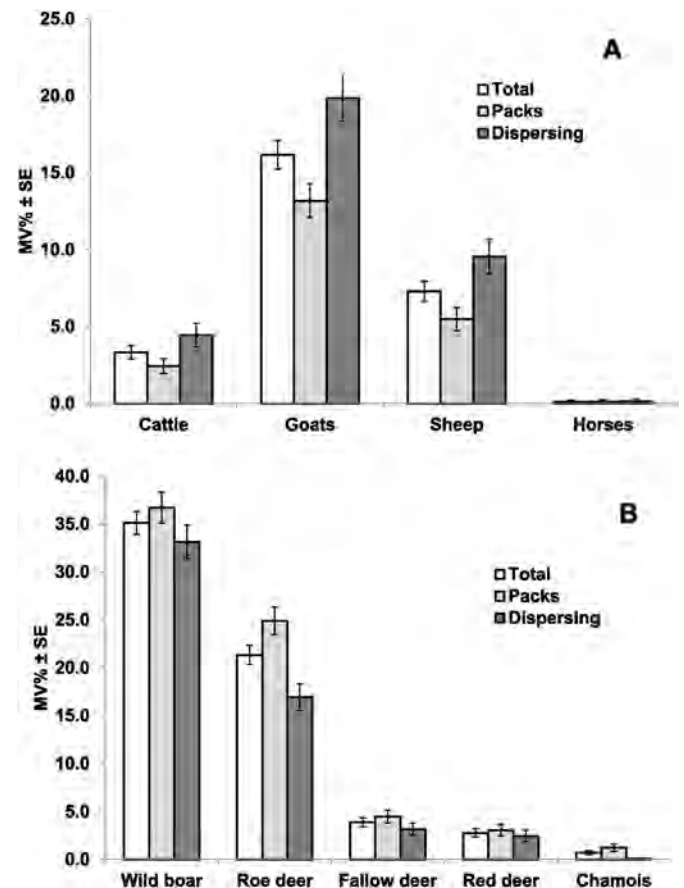
Fig. 3. Mean percent volume ± SE of livestock (A) and wild ungulate species (B) in wolf diet (Liguria region 2008–2013).

Table 3

Seasonal variations of mean percent volume (MV%) and frequency of occurrence (FO%) of categories and prey species in wolf diet (Liguria region, N-Italy, 2008–2013).

Categories and species	Grazing season		Non-grazing season	
	n = 863		n = 593	
	MV%	FO%	MV%	FO%
Livestock	28.1	32.0	25.1	29.2
Ovisaries	2.9	11.2	3.9	18.5
Capra hircus	17.1	62.7	14.8	59.0
Bos taurus	8.1	28.6	6.2	25.4
Equus caballus	0.1	0.4	0.2	0.6
Wild ungulates	62.7	68.7	65.9	71.0
Sus scrofa	29.2	48.9	43.7	68.2
Capreolus capreolus	25.5	43.5	15.6	25.4
Cervus elaphus	3.3	5.4	2.0	3.1
Dama dama	4.2	7.8	3.4	6.2
Ovis aries musimons	0.0	0.0	0.3	0.5
Rupicapra rupicapra	0.5	0.8	1.0	1.4
Medium-sized mammals	3.1	4.8	2.7	4.0
Small mammals	2.2	3.4	1.6	2.5
Invertebrates	0.0	0.2	0.0	0.0
Fruits	0.6	1.9	1.1	3.2
Grasses	1.9	7.1	2.9	11.1
Garbage	0.02	0.2	0.01	0.3

species resulted different between packs; in particular wild boar were consumed mainly by Imperia and Beigua packs, roe deer by Savona and Beigua packs, red deer by Savona pack, fallow deer by Savona and Antola packs, and chamois by Imperia pack (Table 4).

Comparing the diets of individuals belonging to a pack and the dispersing ones, we found overall significant differences in the use of prey categories (NPMANOVA: F = 32.24; P < 0.0001). In particular, a higher consumption of livestock (H = 29.44; df = 1; P < 0.0001) and medium-sized mammals (H = 10.98; df = 1; P = 0.001) resulted for dispersing wolves, whereas the contrary was the case for wild ungulate use, higher in pack diet than in that of dispersing individuals (H = 40.01; df = 1; P < 0.0001) (Fig. 2). Significant differences resulted also considering livestock and wild ungulate species. In particular goats

and cattle were more consumed by dispersing individuals (H = 9.17; df = 1; P = 0.002 and H = 7.65; df = 1; P = 0.006 respectively) but packs consumed more roe deer (H = 15.33; df = 1; P = 0.0001) and chamois (H = 5.67; df = 1; P = 0.017) (Fig. 3A and B). The diet of dispersing wolves differed significantly from that of each pack (P ≤ 0.003 for all pairwise comparisons), with the exception of Spezia pack (P = 0.623).

3.5. Livestock use versus availability

The livestock density was greater in pack territories than in the remaining part of the study area with the exception of Antola and Savona packs (Table 5). During the study period we recorded a total of 176 predations on livestock 15 of which upon cattle and 161 upon sheep and goats. Considering predation cases on livestock species we found significant differences between observed and expected frequencies of events across packs and dispersing wolves for cattle ($\chi^2 = 4167.78$; df = 5; P < 0.0001), sheep and goats ($\chi^2 = 4107.74$; df = 5; P < 0.0001), and for the species pooled ($\chi^2 = 187.83$; df = 5; P < 0.0001). In particular cattle was preyed in proportion to the availability by Antola and Savona packs, avoided by Beigua, Imperia and Spezia packs, and used more than the availability by dispersing wolves. Sheep and goats were used as available by Antola and Spezia packs, underused by Beigua, Imperia, and Savona packs, and overused by dispersing wolves. Pooled species were used in proportion to the availability by Antola pack, less than the availability by the other packs, and more than the availability by dispersing wolves (Table 6). Considering the packs pooled the frequency of predation events was significantly less than expected for sheep and goats ($\chi^2 = 97.73$; df = 1; P < 0.0001), and for the species pooled ($\chi^2 = 103.64$; df = 1; P < 0.0001) but for cattle ($\chi^2 = 4.29$; df = 1; P = 0.066); pooled packs underused cattle, sheep and goats, and the pooled species (Table 6).

3.6. Model of livestock consumption

By the Multiple Linear Regression Analyses on the subsets of uncorrelated predictors, we obtained only one model, the others having

Table 4

Mean percent volume (MV%) and frequency of occurrence (FO%) of categories and prey species in the diet of wolf packs (Liguria region, N-Italy, 2008–2013).

Categories and species	Imperia pack		Savona pack		Beigua pack		Antola pack		La Spezia pack	
	n = 297		n = 102		n = 213		n = 137		n = 64	
	MV%	FO%	MV%	FO%	MV%	FO%	MV%	FO%	MV%	FO%
Livestock	24.2	27.9	17.6	20.6	13.1	14.6	18.2	27.0	46.0	50.0
Ovis aries	2.6	14.5	1.9	9.5	2.9	22.6	1.7	16.2	2.9	6.3
Capra hircus	11.7	53.0	13.1	76.2	8.2	64.5	12.9	70.3	37.2	81.3
Bos taurus	9.7	42.2	2.6	14.3	2.0	19.4	3.6	16.2	5.9	12.5
Equus caballus	0.3	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Wild ungulates	69.7	73.1	75.0	83.3	81.3	84.5	64.6	78.1	44.4	50.0
Sus scrofa	45.3	66.4	19.2	27.1	38.7	51.7	30.0	47.7	31.6	75.0
Capreolus capreolus	19.8	29.5	35.1	48.2	35.2	48.9	19.3	33.6	11.3	25.0
Cervus elaphus	1.6	2.3	9.8	12.9	3.6	4.4	1.9	2.8	0.0	0.0
Dama dama	0.0	0.0	10.0	11.8	3.8	5.6	13.4	24.3	0.0	0.0
Ovis aries musimons	0.3	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rupicapra rupicapra	2.6	3.7	1.0	1.2	0.0	0.0	0.0	0.0	1.5	0.0
Medium-sized mammals	1.0	1.0	0.4	1.0	1.0	1.4	3.1	8.0	7.7	7.8
Small mammals	2.2	3.0	3.3	0.0	0.9	0.9	4.3	5.1	0.0	7.8
Invertebrates	0.002	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fruits	0.1	0.3	1.4	3.9	0.0	0.0	2.9	8.0	0.2	1.6
Grasses	0.4	5.4	2.4	4.9	1.9	7.0	7.9	19.7	0.3	4.7
Garbage	0.02	0.7	0.2	2.0	0.0	0.0	0.0	0.0	0.0	0.0

NPMANOVA pairwise comparisons between packs: Imperia–Beigua P = 0.008; Imperia–La Spezia P = 0.001; Savona La Spezia P = 0.001; Beigua–Antola P = 0.01; Beigua–La Spezia P = 0.001; Antola–La Spezia P = 0.001.

Livestock: H = 36.31; df = 4; P < 0.0001; wild ungulates: H = 45.59; df = 4; P < 0.0001; medium-sized mammals: H = 24.97; df = 4; P < 0.0001.

Fruits: H = 34.10; df = 4; P < 0.0001; grasses: H = 31.59; df = 4; P < 0.0001.

Capra hircus: H = 38.08; df = 4; P < 0.0001; *Bos taurus*: H = 20.54; df = 4; P < 0.0001.

Sus scrofa: H = 27.26; df = 4; P < 0.0001; *Capreolus capreolus*: H = 34.92; df = 4; P < 0.0001; *Cervus elaphus*: H = 24.17; df = 4; P < 0.0001.

Dama dama: H = 69.57; df = 4; P < 0.0001; *Rupicapra rupicapra*: H = 9.53; df = 4; P = 0.049.

Table 5
Percentage of pastures and density (heads per km²) of livestock species in pack territories and in non-pack area.

Pack	Pastures (%)	Cattle	Sheep and goats	Total
Antola	7.6	1.4	0.1	1.5
Beigua	4.7	1.9	3.3	5.2
Imperia	8.5	3.7	14.1	17.8
Savona	1.8	0.5	0.5	1.0
Spezia	8.6	7.5	2.5	10.0
Pooled packs	4.7	2.1	5.1	7.3
No pack	2.6	0.8	1.7	2.5

Table 7
Results of multiple regression analysis of mean percent volume of domestic ungulates in the wolf diet vs. the transect variables (N = 34).

Transect variables	Regression coefficients (SE)	Standardized coefficients	t	P	VIF
Intercept	57.2 (6.16)		9.29	<0.0001	
Pack presence	−31.4 (3.28)	−0.85	9.59	<0.0001	1.3
Pasture number	0.9 (0.15)	0.56	6.45	<0.0001	1.2
Prevention (%)	−37.5 (7.08)	−0.45	5.29	<0.0001	1.1
Roe deer abundance (IKA)	−15.7 (3.92)	−0.36	3.99	0.001	1.3
Deciduous woods (%)	−0.4 (0.12)	−0.29	3.48	0.002	1.1
Wild Ungulate Diversity Index	9.8 (4.27)	0.21	2.29	0.031	1.4

$R^2 = 0.807$. SEE = 7.68. F = 22.59. df = 6,25. P < 0.0001.

ΔAICc > 2 (Table 7). Six variables with significant regression coefficients entered the model explaining 80.7% of the variance of the mean percent volume of livestock in the wolf diet. The presence of packs, prevention methods, deciduous woods and roe deer abundance had a negative effect on livestock consumption, whereas the number of pastures in the areas covered by transects and the diversity of wild ungulate community had a positive effect (Fig. 4). The presence of a pack (by opposition to dispersing wolves) had the strongest influence followed by the number of pastures, the percentage of pastures with prevention methods, roe deer abundance, percentage of deciduous forest, and finally wild ungulate diversity index (Table 7). The Variance Inflation Factor revealed no collinearity among predictors, and the residuals of the model were normally distributed (Shapiro–Wilk test = 0.98, P = 0.736), not auto-correlated (Durbin–Watson statistic = 2.30) and the homoscedasticity was respected (Breush–Pagan statistic = 6.32; df = 6; P = 0.389). Examining the relationships between predictors, transects with wolf packs were characterized by a greater presence of pastures, percentage of deciduous woods, and roe deer abundance in respect to those with dispersing wolves, whereas the percentage of livestock farms with prevention methods and the wild ungulate diversity index were lower (Fig. 5). However these differences were not significant (Mann–Whitney U test, P > 0.05 in all cases).

4. Discussion

The diet of wolves in the Liguria region is characterized by a medium–high occurrence of wild ungulates and by an important part consisting of large domestic prey, the other food categories being a negligible fraction of the diet. This picture places the food habits of wolves in our study area between those of populations preying almost exclusively on wild herbivores and those of wolves living mainly at the expense of livestock and other food of human origin, that can be found in human altered landscapes of some South and East European countries such as Portugal, Spain, South-central Italy, Greece, Bulgaria, Ukraine, Moldova, and Azerbaijzan (Meriggi and Lovari, 1996; Meriggi

Table 6
Results of Bonferroni simultaneous confidence interval analyses for the differences between expected (EUP) and observed usage proportion (OUP) of livestock species across packs and dispersing wolves.

Pack	Cattle (n = 15)		Sheep and goats (n = 161)		Pooled species (n = 176)	
	EUP	OUP	EUP	OUP	EUP	OUP
Antola	0.030	0.133	0.001	0.012	0.010	0.023
Beigua	0.024	0.000[a]	0.019	0.000[a]	0.020	0.000[a]
Imperia	0.302	0.000[a]	0.511	0.019[a]	0.447	0.017[a]
Savona	0.060	0.067	0.026	0.000[a]	0.037	0.006[a]
Spezia	0.116	0.000[a]	0.017	0.012	0.048	0.011[a]
Pooled packs	0.532	0.200[a]	0.575	0.043[a]	0.562	0.057[a]
No pack	0.468	0.800[a]	0.425	0.957[a]	0.438	0.943[a]

[a] Differences at minimum level of α = 0.05.

et al., 2011; Migli et al., 2005; Papageorgiou et al., 1994; Peterson and Ciucci, 2003; Vos, 2000; Zlatanova et al., 2014). Usually the former are found in areas where there are rich and abundant wild ungulate guilds and where livestock is inaccessible because of the husbandry methods, and the latter where wild ungulates are rare and livestock is free ranging and unguarded (Cuesta et al., 1991; Meriggi and Lovari, 1996; Okarma, 1995; Peterson and Ciucci, 2003; Zlatanova et al., 2014). Considering Europe as a whole, the importance of wild ungulates in the wolf diet seems to follow a cline decreasing from North to South and an increasing trend in particular after the eighties in the last century (Meriggi and Lovari, 1996; Meriggi et al., 2011; Okarma, 1995; Zlatanova et al., 2014). Wolves in the Liguria region use fewer wild ungulates and more livestock than those of other close areas located in the northern Apennines (Capitani et al., 2004; Mattioli et al., 1995, 2004, 2011; Meriggi et al., 1996, 2011, 2015; Milanesi et al., 2012). These differences can be related to the characteristics of wild prey community in Liguria where there are two widespread species locally very abundant (wild boar and roe deer), other two localized but with high density populations (fallow deer and chamois) and the last two (red deer and mouflon) are at present rare. Moreover few livestock farms adopt prevention methods, leaving herds, in particular goat flocks, free ranging and unguarded on pastures during the grazing season.

This situation could also cause the annual variations of the use of wild ungulates and livestock; both being probably related to the fluctuations in abundance of the main wild prey species (wild boar and roe deer) because of the quite constant number of livestock heads reared in the Liguria region. The close negative relationships between the importance of the two main food categories in the wolf diet over the study period demonstrates that livestock is more used when wild herbivores are less available (Meriggi and Lovari, 1996; Meriggi et al., 2011). In any case, wild herbivores showed an increase in the wolf diet during the study period in accordance with the general trend already found in Europe and in particular in Italy, and in agreement with the ability of wolves to respond in a short time to the changes in abundance of the preferred prey species (Meriggi and Lovari, 1996; Meriggi et al., 2011, 2015; Peterson and Ciucci, 2003).

Wolves in Liguria consumed mainly wild boar, the main wild prey in the Mediterranean range of the wolf (Meriggi and Lovari, 1996; Meriggi et al., 2011; Okarma, 1995; Zlatanova et al., 2014). This choice could be due to the high wild boar abundance, and to the fact that the species lives in large groups easily detectable by a predator. Furthermore, births occur all year round, causing the removal from the matriarchal groups of sub-adults; these individuals are profitable prey because they have the body size of an adult without its experience so that the handling time can be minimized (Meriggi et al., 1996, 2011, 2015; Milanesi et al., 2012).

The second wild ungulate in order of importance was the roe deer; roe deer has solitary behavior so its detectability and its encounter rate are low compared to the wild boar, with the exception of the areas where the species is present with high density (Meriggi et al.,

Fig. 4. Relationships between mean volume (%) of livestock in wolf diet and the transect variables entered in the regression model.

2011, 2015; Milanesi et al., 2012). Among the other wild ungulate species only fallow deer reached a limited importance in the last study year; this species, together with the chamois, is locally abundant but

the latter is more difficult to prey upon because of the low accessibility of the habitats (Meriggi and Lovari, 1996; Patalano and Lovari, 1993; Poulle et al., 1997). Red deer and mouflon are used only occasionally
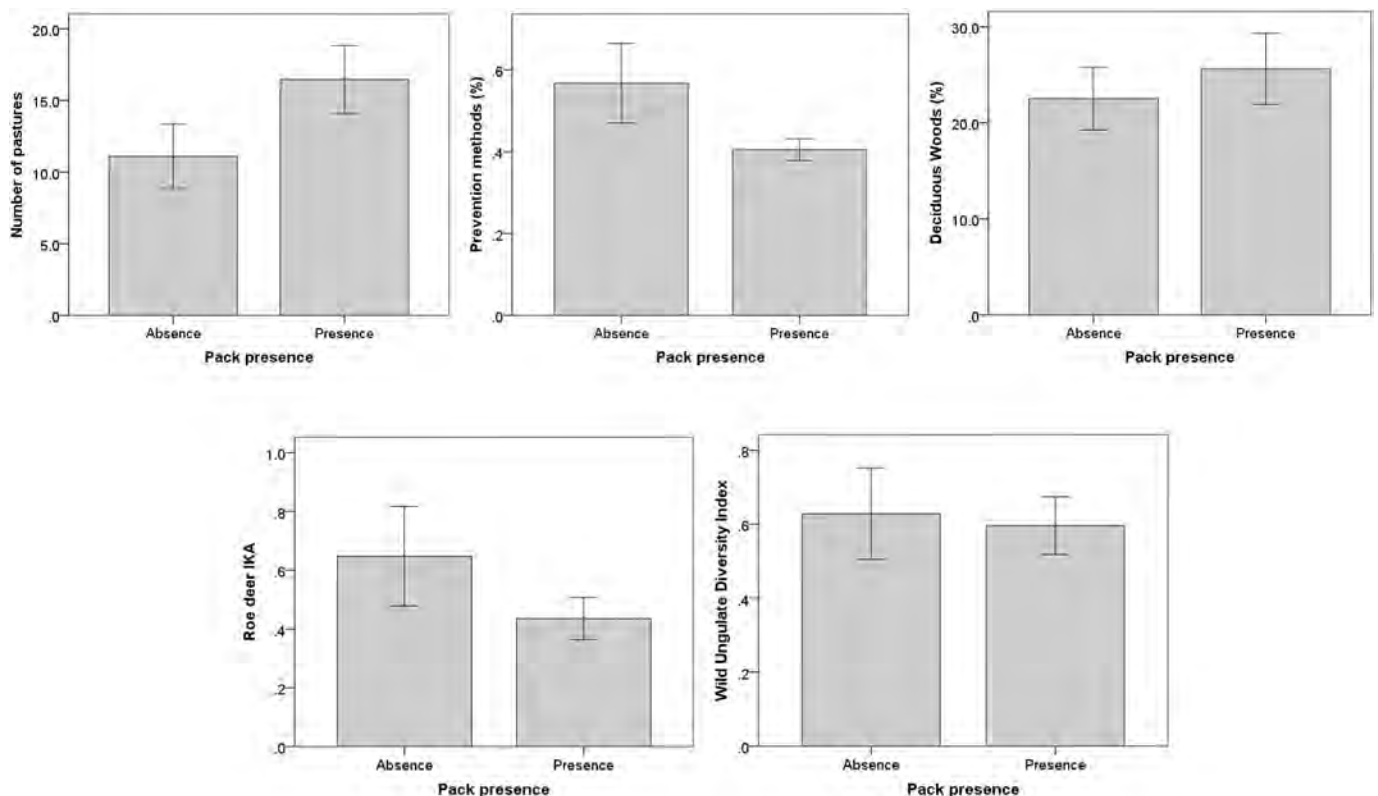
Fig. 5. Average values (±SE) of transect variables entered the model of livestock consumption in relation to the pack presence.

because of their rarity. Despite the annual variations of the wild ungulate species in the wolf diet, only for roe deer did we find a trend with an increase of three times the importance from the first to the last study year. This is in accordance with the general increase of the Italian population of roe deer in the last decades (Carnevali et al., 2009).

The importance of livestock species in the wolf diet in Liguria region was not in agreement with their respective abundance; indeed, the main prey species were goats and cattle that are respectively the third and the second in number. Goats are particularly vulnerable to wolf predation because they are left unguarded and free ranging on mountains; moreover goats lost in the mountain can survive, forming groups of feral animals, available all year round for wolves, and these groups of feral goats are increasing in number and size in Liguria. As far as cattle are concerned, wolves prey almost exclusively upon calves born during the grazing period on pastures, whereas adult cows are rarely attacked; so only cattle farms that adopt calf births on pastures are vulnerable (Brangi et al., 1992; Meriggi et al., 1991, 1996).

Surprisingly, we did not find significant changes of the food categories from grazing to non-grazing seasons, with the exception of fruits that were more eaten in the grazing one. As for wild ungulates, wolves used wild boar in winter and roe deer in summer; in summer, roe deer are more vulnerable because of the presence of young, and in winter, several wild boars are injured and not retrieved by hunters during drive hunts and consequently are easily found and caught by wolves. Moreover snow depth makes wild boars more vulnerable to predation (Okarma, 1995). As for livestock, we found that wolves eat it, particularly goats, also in winter, although in this season they should be in the sheepfolds. This pattern was also found by Patalano and Lovari (1993) in the Abruzzo National Park (central Italy). Two reasons can be proposed: firstly, the scat analysis does not permit the making of distinctions between consumption of preyed animals and of carcasses, thus wolves can feed on carcasses of lost animals during winter that have been well conserved by snow; also shepherds sometime leave their livestock on pastures for a part of winter, exposing it to wolf attacks during the cold season.

The highlighted differences of the diets between packs seem to be partially related to the local variation of wild ungulate species, and consequently to the composition of the wild ungulate community. In particular, the packs located in the provinces with the highest density of roe deer (Savona and the western part of Genoa, respectively 38.6 and 46.7 individuals per km^2) consumed more roe deer than the other packs; moreover, fallow deer and chamois occurred almost exclusively in the diet of packs living in the areas where these species are present or abundant. Moreover, Spezia pack has a diet with a high percentage of livestock compared to the other packs. In this case, pack adaptation to feeding on livestock could be the result of the scarcity of wild prey (Meriggi and Lovari, 1996; Meriggi et al., 2011; Vos, 2000). However packs do not hunt only according to prey abundance, but accessibility, vulnerability and profitability of prey as well as composition of ungulate community, wolf foraging behavior, previous hunting experience, cultural transmission, and learning from parents can heavily affect food choice and predator diet (Curio, 1976; Endler, 1991; Huggard, 1993; Meriggi et al., 1996).

We also found that the packs consume more wild ungulates than the dispersing wolves, and dispersing individuals showed a greater use of livestock than packs. Dispersing wolves are mainly young individuals and their hunting success is usually lower than that of older ones; because of this they could direct predation on livestock that, because of domestication, have less effective defenses against predators than wild large prey (Meriggi and Lovari, 1996; Meriggi et al., 1996). Moreover, dispersing wolves can cover great distances in a short time and therefore do not have the time to learn the wild prey distribution (Linnell et al., 1999); as a consequence dispersing individuals can attack livestock herds that have a greater detectability because of their highly clumped distribution and their small movement. This finding is confirmed by the use vs. availability analyses that showed

selection for livestock species by dispersing wolves whereas packs underuse or use as availability both cattle or sheep and goats or the species pooled.

The model of livestock consumption explained a high percentage of the variance and it was therefore very informative. The presence of packs, unlike the case of dispersing individuals, had a negative effect on livestock consumption. This is in accord with the lower use of livestock species that we found in the pack diet compared to that of dispersing wolves; structured packs hunt on their territory and know where to find wild prey, whereas dispersing individuals, new to the area, do not know it and hunt the first potential prey they encounter. The number of pastures had a positive effect on consumption of livestock because if the pastures are fragmented and scattered in the forests, the contact zone between woods and pastures increases and this can enhance the predation risk facilitating the attacks by wolves (Dondina et al., 2014; Kaartinen et al., 2009; van Lière et al., 2013). Prevention methods negatively affected the livestock consumption; the effect of the adoption of different methods (nocturnal shelter, presence of shepherds and dogs, electric fences) of herd and flock protection in reducing predator attacks and their success was demonstrated by several studies even if in some cases they fail or are impossible to adopt (Dondina et al., 2014; Espuno et al., 2004; Landry et al., 1999; Mech and Boitani, 2003; Miller, 2015). Roe deer abundance also decreased the use of livestock; the presence of roe deer corresponds to the presence of a second potential prey species for wolves, the first one being wild boar that is present in the whole region at high density. In this situation, if the abundance of one of the two species drops, wolves can compensate with the other one to satisfy their food requirements and thus neglect livestock. In particular, wild boar populations are subject to substantial fluctuations related to the occurrence of mast seeding years and the presence of a secondary prey at medium–high density can stabilize the overall availability of prey species (Bieber and Ruf, 2005). This is in accord with Meriggi and Lovari (1996) and with Meriggi et al. (2011) which suggest the increase of the diversity of wild ungulate community as a measure to mitigate the conflicts with husbandry. The extent of deciduous woods decreased livestock consumption, probably in relation to the great density of wild ungulates (wild boar and deer) that can be find in this kind of vegetation (Focardi et al., 2009; Fonseca, 2008); in fact, usually the presence of large wild herbivores decreases predation on livestock by wolves (Meriggi and Lovari, 1996; Meriggi et al., 1996, 2011). Surprisingly, the diversity of wild ungulate community had a positive effect on livestock use, a rich and abundant community of wild ungulates reducing the consumption of livestock elsewhere (Meriggi et al., 1996; Meriggi and Lovari, 1996). In our case the wild ungulate diversity index was positively related to the presence of chamois; this species is very localized and abundant only in the Imperia province where the roe deer density and wild boar abundance are lower than in other parts of Ligurian region. If wolves have the choice between chamois and easier prey, e.g. livestock, they will prefer the latter.

5. Conclusion

In Liguria, as in many countries of southern Europe, conflicts between wolf conservation and husbandry are far from being solved and they are an important threat to wolf conservation, as the high number of wolves found illegally killed demonstrates (12 individuals out of 16 confirmed dead between 2007 and 2014 in the whole region). Poaching by shooting and poisoning is the main mortality factor of wolves in the region and in Italy, and can be related to the damage to livestock farms (Lovari et al., 2007). Consequently it is important for wolf conservation to adopt management options that can effectively protect Ligurian wolves, to maintain a connection between sub-populations of Alps and Apennines, avoiding the isolation of Alpine wolves, and to permit the linkup between Italian and Balkan populations.

The main results of our study useful to improving wolf conservation and planning effective management actions aimed at conflict mitigation are as follows: i) the relationship between livestock and wild ungulate consumption, ii) the differences in livestock and wild ungulate use between packs, iii) the differences in diet between packs and dispersing wolves, and iv) the model of livestock consumption showing that the main factors negatively affecting predation upon livestock species are the presence of packs, the adoption of prevention methods, and roe deer abundance.

In order to limit the damage that wolves cause on husbandry, conservation measures should be primarily aimed at restoring a rich and abundant wild ungulate community. This goal can be achieved by a better regulation of wild boar and roe deer hunting and by more effective harvest plans in order to maintain stable the population of the former, and to increase the density of the latter, in particular in those areas where it is at low density. Moreover, reintroductions of red deer should be carried out to increase its presence in the region.

Another important step for conflict mitigation is to encourage the presence of wolf packs that at present are limited in number in respect to the availability of suitable areas in the region (Meriggi et al., 2013, unpublished report). If all available and suitable areas were occupied by packs the presence of erratic wolves would be reduced because of the intolerance of packs members towards foreign individuals (Mech, 1970; Mech and Boitani, 2003), and livestock depredation lowered. To enhance the pack numbers in Liguria the main action is poaching repression; illegal kills can cause pack break up and social disruption with an increase of dispersal and the formation of new breeding pairs in other areas, the ultimate effect of this being a low effectiveness of wild prey use and a consequent increase of livestock depredation (Haber, 1996; Sand et al., 2006; Wielgus and Peebles, 2014).

Prevention methods are important in reducing livestock consumption but they are not applicable everywhere, in particular on very large pastures and because of the increased costs of breeding.

On the basis of our results numeric control seems to be questionable. In a pack, removal of one of the two alpha members can lead to its break up and the other individuals leave the territory (Mech and Boitani, 2003). Consequently, livestock attacks can decrease drastically, the wolves not being any longer present in the area. However, it is a brief effect because empty suitable areas are rapidly recolonized by dispersing individuals, who have a bigger consumption of livestock than packs; these dispersing individuals should quickly change into residents and form a pack but this process requires several years during which livestock depredation increases. So removal measures do not solve the problem in the long run but conversely they can amplify it also putting at risk the wolf population because of the direct and indirect effects of harvest on recruitment (Ausband et al., 2015; Wielgus and Peebles, 2014). Use of prevention tools, promotion of a rich wild ungulate community and avoiding numerical control and poaching must be used together to mitigate conflicts between wolf conservation and husbandry. They have to be combined with good monitoring of wolf populations, so that which stage of colonization wolves are at can be known.

Acknowledgments

Appendix A. Environmental variables measured in the 13-km buffers around the transects and used to model livestock consumption

Environmental variables	Unit
Mixed woods	%
Deciduous woods	%
Coniferous woods	%
Scrublands	%
Pastures	%
Rocky areas	%
Water (streams and lakes)	%
Urban areas	%
Altitude	Meters a.s.l.
Slope	Degree
Annual insolation	kW/m^2

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Dead or alive? Comparing costs and benefits of lethal and non-lethal human–wildlife conflict mitigation on livestock farms

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Abstract Livestock depredation has implications for conservation and agronomy; it can be costly for farmers and can prompt retaliatory killing of carnivores. Lethal control measures are readily available and are reportedly perceived to be cheaper, more practical and more effective than non-lethal methods. However, the costs and efficacy of lethal vs non-lethal approaches have rarely been compared formally. We conducted a 3-year study on 11 South African livestock farms, examining costs and benefits of lethal and non-lethal conflict mitigation methods. Farmers used existing lethal control in the first year and switched to guardian animals (dogs *Canis familiaris* and alpacas *Lama pacos*) or livestock protection collars for the following 2 years. During the first year the mean cost of livestock protection was USD 3.30 per head of stock and the mean cost of depredation was USD 20.11 per head of stock. In the first year of non-lethal control the combined implementation and running costs were similar to those of lethal control (USD 3.08 per head). However, the mean cost of depredation decreased by 69.3%, to USD 6.52 per head. In the second year of non-lethal control the running costs (USD 0.43 per head) were significantly lower than in previous years and depredation costs decreased further, to USD 5.49 per head. Our results suggest that non-lethal methods of human–wildlife conflict mitigation can reduce depredation and can be economically advantageous compared to lethal methods of predator control.

Keywords Carnivore conservation, conflict mitigation, human–wildlife conflict, lethal control, livestock depredation, non-lethal mitigation techniques, profit/loss ratio

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Introduction

Depredation of livestock is a principal cause of human–wildlife conflict (Sillero-Zubiri & Laurenson, 2001). It incurs high costs for livestock-keepers and provokes both retaliatory and preventative killing of carnivores, which may threaten their survival locally or globally (Kruuk, 2002; Ray et al., 2005; Macdonald et al., 2013). Pastoralists in the Serengeti have reported that the cost of depredation amounts to c. 19% of their annual cash income (Holmern et al., 2007), and in Bhutan attacks on livestock by carnivores cost farmers over two-thirds of their annual cash income, on average (Wang & Macdonald, 2006). In the USA the annual cost of depredation to the livestock industry is USD 40 million (Conner et al., 2008). Even greater losses are reported in South Africa, where a survey in 2010 estimated that the annual cost of depredation to the livestock industry is USD 171 million (van Niekerk, 2010), although a 2007 census estimated the cost to be USD 22 million (Statistics South Africa, 2010). The disparity between these two estimates raises uncertainty as to their accuracy but both reveal a perception that losses to carnivores are high.

Ideally tools for reducing depredation should benefit both farmers and wildlife conservation. Desirable features of interventions include persistent efficacy, minimal unintended environmental consequences, selectivity towards problematic individuals, lower cost than that of the depredation prevented, and social acceptability. Traditionally farmers have attempted to prevent depredation, or retaliate, by killing predators (Hone, 1994; Macdonald et al., 2010), often with negative effects on carnivore populations (Sillero-Zubiri & Laurenson, 2001; Woodroffe et al., 2005; Loveridge et al., 2010). In South Africa, encouraged by the government, farmers have employed lethal control of predators, using methods such as gin-traps (leg-hold traps), gun-traps, poison and hunting, with and without hounds, to eradicate carnivores and other problem animals (Daly et al., 2006). As recently as the 1990s formal bounty systems were in place for most of the terrestrial mammal species that were perceived to cause conflicts with commercial agriculture, and lethal control is still common on livestock farms (Daly et al., 2006). Despite these measures depredation remains a problem in the livestock farming sector, with indications that losses are increasing (Avenant & du Plessis, 2008).

Lethal control is often considered the cheapest and most effective method of reducing depredation (Conover, 2001; Mitchell et al., 2004) but it is not without problems: it may

miss problem individuals and it often fails to eradicate depredation (Avenant & du Plessis, 2008) and involves ongoing commitment and expense (Conover, 2001; Mitchell et al., 2004). It is commonly unselective and there is little evidence of cost-effective diminution of livestock losses (Treves & Naughton-Treves, 2005; Berger, 2006), as predators learn to avoid control efforts (Brand et al., 1995; Knowlton et al., 1999). Methods such as leg-hold traps, snaring and poisoning are largely indiscriminate and often kill non-target species (Rochlitz et al., 2010); in South Africa, this includes threatened species such as Cape vultures *Gyps coprotheres* (Bamford et al., 2007). Unintended outcomes of removing territorial predators can include an influx of replacement individuals, potentially increasing the local predator population and the risk of depredation (Crooks & Soulé, 1999; Knowlton et al., 1999), through what are known generically as perturbation effects (Tuyttens & Macdonald, 2000). Furthermore, lethal control has led to the extermination of populations of large carnivores (Kruuk, 2002), resulting in debates amongst conservationists, farmers and the general public (Treves & Karanth, 2003; Graham et al., 2005).

The inadequacies of lethal control methods have focused attention on possible non-lethal interventions. One advantage of non-lethal control for territorial species is that it does not cause social perturbation in the way that lethal control can do; instead, the target individual is allowed to remain in its territory and although its behaviour may be altered (e.g. in the case of learned food aversions) other ecological relationships remain intact, including exclusion of potentially invading conspecifics (Reynolds, 1999). Possible non-lethal interventions include corralling livestock during periods of vulnerability (Schiess-Meier et al., 2007), installing predator-proof fencing around small vulnerable areas (Breitenmoser et al., 2005), using shepherds (Shivik, 2006), installing fladry (Davidson-Nelson & Gehring, 2010), translocating species (Bradley et al., 2005) and using conditioned taste aversion (Cox et al., 2004), other learned food aversions (Macdonald & Baker, 2004; Baker et al., 2008) or odour (Atkinson & Macdonald, 1994), chemical, visual or acoustic repellents (Mason et al., 2001). Guardian animals, particularly livestock guardian dogs, are another popular method and have been found to decrease depredation by 10–100% on ranches in the USA (Linhart et al., 1979; Coppinger et al., 1988; Andelt & Hopper, 2000; Gehring et al., 2010). They have also proved effective in southern Africa: in Namibia, 73% of farmers who used guardian dogs reported a significant decline in livestock depredation (Marker et al., 2005, 2010). Other guardian animals that behave aggressively towards stock-predators can also be effective, such as donkeys *Equus africanus asinus*, alpacas *Lama pacos* and llamas *Lama glama* (Conover, 2001). A promising but largely untested technique is the use of protective collars made of a strong epoxy–metal mesh.

Carnivores typically kill their prey by a fatal bite to the neck, and these collars protect the vulnerable neck area, increase the effort needed by predators to kill livestock, and reduce the likelihood of a fatal bite.

Such methods have the potential to be more selective than lethal predator control, targeting only those animals attempting to kill livestock. There is evidence that non-lethal interventions can reduce depredation (Breitenmoser et al., 2005), with the added benefits of favourable public perception, improved animal welfare and reduced non-target casualties (Treves & Naughton-Treves, 2005). Non-lethal methods may be more compatible with conservation objectives and less likely to trigger perturbation effects, including counter-productive ecological cascades such as mesopredator release (Beasom, 1974; Crooks & Soulé, 1999). However, some controls can have negative consequences: from the early 1900s to the 1960s most farms in South Africa were fenced to prevent depredation (Beinart, 2008) but fencing large areas may restrict the movement of wildlife (Knowlton et al., 1999). Livestock guardian dogs may attack wildlife if not properly managed (Green et al., 1984). Furthermore, although comprehensive audits are few, non-lethal mitigation techniques are sometimes considered more expensive (Mitchell et al., 2004) and less long-lasting than lethal predator control (Shivik, 2006). There is a dearth of rigorous accounting of the full life-cycle costs and benefits of alternative interventions. Here we assess the efficacy and economics of lethal control of carnivores compared to three non-lethal mitigation techniques over a 3-year period.

Study area

Our study took place on 11 commercial livestock farms at altitudes of 500–2,000 m in the Eastern Cape Province of South Africa (Fig. 1). Mean farm size was 4,291 ha (1,500–10,000 ha) and the farms covered a total of 47,200 ha and received annual rainfall of 230–480 mm. During the period of the study no unusual climatic conditions were experienced. There was extensive grazing on all farms apart from Farm 2, where high-intensity, short-duration planned grazing rotation was employed (Savory, 1983). Farms were subject to varying degrees of depredation and different environmental conditions, and represented at least one of four major biomes: (1) Albany thicket, with relatively dense, woody vegetation of mean height c. 2–3 m (Mucina & Rutherford, 2005), dominated by *Portulacaria afra* (spekboom) and *Rhus* sp.; (2) Afrotemperate forest (Mucina & Rutherford, 2005), with yellowwood *Afrocarpus falcatus* and forest elder *Nuxia floribunda* in mountainous gorges; (3) Sandstone fynbos, which was prolific on higher-altitude farms and commonly included *Protea* and *Erica*; and (4) Nama-Karoo, which is characterized by low sweet thorn *Acacia karroo* in annual river beds, shrubs intermixed with grasses, and succulent plants. All farms had
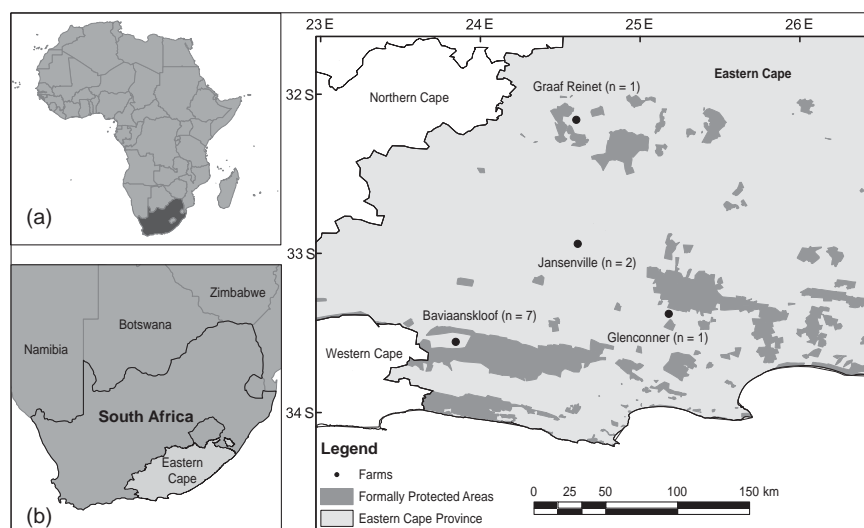
FIG. 1 The distribution and number of trial farms in the Eastern Cape Province, South Africa. The black shaded area in (a) indicates the location of South Africa, and (b) indicates the location of the Eastern Cape Province.

black-backed jackal *Canis mesomelas* and caracal *Caracal caracal* present and Farms 5–11 also had leopard *Panthera pardus* present.

Methods

We conducted interviews with farmers from the 11 farms in September 2007, 2008 and 2009. The semi-structured questionnaire focused on farm description, quantity of livestock, number of losses and their perceived causes, depredation control methods, expenditure on control methods, and willingness to adopt non-lethal control methods. The same questionnaire was administered in person by the same researcher each year.

During the lethal-control year all farms except 1, 4 and 10 used gin-traps and hunting as their control methods. Farm 1 used gun-traps in addition to these methods, Farm 4 used only gin-traps, and Farm 10 used only hunting. During the non-lethal control years implementation and running costs (e.g. veterinary costs and food for livestock guardian animals) were sponsored for nine farms for the duration of the study, after which each farmer took responsibility for any costs. Two farms (2 and 4) chose to pay the implementation and running costs of their preferred control methods for the duration of the study and thereafter. The recruitment of farmers was facilitated by sponsorship of the controls.

The allocation of the various non-lethal controls was based on the farmers' willingness to work with livestock guardian animals, and on local conditions. To ensure accurate identification of causes of livestock losses, farmers attended training workshops and received detailed identification kits and descriptive manuals on kill identification (Smuts, 2008). When livestock was depredated, trained conservation officials and/or one of the researchers, and the farmer, undertook carcass inspections to determine if the death was caused by a predator and, if so, by which species. If there was doubt, photographs were taken and conclusions were made by external experts. Because of the size of the farms, sometimes carcasses were not discovered until it was impossible to determine the cause of death. These were excluded from analyses and cause of death was recorded as unknown.

Initial data were collected during August 2006–August 2007 (the lethal-control year) and all farms converted to non-lethal control in September 2007. Follow-up surveys were conducted at the end of September 2008 to collect data on the first non-lethal year, and at the end of September 2009 for the second non-lethal year. Therefore, the dataset for the first non-lethal year includes the initial conversion from lethal to non-lethal methods. Three farms received livestock guardian dogs (two received one dog each and the other received five), one farm received seven alpacas and the remaining seven farms received 'Dead-Stop' livestock protection collars (Klaas Louw, Cape Town, South Africa) for all stock.

Farmers received a one-off payment in the first year of implementation to cover the cost of purchasing guardian animals or collars (USD 553 per dog, USD 860 per alpaca and USD 3.50 per collar). Ongoing maintenance costs for guardian animals, such as feeding and veterinary care, averaged USD 432 per dog and USD 98 per alpaca per year. There were no running costs for collars in the first year but in the second year there was an additional replacement cost of USD 0.35 per collar for wear and tear (10% replacement). Maintenance costs for guardian animals remained the same in the second year. If the number of livestock increased between the first and second years of non-lethal control, costs for additional collars (one per additional stock animal) were included in year two. The cost of lethal control varied according to the different methods used by farmers. The cost of tools such as gin-traps and gun-traps was calculated

as the cost of one labourer at minimum wage (USD 8.20 per day) because legally the devices must be checked once per day and most farmers assigned one worker to check and set these devices. The cost of hunting was calculated based on daily rates charged by professional vermin hunters (USD 79) and the number of days these hunters were employed (2–12 days per year). For each individual of a target species (jackal or caracal) shot by the hunter, an additional USD 122 was charged. To standardize depredation costs, the cost of one depredated animal was calculated at USD 147.42, the mean price for a weaned lamb. We use November 2011 prices and the exchange rate at that time of ZAR 8.14 = USD 1.

Total costs during the lethal-control year were calculated as the sum of running costs and depredation costs, in the first year of non-lethal control as the sum of implementation, running costs and depredation, and in the second non-lethal control year as running costs plus depredation. As lethal control had been used prior to the study, implementation costs for equipment such as gin-traps, gun-traps and poisons were not accounted, and therefore the overall cost of lethal control may be under-estimated. However, the running costs were considered a close representation of overall costs because items such as gin-traps lasted several years and hunting was calculated as a service rather than permanent equipment. Data were not normally distributed so we represented the range of variance of the results in the data between the comparative sites. However, when comparing our results with other studies that used mean data we used means in describing the central tendency. The Wilcoxon signed-rank test for related samples was used to compare different years at the same sites and the Kruskal–Wallis χ^2 test was used to compare continuous variables between different farms. All analyses were conducted using *SPSS v. 16.0* (SPSS, Chicago, USA).

Results

Costs of lethal predator control and non-lethal conflict mitigation

During the year of lethal control the cost of control measures was USD 3.30 per head of stock and the mean cost of depredation was USD 20.11 per head of stock (Supplementary Table S1). With a mean total cost of USD 23.41 per head of stock (Supplementary Table S1), the cost to each farmer was USD 3,552–69,290 depending on their stock holdings (mean USD 29,046). There was no significant difference in total cost per head between farms that would later receive livestock guardian dogs, alpacas or collars ($\chi^2 = 3.81$, df = 2, P = 0.149). When implementing lethal control farmers lost 4.0–45% of their stock (mean 13.6%; Supplementary Table S2) to depredation, which, given their stock holdings (Supplementary Table S1), equated to a mean cost of USD 25,306 per farm (range USD 3,392–66,340).

The mean cost of implementing non-lethal techniques was USD 2.91 per head of stock (Supplementary Table S1). During the first year of non-lethal control the mean running cost was USD 0.17 per head of stock (Supplementary Table S1), or USD 336.76 per farm (range USD 0–2,160; there were no running costs during the first year for farms using collars; Supplementary Table S1). The mean combined implementation and running cost during this year was USD 3.08 per head, similar to the running costs of lethal control (Z = −255, P = 0.799). During the same year depredation was significantly lower than when using lethal control (Z = 2.93, P = 0.003). The mean decline in depredation was 69.3%, with depredation accounting for 4.4% of stock (range 0.1–15.0%; Supplementary Table S2) and costing farmers a mean of USD 6.52 per head of stock (Supplementary Table S1).

Therefore, the mean total cost per head during the first year of non-lethal control was USD 9.60 (range USD 1.49–28.82; Supplementary Table S1), significantly less (59.0%) than the cost when using lethal control (Z = −2.85, P = 0.004). The cost decreased on 10 of the 11 farms (range 41.8–89.9%) but on one farm (Farm 10) there was an 8.1% increase in costs relative to the lethal-control year (Supplementary Table S1). There was no significant difference in the decline in costs per head between farms using alpacas, dogs or collars ($\chi^2 = 4.33$, df = 2, P = 0.115).

The second year of non-lethal control involved no implementation costs; mean running cost was USD 0.43 per head (Supplementary Table S1). This was significantly lower than both the running costs of lethal control (Z = −2.85, P = 0.004) and the combined running and implementation costs during the first year of non-lethal control (Z = −2.94, P = 0.003), although the costs were significantly higher than the running costs (excluding implementation costs) of the first year of non-lethal control (Z = −2.31, P = 0.021; Supplementary Table S1). Depredation, which accounted for 0.1–14.2% of the herd (mean 3.7%: Supplementary Table S2), at a mean cost of USD 5.49 per head (Supplementary Table S1), declined by 72.7% compared to the lethal-control year, which is a significant difference (Z = −2.93, P = 0.003; Supplementary Table S2). Therefore, the cost of depredation declined by a mean of 15.8% compared to the first year of non-lethal control (Z = −1.79, P = 0.074), although on two farms using collars, depredation levels increased between the first and second years of non-lethal control (Supplementary Table S2). Based on stock holdings, during the second year of non-lethal control depredation declined by 73.9% compared to the lethal-control year and by 13.3% compared to the first year of non-lethal control.

The mean total cost per head of non-lethal control in the second year was USD 5.92 (range 0.72–21.62; Supplementary Table S1); this was significantly lower than the cost

during the lethal-control year (Z = −2.93, P = 0.003). All farms reported lower total costs than during the lethal-control year, with a mean saving of 74.6% (range 54.1–95.1%; Supplementary Table S1). Overall costs were also significantly lower than during the first year of non-lethal control on all farms (Z = −2.93, P = 0.003), with a mean decline of 43.9% (range 25.0–76.7%; Supplementary Table S1). The saving per head in the second year of non-lethal control did not differ significantly between farms using different forms of control, when compared to the lethal-control year (χ^2 = 2.04, df = 2, P = 0.360) or the first year of non-lethal control (χ^2 = 2.51, df = 2, P = 0.285).

Avoided depredation and profit : loss ratios in different years

Although switching from lethal to non-lethal control resulted in significant declines in both depredation and total costs, this does not fully reflect the economic savings that were made. The non-lethal measures led to considerable cost savings through avoided depredation, assuming that depredation would have remained at the same level as under lethal control. Implementing non-lethal control saved farmers a mean of USD 13.58 per head of stock in avoided depredation (Supplementary Table S3), which equates to a saving of USD 20,384 per farmer, based on the mean herd size of 1,501 in the first year of non-lethal control. Combined with a saving on running costs of USD 0.21 per head of stock (Supplementary Table S3), the overall saving compared to what would have been expected under lethal control was USD 13.79 per head, a mean saving of USD 20,699 per farmer. Given the total cost of implementation, running expenses and depredation during the first year, this gives a mean profit : loss ratio of 2.11 : 1, with all but one farmer showing a profit (Supplementary Table S3). Where the running cost of lethal control was cheaper than that of non-lethal techniques, the lower-than-expected depredation still resulted in a profit (Supplementary Table S3). There was no significant difference in the profit : loss ratio between different forms of non-lethal control (χ^2 = 1.82, df = 2, P = 0.403).

In the second year of non-lethal control, farmers saved a mean of USD 17.41 per head of stock (range USD 3.29–47.67; Supplementary Table S3) compared to what would have been expected under lethal control. All farms had a positive profit : loss ratio compared to lethal control, saving a mean of USD 5.36 for every USD 1 spent (range USD 1.16–18.11; Supplementary Table S3). As in the first year of non-lethal control, there was no difference in the mean profit : loss ratio between farms using different non-lethal methods (χ^2 = 2.04, df = 2, P = 0.360).

Comparing the 2 years of non-lethal control, two farms (18%) experienced higher levels of depredation in the second year and nine (82%) experienced slightly lower depredation (Supplementary Table S2). Compared to the first year of non-lethal control, these changes amounted to a profit : loss ratio of 1.23 : 1 (Supplementary Table S3). This ratio did not differ significantly according to the non-lethal method implemented (χ^2 = 0.90, df = 2, P = 0.637).

Post-trial follow ups

Observations made 13 months after the study finished revealed that 55% of the farms continued to use non-lethal control. All farms with livestock guardian animals (Farms 1–4) retained them at their own expense, two others (6 and 11) acquired livestock guardian animals in addition to existing methods, and one (Farm 10) only retained the collars. Just under half the farms (45%) combined both lethal and non-lethal methods after cessation of the trial; Farms 5, 7, 8 and 9 used both hunters and collars and Farm 3 used gin-traps, hunting dogs, hunting and collars.

After 30 months 36% of farms (2, 4, 8 and 10) used only non-lethal control, 46% (1, 3, 5, 6 and 11) combined lethal and non-lethal control, and 18% (7 and 9) used only lethal control. Depredation was reported to have remained the same by 30% of farms (4, 5 and 8), 30% reported an increase in depredation (7, 9 and 11) and 40% reported a decrease (1, 2, 3 and 10) since the end of the trial. This information was not available for Farm 6 because livestock farming was only reinstated 1 month prior to the interview. Six farms used livestock guardian animals (1–4, 6 and 11) but the dog on Farm 1 was shot by a neighbour who feared it would cause damage to livestock. The farmer did not replace the dog but instead placed lambing ewes in fenced camps to avoid losses at vulnerable times. Farms 3 and 4 made no changes to management and Farms 6 and 11 stopped farming livestock 19 months after the trial ceased, until April 2013 and December 2012, respectively. When livestock farming was re-established Farm 6 re-acquired a livestock guardian dog and Farm 11 used shepherds and electrified lambing camps. Farms 7 and 9 used only lethal controls. Farm 9 reported that it was easier to implement because it was managed by a neighbour; Farm 7 undertook call-and-shoot hunting over several farms to reduce predator numbers and avoid losses. Farm 8 used three livestock guardian dogs and Farm 10 used shepherds in mountainous areas. All farms except Farm 7 remained willing to pay for non-lethal controls; Farm 7 indicated that payment to use non-lethal control would increase the likelihood of its use.

Discussion

Large carnivores are often highly valued at a global scale but have a low or negative economic value at a local scale

(Dickman et al., 2011). To address this, local revenue from carnivore presence should outweigh the costs of coexistence. This can be achieved by generating more local revenue, for instance through tourism or payments for presence (Sillero-Zubiri et al., 2004; Dickman et al., 2011), and also by reducing the costs incurred locally as a result of carnivore presence. Our findings suggest that non-lethal mitigation can effectively reduce depredation and the economic costs of carnivores in the vicinity of livestock farming. Farmers saved 55.1 and 74.6% during the first and second years of non-lethal control, respectively, compared to expected losses during lethal control. Even where lethal controls were cheaper to implement than non-lethal methods, the lower-than-expected depredation resulted in savings in both years when non-lethal controls were used. There was a mean saving of USD 13.79 per head of stock in the first year of non-lethal control and USD 17.41 per head in the second, compared to what would be expected when using lethal control only. Overall, farmers saved a mean of > USD 20,000 during the first year of switching to non-lethal measures, which was equivalent to the value of 138 livestock. Initiating and operating non-lethal control during the first year was cheaper than continuing lethal control on the majority of study farms, and depredation rates were invariably lower. In short, non-lethal measures were cheaper than lethal control on 91% of the farms in the first year of implementation. On the one farm where the implementation costs were lower for lethal control, only low-intensity control was employed (Supplementary Table S1). In the second year, depredation remained low, running costs were minimal and all farms reported lower costs per head than under lethal control. The economic case for non-lethal approaches is further strengthened if the avoided losses from depredation under lethal control are considered. This made non-lethal predator control twice as lucrative during the first year and > 5 times so during the second year.

Large-scale, intensive and expensive lethal-control experiments have resulted in a 51–68% reduction in depredation rate (Guthery & Beasom, 1978; O'Gara et al., 1983; Wagner & Conover, 1999; Greentree et al., 2000). This benefit is similar to, or less than, the 69.3 and 73.9% reduction we found during the first and second years of implementing non-lethal measures. Given the higher cost of lethal control, this suggests that non-lethal measures are a more economical option.

We are mindful that the design of our study lacked a formal control, as there was no sample of farms in the second and third years on which lethal control continued for comparison. Nonetheless, the reductions in cost and depredation were similar across all farms (irrespective of locations, biomes and environmental conditions). We do not have grounds to believe that the reduction in depredation that occurred during non-lethal control would

have occurred without our experimental intervention, or that such a reduction occurred on comparable farms that continued to use lethal control. Farms neighbouring the study farms may have increased the intensity of their predator control but we have no evidence for this and it seems unlikely that this would have happened across all the disparate locations. Furthermore, seven of the experimental farms (Farms 5–11) were adjacent to protected areas, where there would have been no scope, legally, for control of predators; the remaining four had neighbours that practised lethal control. Some other confounding factor, such as infectious disease, could have reduced predator populations during the second and third years of our trial on all sampled farms but there was no evidence for this and it is unlikely to have occurred at all of the different sites. Farmers may have exaggerated reported losses during the first year of the survey to demonstrate their need for help, thereby distorting our findings, but this is unlikely to have occurred in every case. Although other studies have identified a positive correlation between carnivore absence and human presence (Ogada et al., 2003; Bunnefeld et al., 2006) there is no evidence that local human activity was substantially higher in the years when non-lethal control was implemented. Another possibility is that experimental cessation of lethal controls somehow diminished losses of non-target species, and consequently natural prey numbers increased more than the target predators, relieving the pressure on domestic stock. Although none of these potential explanations appears to be likely, we suggest that future studies are run with control sites and non-lethal trials concurrently for longer periods, to determine if and when predators either adapt to non-lethal measures (Brand et al., 1995) or repopulate to a level at which the control measures become ineffective (Gese, 2005), and whether depredation and costs of control remain low in the long term. Understanding the effect of lethal controls on non-target species population densities could help to determine whether changes occur in their availability and frequency and whether this could affect depredation on livestock.

Although, under the particular circumstances of our trial, non-lethal methods yielded significant cost-savings, using lethal control is not purely an economic decision. Hunting of carnivores is often culturally and socially embedded and may provide intangible benefits such as social prestige and enjoyment (Hazzah et al., 2009; Marchini & Macdonald, 2012). It is likely that many farmers will want to continue some form of carnivore hunting but if non-lethal methods continue to be effective it will be clear that this is driven more by cultural norms and satisfaction than economics. Furthermore, the adoption of non-lethal methods will depend on the local context; for example in many areas livestock-keepers may not have the means or the inclination to invest time, care and resources in livestock guardian dogs or exotic animals such as alpacas.

Determining the most appropriate methods for the local socio-economic and cultural environment is a vital step in encouraging farmers to adopt novel forms of non-lethal control. According to our interviews all 11 farmers were willing to pay for non-lethal control if it effectively reduced losses. However, 9 of the 11 farms were provided with such controls free of charge, which probably accelerated the rate of uptake, and two farmers bought and implemented the controls without financial support. Therefore, although many farmers may be willing to implement non-lethal controls they may not do so without incentives or support of some kind. However, attitudes towards predators are rarely based on economics alone but are influenced by a variety of personal factors, including beliefs and values, education, upbringing, tradition and culture (Zimmermann et al., 2005).

Our observations indicate that after non-lethal controls are introduced, in most cases (82%) their use is continued or alternative non-lethal methods are tried, either in isolation or alongside lethal controls. Depredation increased on the two farms where only lethal controls were used and decreased on 50% of farms where only non-lethal methods were implemented. On the other 50% there was no change in the level of depredation. Where lethal and non-lethal controls were combined, losses to depredation decreased on 50% of farms, remained the same on 25% of farms and increased on the remaining 25%. Given that depredation increased when using lethal controls, it seems that the use of such controls is influenced by the attitudes of farmers and their neighbours as much as by any realized economic advantages.

Further and long-term controlled trials are needed to investigate whether the benefits we observed as a result of non-lethal controls are sustainable. Such trials could also evaluate predator habituation to non-lethal techniques and the effectiveness of methods such as using alpacas to guard against larger predators such as leopards. Our results suggest that non-lethal forms of livestock protection, whether livestock guardian animals or barriers such as collars, can efficiently and cost-effectively reduce depredation on domestic stock. These methods reduced the economic cost of livestock depredation by carnivores for at least 2 years, which is important for improving the local cost : benefit ratio of carnivore presence. They may also benefit conservation by reducing the motivation for retaliatory or pre-emptive killing of carnivores, and by reducing the effects of control on non-target species. The use of non-lethal conflict mitigation approaches may also be useful in reducing edge effects (Woodroffe & Ginsberg, 1998) on species and provide safety buffer zones adjacent to protected areas or along important wildlife corridors. Since this study was completed there has been a strong uptake in the use of various livestock protective collars, including in Iran.

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Biographical sketches

JEANNINE MCMANUS has experience in restoring wildlife habitat and addressing the conflict caused by economic losses to the livestock industry as a result of carnivore predation. AMY DICKMAN has been researching human–carnivore conflict in Africa for 15 years, with a particular focus on testing the efficacy of non-lethal conflict mitigation techniques. DAVID GAYNOR is a specialist in mammal behaviour ecology and is also a livestock farmer. BOOL SMUTS has been involved in human–wildlife conflict mitigation efforts since 2004. He develops projects integrating environmental ethics, viable economics and social responsibility. DAVID MACDONALD's research interests lie in the behavioural ecology of carnivores, especially with relevance to human–carnivore conflict. He has studied large felids in Africa, Asia and South America.

Project to Reform Public Land Grazing in Northern California
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A report to sponsors, allies and supporters on efforts in 2015 to Reform Public Land Grazing

By Felice Pace, Project Coordinator

Introduction

In 2015 the Project to Reform Public Land Grazing in Northern California completed its sixth year monitoring grazing management on the ground in Northern California's national forests. As in past years, our objective was to document the impacts of poorly managed grazing on water quality and habitat and to recommend to responsible Forest Service officials and regional water quality regulators what needs to be done to manage grazing responsibly. Responsible grazing would reduce to insignificance or eliminate the adverse impacts of poorly managed grazing.

Four volunteers logged 224 hours (28 person days) monitoring 14 national forest grazing allotments on-the-ground in 2015. That is nearly double the monitoring hours logged in 2014. In 2015 we monitored grazing allotments from the Oregon-California border to the McCloud Flats South of Mount Shasta.

In the north, three volunteers monitored the Elliot and Beaver-Silver grazing allotments north of the Siskiyou Crest on the Rogue-Siskiyou National Forest and the Horse Creek, Dry Lake and East Beaver Grazing Allotments on the Klamath National Forest south of the Crest. Running west from Mount Ashland, the Siskiyou Crest contains a complex of sensitive lands and roadless areas. Grazing degradation there began in the 1800s and continues today.

The three grazing allotments south of the Crest extend to lower elevation lands near the Klamath River. Both the Beaver and Horse Creek Watersheds include miles of streams that have been designated Critical Habit for Coho Salmon.

Farther south, Project volunteers monitored the Big Meadows grazing allotment in the Marble Mountain Wilderness and the Carter Meadows and Mill Creek grazing allotments in the Trinity Alps Wilderness. Those allotments are on the Klamath National Forest; the Mill Creek allotment includes meadows and headwater basins on both the Klamath and Shasta-Trinity National Forests.

On the following page you'll find a map on which the twelve grazing allotments on the Klamath National Forest which the Project has monitored are depicted and can be located.

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Grazing Allotments in Northern California's Klamath National Forest
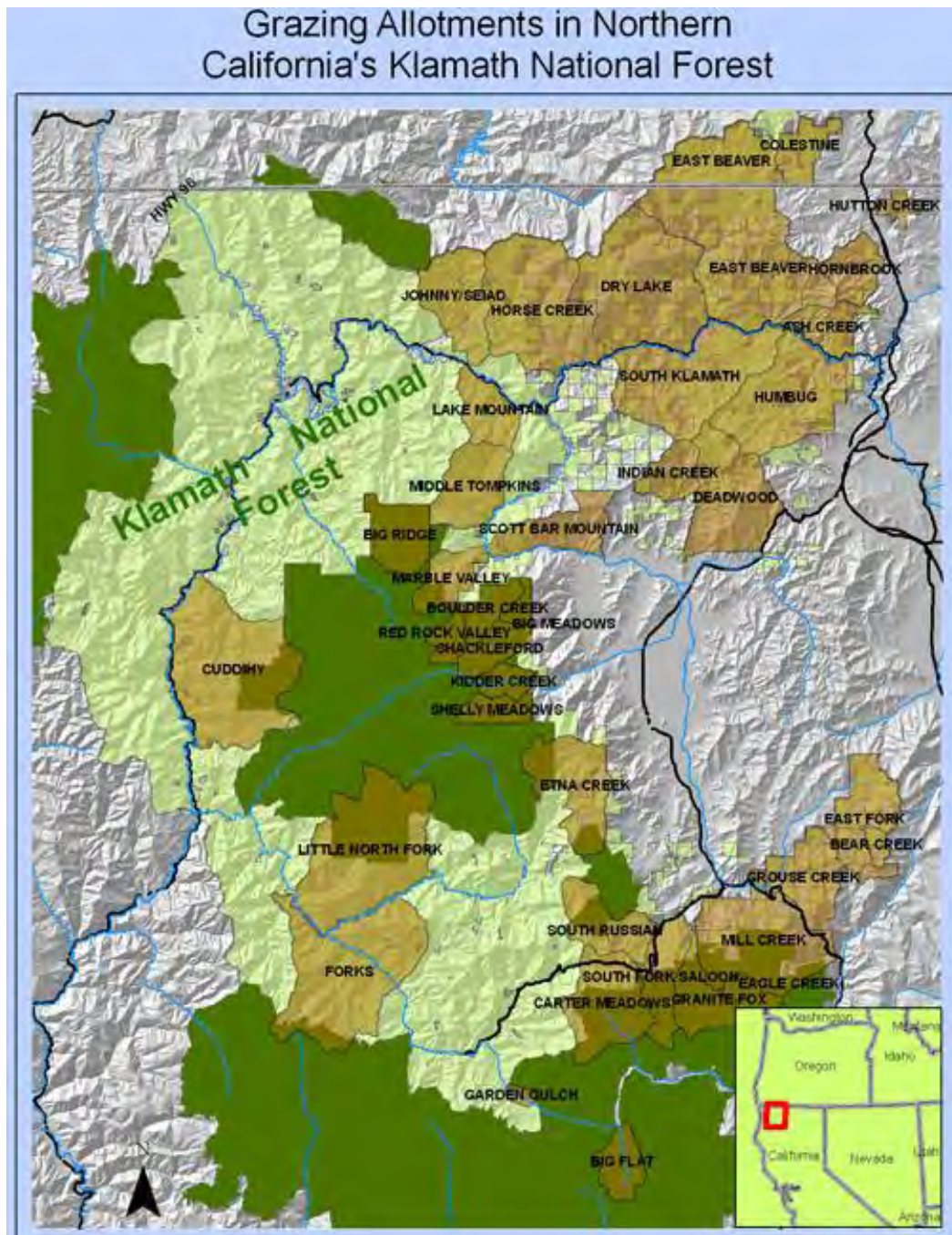
While monitoring grazing on the Big Meadows Allotment, I was joined by hydrologist Jon Rhodes. An expert on meadow hydrology and grazing impacts to water quality, the Project hired Jon to study and report on the impact of Big Meadows grazing on water quality, meadow hydrology, water supply, riparian vegetation and wetlands. As I write this annual report we await Jon's Big Meadows report which we will use to "encourage" Forest Service managers to implement needed grazing management reforms. To learn about Jon's work around the West to reform and challenge irresponsible and damaging public land grazing see his web site at this link.

There was a Project milestone in 2015 when we monitored grazing in the Mount Shasta area of the Shasta Trinity National Forest (STNF) for the first time. Project volunteer and former Forest

Service biologist Francis Mangles, who before he retired managed STNF grazing allotments, joined me in monitoring the Bartle Grazing Allotment on the McCloud Ranger District east of Mt. Shasta and the Bear Creek Grazing Allotment on the north and east slopes of Mount Eddy within the Mount Shasta Ranger District.

Retired Forest Service biologist Francis Mangles examines riparian conditions on the Bear Creek Grazing Allotment near Mount Eddy on the Shasta Trinity National Forest

All on-the-ground monitoring by the Project is 100% volunteer, including my time. Thanks to a grant from the Fund for Wild Nature, the Project was able to reimburse volunteers for mileage and expenses incurred while monitoring.

Funding from generous EPIC donors makes it possible for me to also do paid work on public land grazing for EPIC. That work includes commenting on and challenging Forest Service proposals to reauthorize grazing on North Coast and Klamath River Basin national forests.

EPIC is one of three environmental organizations which sponsor The Project to Reform Public Land Grazing in Northern California; Klamath Forest Alliance (KFA) and Montana-based Wilderness Watch are also sponsors. A grant to KFA from the Giles and Elsie Mead Foundation also supports work on grazing. Mead Foundation and EPIC donor funding makes it possible for the Project to use its monitoring findings to challenge and reform public land grazing.

Over the course of the past six grazing seasons, the Project has monitored 16 separate grazing allotments on 3 national forests: 2 allotments on the Shasta-Trinity National Forest, 2 allotments on the Rogue-Siskiyou National Forest and 12 grazing allotments on the Klamath National Forests. We've monitored grazing in the Marble Mountain, Russian Peak and Trinity Alps Wilderness Areas, along the Siskiyou Crest west of Mt. Ashland and in several roadless areas. Most allotments have been monitored multiple-times and in multiple years.

Environmental impacts, including damage to water quality, impairment of meadow hydrology and degradation of fish, amphibian and wildlife habitat, are similar on all the grazing allotments the Project has monitored. Those impacts, however, vary in intensity; the meadows where most grazing occurs are trashed on some allotments while on others they are only damaged.

Management deficiencies are also consistent across all 16 grazing allotments the Project has monitored. The failure of Forest Service managers to require responsible grazing and modern grazing methods are the root cause of the degradation of water quality, wetlands, riparian areas and wildlife habitat which we have documented. In the following sections I illustrate those degraded conditions and the management deficiencies which cause the degradation of what should be our highest quality waters.

The environmental impact of grazing on Northern California's national forests includes degradation of water quality, the fragmentation and degradation of wetlands, the devegetation of dry meadows and negative impacts to wildlife and the habitats on which wildlife depend.

Water Quality Degradation

Grazing on national forest land in Northern California degrades water quality in violation of Clean Water Act standards. Water quality degradation related to poorly managed grazing includes excessive sedimentation, fecal bacteria and nutrient pollution and unnaturally high stream water temperature.

Excessive and nuisance sedimentation is the result of cattle weighing up to and over 1,200 pounds trampling springs and streambanks. When cattle are not herded frequently they will spend an inordinate amount of time grazing while standing and walking in springs, in streams and on streambanks.

Below are photos illustrating the streambank and spring trampling which the Project has found consistently on national forest grazing allotments. On many of the 16 grazing allotments we've monitored it is hard to find a spring that has not been trampled and streambank trampling is common in preferred areas where poorly herded cattle remain for long periods.

A trampled streambank on East Boulder Creek, Mill Creek Grazing Allotment in the Trinity Alps Wilderness

Trampling and deposition of bovine waste into Mud Springs
near the Siskiyou Crest on the Dry Lake Grazing Allotment

Project volunteer Luke Ruediger examines cattle damage to a riparian area. This
is part of the Elliot Creek Grazing Allotment on the Rogue-Siskiyou National Forest.

Poorly managed cattle grazing removes shade which raises the temperature of the water

Over the past seven years the Quartz Valley Indian Reservation, a federally recognized tribe, has monitored water quality in streams issuing from national forest grazing allotments and at other stream locations within the Scott River Basin. The Tribe, which has its own certified water quality laboratory, has documented multiple violations of North Coast Water Board and EPA standards for fecal bacteria pollution as well as nutrient pollution in streams below the grazing allotments. A report summarizing "Patterns in Fecal Indicator Bacteria in the Scott River Watershed, 2007-2014" can be accessed and downloaded at this link.

QVIR water quality testing was the main factor motivating me to begin the Project to Reform Public Land Grazing in Northern California six years ago. It started as an effort to document on-the-ground management failures causing the Clean Water Act violations the Tribe found.

The #1 cause of fecal bacteria and nutrient pollution in lakes and streams on and flowing from national forest grazing allotments is direct deposition of bovine waste into streams and onto streambanks. The photo below shows direct deposition of waste into Taylor Lake, a popular swimming lake in the Russian Peak Wilderness just ½ mile from the trailhead.

Cattle manure in Taylor Lake, a popular swimming lake in the Russian Peak Wilderness

Taylor Lake trail is accessible to individuals with disabilities; the lake is a popular place for locals to take youngsters swimming.

When cattle are poorly managed they spend an inordinate amount of time grazing within the riparian areas adjacent to streams. While on the streams cattle also browse riparian vegetation. One typical result is the removal of shade from the stream. Opening the streams to increased solar radiation raises the water's temperature which impacts all those species which depend on cold water stream habitat including frogs, other amphibians like the Pacific Giant Salamander, trout and salmon in the streams below.

The Pacific Giant Salamander is a top predator in healthy Northern California headwater streams

The impact of grazing in the headwater basins of key national forest salmon and steelhead watersheds has gone largely unassessed and is denied by Forest Service managers. Managers appear to prefer to not know what might require actions that would likely cause conflict with the ranchers who graze on public lands. In light of what is occurring on the Malheur Wildlife Refuge in eastern Oregon as I write this report, one can understand why most Forest Service grazing managers prefer to ignore the environmental impacts of poorly managed grazing. But avoidance of conflict is not a valid justification for managers who refuse to enforce the regulations and require the practices that protect water quality, public lands and wildlife habitat from degradation.

Wetland degradation and fragmentation

As noted above, when they are not adequately herded to rotate grazing among the various pastures on a grazing allotment, cattle find a preferred area and remain there until they are herded to a different area or until all available forage has been consumed. Often those preferred locations are in lower gradient meadow systems in which there are large wetlands dominated by willow species.

Most healthy Northern California willow wetlands found on national forests are from ½ to 2 acres in extent and from 5 to 15 feet in height. They contain continuous dense vegetation from the tops of the willows to the ground rendering them nearly impenetrable to humans.

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Healthy, ungrazed willow wetlands in the Marble Mountain Wilderness

Poorly herded cattle push into and through the willow wetlands to get to the tender grasses and sedges growing under the willows. The bovines also browse the willows, especially in fall after the first frosts. When that sort of use is allowed to continue for long periods and year after year the willow stands are progressively fragmented and degraded. Bovine trampling dries out the wetlands over time. In the most extreme cases willow wetlands are being slowly converted into grasslands.

This severely fragmented and degraded willow wetland in the Black Meadows pasture
of the Big Meadows Grazing Allotment is being slowly converted into a grassland

Large and dense willow wetlands provide breeding habitat for the Willow Flycatcher, a bird species listed as "endangered" under provisions of the California Endangered Species Act. The diminutive flycatcher is also a "management indicator species" for California national forests. That means every national forest in California is supposed to monitor either the bird itself or its breeding habitat.

The forest plan for the Klamath National Forest calls for breeding ground surveys to determine if Willow Flycatchers are present in the large willow wetlands which are the birds breeding habitat. But the Forest Service has mostly failed to conduct those surveys and has never conducted surveys on grazing allotments. Nor does the Klamath National Forest monitor to determine the quality and suitability of Willow Flycatcher breeding habitat. It appears that Forest Service managers would prefer not to know whether what is supposed to be a "management indicator species" is breeding successfully and whether the species' breeding habitat is suitable or degraded.

In response to the FS failure to monitor Willow Flycatcher breeding and habitat, the Project began conducting breeding ground Willow Flycatcher surveys under established protocols three years ago. We've monitored what should be suitable breeding habitat both within and outside national forest grazing allotments. In spite of monitoring before the cattle arrive, which is usually in mid-July, we've never heard a Willow Flycatcher respond to the territorial bird calls we've broadcast near willow wetlands that are grazed. We have received responses, and once positively identified a Willow Flycatcher, when we've monitored suitable habitat outside grazed areas.

According to the scientific literature on Willow Flycatcher, the main reason the diminutive bird is C-ESA listed and a management indicator species is its sensitivity to grazing. When cattle are allowed to push into and fragment large willow wetlands, the bird's nesting habitat (dense vegetation in the interior of the stands within 5 feet of the ground) is destroyed. The Project has confirmed what is stated in the scientific literature: poorly managed grazing destroys Willow Flycatcher nesting habitat, extirpating the species from national forest grazing allotments.

Dry meadow devegetation

In Northern California and throughout the West most dry meadows and grasslands in a natural condition are dominated by native bunchgrass. Ungrazed bunchgrass stands are dense, vibrant and quite beautiful, particularly in springtime which, in the higher mountains where most public land grazing in Northern California occurs, can extends into August.

A healthy bunchgrass stand in an ungrazed portion of the Marble Mountain Wilderness

Unfortunately western bunchgrasses, which co-evolved with widely ranging herds of native ungulates, are particularly sensitive to repeated grazing during a single season. That makes the bunchgrasses vulnerable to cattle because, unlike native ungulates, cattle do not naturally range widely, especially if they are not herded regularly.

Forest Service managers do not require regular herding. As a result, native bunchgrass stands within Northern California national forest grazing allotments are degraded. In many of the preferred areas where unherded cattle congregate for long periods, bunchgrass has been totally extirpated from large areas of dry meadow creating barrens. The loss of dryland bunchgrasses on national forest grazing allotments has made the cattle which graze there more dependent on riparian areas and wetlands and that accelerates degradation of water quality, streambanks and wetlands.

In the preferred areas where unherded cattle congregate for long periods bunchgrasses have been wiped out and barrens have been created.

The Project has monitored a few national forest locations where grazing ended several years back because there were no ranchers who wanted those allotments. We've watched bunchgrass stands in dry meadows recover slowly in those locations once grazing ends. Preventing cattle from grazing a dry meadow more than once during a single season might lead to bunchgrass recovery. But that is not the way the national forest grazing allotments the Project has monitored are managed.

Competition with wildlife

Reintroduced and recovering elk herds are expanding their range across Northern California. The expansion has brought elk back to many of the grazing allotments which the Project monitors. Like cattle, elk are primary grazers which also browse on woody vegetation. Unlike cattle, elk do not remain in preferred locations for long periods; except for mothers when they are with young foals, elk typically move constantly within their territories.

In those portions of the national forests where elk and cattle range overlaps, they compete for the available forage. Responsible Forest Service managers would reduce the number of cattle allowed to graze when elk reoccupy a grazing allotment because there is only so much forage available in a given year. Failure to adjust what is referred to as cattle "stocking" when elk reoccupy national forest land where livestock grazing occurs results in overgrazing and accelerated degradation of meadows, riparian areas and willow wetlands.

Elk sign near Reeves Ranch Spring along the Siskiyou Crest on June 1, 2015. Horse Creek Allotment cattle had not yet reached this location but elk had already consumed most of the available forage.

The following two photos show two of the classic indicators of overgrazing: *trailing* and *pedestalling*. The Project has documented *trailing* and *pedestalling* on most of the grazing allotments we've monitored.

"Trailing" which refers to the multiple trails which cattle sometimes create is a classic indicator of overgrazing.

"Pedestalling" refers to vegetation perched on a soil pedestal. It is another classic indicator of overgrazing

Forest Service (mis)management

In describing the environmental degradation which Project monitors have documented, I have often referred to "poorly herded" and "unherded" cattle or livestock. The technical term for managing livestock without regular herding to move them out of wetlands and rotate them among the various pastures on a grazing allotment is "passive, season-long grazing."

"Passive season-long grazing' is not a valid grazing management method but rather the lack of a method. On every one of the sixteen national forest grazing allotments we've monitored, "herding" is mentioned in Allotment Management Plans and in the Annual Operating Instructions issued each year to grazing permit holders. But reality on the ground is that herding is only required when there is a complaint in which case a Forest Service range technician or ranger will ask the permit holding rancher to go out and move the cattle. The ranchers usually, but not always, comply. But even in those cases were the cattle are moved, they are not moved far and often return to the area from which they were removed within a few days.

Passive season-long grazing is not compatible with maintaining water quality and wildlife habitat on Northern California national forests. That's why the Project to Reform Public Land Grazing in Northern California advocates that Forest Service managers require modern grazing methods.

Because virtually all Northern California grazing allotments contain several distinct and separate pastures, it is entirely feasible to implement modern rest-rotation grazing methods. Where pastures are not sufficiently isolated, drift fences can be used to prevent cattle from returning to preferred areas. Implementing modern grazing technologies would spread impacts more evenly across the allotments and would result in improved water quality and less damage to riparian areas and wetlands.

Unfortunately, Forest Service managers have ignored the Project's documentation of the serious environmental degradation that occurs as a result of "passive continuous grazing." Responsible Forest Service officials fail to require the regular range riding and modern grazing methods which are essential if environmental degradation is going to be reduced. As the situation in early

2016 on the Malheur Refuge in Oregon and the earlier standoff with the Bundy Rancher Militia in Nevada demonstrate, when public land managers require good management (or even the payment of grazing fees) they are often subjected to threats, intimidation and worse. To avoid conflict, most public land grazing managers prefer to ignore the impacts of poorly managed grazing in order to avoid confrontation with ranchers and their radical supporters.

The situation has become so bad on the Klamath National Forest that Forest Service managers no longer require ranchers to remove their cattle from the range when the grazing permit says they should be removed. A growing number of those ranchers now do not even go out to gather their cattle and move them to the home ranch at the end of the grazing season. Instead they allow the cattle to walk home on their own, grazing on national forest land along the way for up to a month after those cattle were supposed to be removed from national forest land.

A steer on the Klamath National Forest walking home 10 days after all
Cattle ere supposed to have been removed from public land

Forest Service managers are directed to charge *excess use* fees when a grazing permit holder allows his or her cattle to remain on national forest land after the date by which the grazing permit says all livestock are supposed to have been removed from national forest land. After observing that some permit holders on the Klamath National Forest don't even begin gathering their cattle until the official *off date* and that others allowed their cattle to wander home on national forest land for up to a month after the permit said they should be removed, the Project used the Freedom of Information Act to obtain billing records for *excess use* charges. We wanted to see if grazing managers were collecting the extra grazing fees officially required.

Over the course of the past ten years, managers of the Klamath National Forest issued only one bill for *excess use* when a rancher allowed his cattle to remain on the range all winter. For most KNF grazing permit holders, however, there are never consequences, financial or otherwise, when they ignore grazing permit requirements; No wonder several don't remove their cattle by the *off date*. Unfortunately, it is the land, wildlife and water quality which suffer as a result, while for the Forest Service managers who fail to do their duty there are also no consequences.

The future

For six years the Project to Reform Public Land Grazing in Northern California has been meticulously documenting the lack of responsible management on Forest Service grazing allotments and the resulting environmental degradation. For six years we've written reports presenting what we found on-the-ground and calling on Forest Service managers to correct management deficiencies. Above all else, we have asked responsible Forest Service officials, the district rangers, to require regular herding that moves cattle to lessen the negative impacts of grazing. The response has been profoundly disappointing.

The failure of Forest Service managers to reform grossly inadequate and retrograde grazing management has caused the Project and its sponsors to adopt a new approach. We will now ask the superiors of those who mismanage grazing and those whose job is oversight of the Forest Service to correct the mismanagement. And we will begin to challenge the reauthorization of grazing on national forest land unless modern grazing methods are required.

The Project does not seek to end national forest grazing. What we seek is proper and responsible grazing management. If ranchers want to continue grazing their cattle on public land, they need to properly manage their livestock using modern methods. If ranchers are not willing to manage grazing properly, they have no business grazing public land.

In 2016 we will also seek to expand on-the-ground public land grazing monitoring to more national forests and to other public lands in Northern California. But that will depend on whether there are volunteers willing to go out on the grazing allotments to document conditions and how the cattle are being managed, if at all. As always, the Project is on the lookout for volunteers and interns who we will train to do the monitoring work Forest Service managers refuse to do.

Throughout this report I have referred to "poorly managed" national forest grazing. In reality, grazing on the national forest grazing allotments the Project has monitored is not just "poorly managed" it is virtually unmanaged. The project is determined to change that reality.

Cattle in need of management: a common sight on Northern California's national forests

SCIENTIFIC REPORTS

Human behaviour can trigger large carnivore attacks in developed countries

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The media and scientific literature are increasingly reporting an escalation of large carnivore attacks on humans in North America and Europe. Although rare compared to human fatalities by other wildlife, the media often overplay large carnivore attacks on humans, causing increased fear and negative attitudes towards coexisting with and conserving these species. Although large carnivore populations are generally increasing in developed countries, increased numbers are not solely responsible for the observed rise in the number of attacks by large carnivores. Here we show that an increasing number of people are involved in outdoor activities and, when doing so, some people engage in risk-enhancing behaviour that can increase the probability of a risky encounter and a potential attack. About half of the well-documented reported attacks have involved risk-enhancing human behaviours, the most common of which is leaving children unattended. Our study provides unique insight into the causes, and as a result the prevention, of large carnivore attacks on people. Prevention and information that can encourage appropriate human behaviour when sharing the landscape with large carnivores are of paramount importance to reduce both potentially fatal human-carnivore encounters and their consequences to large carnivores.

During the last few decades, large carnivore attacks on humans in developed countries have increased over time[1–8] (Fig. 1). This is expected to increase people's apprehension and reduce their willingness to share the landscape with large carnivores. Unfortunately, such rare events are usually overplayed by the media. Indeed, media coverage of such attacks generally includes sensational texts and dreadful pictures (Extended Data 1), appealing more to the public's emotions than their logic. Denominator neglect[9] is a well-studied phenomenon leading humans to overestimate the risk of rare events that evoke strong emotions. Overestimating the risk of large carnivore attacks on humans irrationally enhances human fear and triggers a vicious cycle that may affect the increasingly positive conservation status of many of these contentious species[10–12]. With an increasing number of large carnivore attacks on humans there is, now more than ever, a need for objective and accurate information regarding not only the long-term trend and underlying mechanisms of large carnivore attacks on humans, but also potentially risky situations and risk-enhancing human behaviours[8]. Surprisingly, the few available studies focus on attacks by

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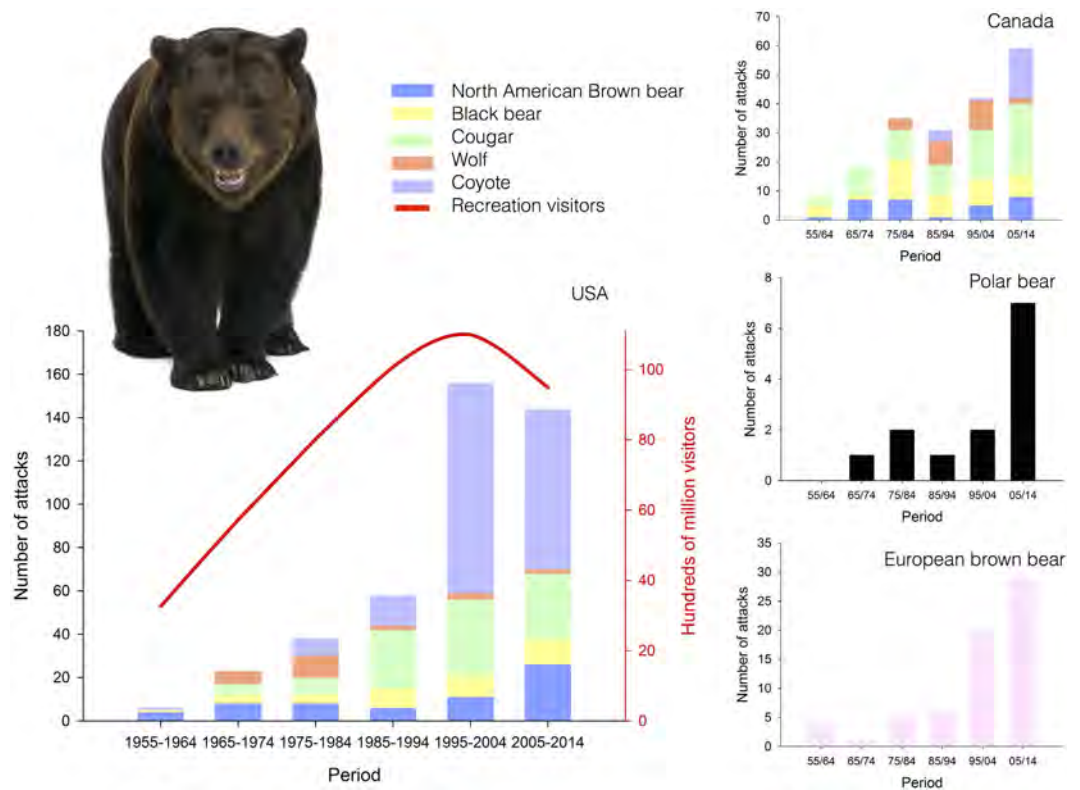
Figure 1. Temporal trends in large carnivore attacks on humans in developed countries. The number of attacks on humans by large carnivores has increased significantly (Extended Data Table 1) during the last few decades for almost all large carnivores. The left panel shows the relationship between the number of large carnivore attacks in the US and the number of visitors (hundreds of millions, red line) in American protected areas since 1955, which has increased significantly over time (Extended Data Table 4). The right panels show (from top to bottom) the temporal trends in large carnivore attacks in Canada, as well as the trends of polar bear (Europe, Russia, the United States and Canada) and European brown bear (Sweden, Finland and Spain) attacks. It is worth noting that: (i) conflicts with polar bears have been increasing in the last decade. Causal factors include a growing human population and more tourists visiting polar bear areas, increased oil and gas development along the Arctic coastline, and decreasing ice volume and seasonal extent due to climate change[63]. Indeed, human-polar bear encounters are expected to increase as the sea ice continues to melt and hungry bears are driven ashore (http://www.polarbearsinternational.org/about-polar-bears/essentials/attacks-and-encounters; http://www.theguardian.com/world/2013/nov/04/polar-bear-attacks-scientists-warn-warming-arctic); (ii) the remarkable increase in coyote attacks may be related to both the recent substantial expansion of the coyote range in eastern North America[64] and increased conflicts in suburban residential areas. In these areas, coyotes can relax human avoidance mechanisms as a result of relying on anthropogenic food resources and even intentional feeding by residents[4]; and (iii) wolves were the only species to show a decreasing trend in the number of attacks, declining from 10 attacks during the decade 1975–1984 to only two or three attacks per decade starting in 1985. (The brown bear picture has been downloaded from 123RF ROYALTY FREE STOCK PHOTOS (http://www.123rf.com), Image ID 7250879, Eric Isselee).

single carnivore species and thus they do not provide a comprehensive perspective concerning the pervasiveness and socio-ecological correlates of this phenomenon in developed countries.

Our main hypothesis is that lack of knowledge of people about how to avoid risky encounters with large carnivores engenders risk-enhancing behaviours, which can determine an increase in the number of attacks if more humans are sharing landscape with large carnivores. Three main predictions arise from this hypothesis: (1) an increased number of people are engaging in outdoor leisure activities in areas inhabited by large carnivores; (2) many people are not prepared to safely enjoy outdoor activities or they behave inappropriately in the countryside; and (3) large carnivore attacks are influenced by the interaction between several human- and animal-related factors.

Thus, we first explored whether the long-term patterns in the number of attacks have been similar among different large carnivore species, and how they varied throughout the year. Then, we evaluated whether there might have been a general long-term change in the attack patterns by assessing whether victim ages and the frequency of attacks on parties vs. lone humans have changed in a congruent manner for the different species. Finally, we assessed the possible relationships between temporal trends of attacks on humans and outdoor activities, as well as the role that risk-enhancing human behaviour can have played in the observed increase in large carnivore attacks.
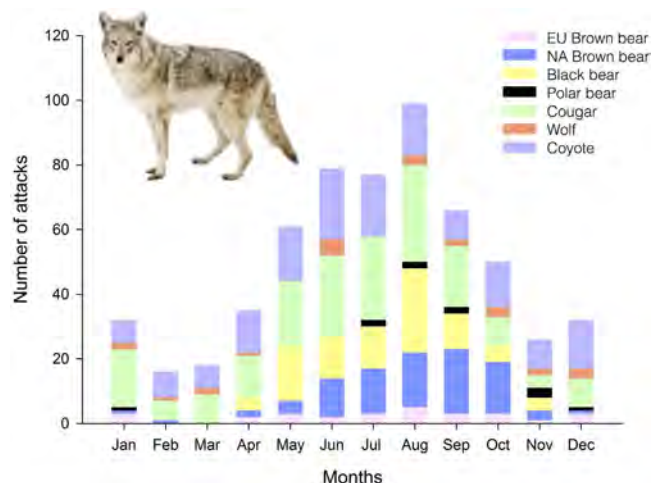
Figure 2. Temporal trends in large carnivore attacks on humans in developed countries: monthly patterns.
Most large carnivore attacks occurred from late spring to early autumn, when most people usually engage in outdoor activities. (The coyote picture has been downloaded from 123RF ROYALTY FREE STOCK PHOTOS (http://www.123rf.com), Image ID 14988151, James Mattil).

We analysed the circumstances of ca. 700 large carnivore attacks on people from 1955 in detail (when more reliable data became available) until the present for six species responsible for most of the large carnivore attacks recorded in North America and Europe: brown/grizzly bear *Ursus arctos*, black bear *Ursus americanus*, cougar *Puma concolor*, wolf *Canis lupus* and coyote *Canis latrans* in North America, brown bear in Europe, and polar bear *Ursus maritimus* circumpolar, i.e. Europe, Russia and North America. We also collected statistics concerning outdoor activities during the same period (see Methods for more details).

The number of large carnivore attacks on people has increased significantly over time, with contrasting trends across species (Fig. 1; Extended Data Table 1). In North America, coyotes (31.0% of the total number of attacks) and cougars (25.7%) were responsible for the majority of attacks, followed by brown bears (13.2%), black bears (12.2%) and wolves (6.7%). A similar increase over time was observed for brown bears (9.3%) in Europe and circumpolar for polar bears (1.9%; Fig. 1). Moreover: (a) the age of victims has also increased significantly over time showing different patterns across species (Extended Data Table 2 and Extended Data Fig. 1); and (b) the propensity to attack lone humans or parties depends on the large carnivore species, and only a slight but non-significant increasing trend of attacks on parties has been observed (Extended Data Table 3 and Extended Data Fig. 2A,B).

The patterns of attacks reported here may also reflect an increasing number of bold individuals in large carnivore populations, as this trait is often correlated with aggressiveness[13,14], and this might lead to more aggressive responses when large carnivores encounter humans. We hypothesise that intense and prolonged human-caused mortality imposes selection pressures on target populations (selective removal of certain phenotypes) and might lead to rapid evolutionary changes[15]. Natural selection maintains a mix of behavioural phenotypes in populations[16], the shy-bold behavioural continuum[17]; bold individuals thrive on risk and novelty, whereas shy individuals shrink from the same situations[18]. Persecution, however, is expected to result in the disproportionate removal of bold individuals, as they are less cautious[19], and thus more likely to be killed. As a consequence, shy individuals might have been overrepresented in remnant large carnivore populations in the past[17,18,20–22]. Additionally, individuals may become more vigilant and actively avoid contact with humans during times of intense persecution[23]. Although the history of large carnivore persecution and conservation differ across regions[9], the contemporary conservation paradigm emerged during the 1960s–1970s[24], when most bounty systems were banned[25] and large carnivores were reclassified from vermins or bountied predators to game or protected species. Since then, although large carnivores have continued to be hunted or managed (Extended Data Fig. 3), most populations have generally increased during the past four decades[9,11,12]. Increasing population trends in conjunction with relaxed artificial selection may potentially engender higher variation in behavioural temperaments[26], which is likely to alter individual responses to human encounters[22]. This significant increase of large carnivore populations in both North America and Europe, and their consequent range expansion, also may contribute to explain the observed increase in the attacks on humans.

However, similar to the increasing trend in attacks, the number of people engaging in outdoor leisure activities also has risen over time, a phenomenon that is significantly correlated with the observed trend in the number of attacks (Fig. 1; Extended Data Table 4, Extended Data Fig. 4A–C). Seasonally, most of the attacks occurred between late spring and early autumn (Fig. 2), when most people pursue outdoor activities[7,8]; in addition, because bears hibernate, they are unlikely to attack people in winter. Such an increase in recreational activities in areas inhabited by large carnivores implicitly increases the probability of a risky encounter and, therefore, a potential attack. However, even with more people visiting those areas, attacks are still extremely rare (Fig. 1): although some people may only focus on the total number of attacks, we have to bear in mind the long time period during which these attacks occurred.
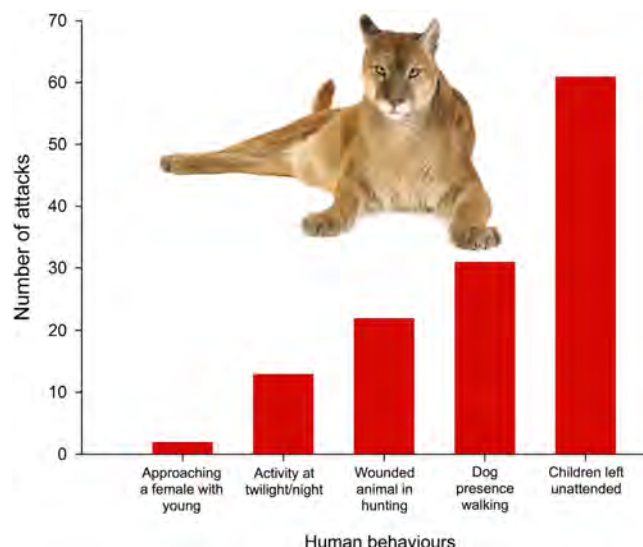
Figure 3. The number of attacks is modulated by human behaviour. Around half of the attacks were associated with risk-enhancing human behaviours. Out of 271 well-documented attacks, 47.6% were associated with certain human behaviours that may have contributed to the probability of suffering an attack. Within the principal category (children left unattended by their parents), the main species responsible for 91.9% of these attacks were cougars (50.8%), coyotes (27.9%) and black bears (13.2%). (The cougar picture has been downloaded from 123RF ROYALTY FREE STOCK PHOTOS (http://www.123rf.com), Image ID 2597979, Eric Isselee).

Remarkably, risk-enhancing human behaviour has been involved in at least half of the well-documented attacks (47.6%; Fig. 3). From highest to lowest, the five most common human behaviours occurring at the time of an attack were (a) parents leaving children unattended, (b) walking an unleashed dog, (c) searching for a wounded large carnivore during hunting, (d) engaging in outdoor activities at twilight/night and (e) approaching a female with young. These are clearly risk-enhancing behaviours when sharing the landscape with large carnivores. For example, the most frequently recorded human behaviour was children left unattended (47.3%), which were most often attacked by cougars (50.8% of the attacks), coyotes (27.9%) and black bears (13.2%). Risk-enhancing human behaviour is not the sole reason behind large carnivore attacks on humans. The causes of the other half of the attacks do not seem to be related to risk-enhancing human behaviour, for example, accidentally walking close to a mother with young or to a carcass with a bear nearby or an encounter with a food-conditioned individual (which is an indirect result of a risk-enhancing human behaviour[8]).

Thousands of interactions occur between people and large carnivores with no human injuries or fatalities. Even if attacks have increased over time, they remain extremely rare events (e.g. a cross-continental average of 24.1 attacks and 3.9 fatalities per year during the last decade, all species pooled; Fig. 1). Other wildlife (bees and mosquitos, spiders, snails, snakes and ungulates) and domestic dogs are far more responsible for human fatalities[1,27]. But humans are not the only victims. When attacks occur, large carnivores are frequently killed and negative attitudes towards large carnivores harden[6]. Lethal removal of 'problematic' individuals is effective in solving the local problem caused by a given individual[28], but generally this happens after an aggressive behaviour, human injury or death has occurred. Consequently, both humans and carnivores suffer from these incidents.

After decades of minimal interaction between humans and large carnivores in many regions of developed countries, many people involved in outdoor activities may lack knowledge about how to avoid risky encounters with large carnivores and what to do when such encounters occur. From an early age most of us learn social norms, rules and how to decrease risks in urban environmental settings, but much less effort is expended to teach us how to safely enjoy outdoor activities or to behave appropriately in the countryside. However, it is up to us to reduce the likelihood of an attack. The increasing human presence in areas inhabited by large carnivores, together with their population recoveries[9,11,12], requires an improvement in information, education and prevention guidelines, and their enforcement, which are of paramount importance to reduce both the risks to humans and the killing of carnivores[1,4,7,28,29]. Educating people that share landscape with large carnivores can represent a crucial factor to help reducing the number of attacks and also the negative attitudes towards large carnivore conservation, especially because of the difficulty to envisage risk estimates. Indeed, scenarios of attacks are extremely different and may depend on many different factors, such as human population and carnivore densities, time of the day, human activities, personality and condition of the large carnivore, party size or even subtle details, like the presence of an unleashed dog at the moment of the attack and/or the landscape features of the area where an attack has happened. As conflicts between humans and large carnivores continue to increase, accurate information becomes crucial to informed human–wildlife conflict management. Communicating about large carnivore-inflicted human injuries and fatalities in a statistical manner contributes to better understanding of common patterns in large carnivore attacks, further reduces chances of injury or death and promotes public appreciation of these species. An important strategy to reduce attacks on humans is to inform people how to avoid

and manage aggressive encounters. But nowadays, educational and interpretive efforts aimed at decreasing the risk of large carnivore attacks should not focus exclusively on people living in rural and wilderness areas. Indeed, many people living in cities should also be included within the category of groups at risk because of the increasing number of them enjoying outdoor activities in areas inhabited by large carnivores and the expanding population of carnivores (mainly coyotes) in suburban areas.

Although large carnivore attacks on humans are influenced by the interaction between multiple human- and animal-related factors, adapting our own behaviours when coexisting with large carnivores has the potential to reduce the number of attacks to about half of today's level. The examples provided by the numerous cases of children injured/killed while left unattended by their parents, attacks on people jogging/walking alone at twilight and during hunting, should make us reflect on our responsibilities, the possibility of decreasing the number of these tragic events and changing the observed trends. Understanding the circumstances associated with large carnivore attacks should help us to reduce them and thereby minimize the role that fear and supposition may play in large carnivore management and conservation.

Methods

Collection of records of large carnivore attacks on humans.
Records of large carnivore attacks (i.e. attacks resulting in physical injury or death) on humans for the brown bear, black bear, cougar, wolf and coyote were collected for North America (the United States and Canada). In addition, with the aim to broaden our research and obtain a general picture of large carnivore attacks on humans in developed countries, we complemented the North American dataset with information on brown bear attacks in three European countries (Sweden, Finland and Spain) as well as data on attacks by polar bears in Europe (Svalbard; Norway), Russia, the United States, and Canada. Our time period spanned from 1955 to 2014 and our search resulted in a total of 697 attacks of large carnivores on people.

We consider that we both recorded the majority of such events occurring during the last six decades in these developed countries and avoided bias due to possible changes in reporting probability given (*i*) the large number of experienced people involved in the work (some of them had their own database on attacks, which started at the beginning of the 1900s), (*ii*) the multiple sources of information used to collect recorded attacks and (*iii*) the sensational nature and media impacts of attacks that end with injuries or the death of the victim since the beginning of the past century. Records of attacks were collected from unpublished reports and PhD/MS theses, webpages (last accessed in November 2014, but currently available at the specific addresses listed by species below), books and scientific articles, as well as personal datasets from some of the co-authors. In addition, to complete the data obtained from the above-cited sources, we also collected dozens of news reports from online newspapers. To do this, for each species and area, we searched on an annual basis for news articles on Google using the combination of the following terms: "species name" + "attack" and "species name" + "attack" + "human". Because of the use of multiple sources, several attacks recurred repeatedly during the search, but we used information such as date, locality and sex/age of the victims to prevent duplicate records in the dataset. However, the lack of some records would still not result in a bias in the general patterns we observed in the present work, because: (*i*) we followed the same procedure for each species and, thus, we collected at least an equally biased sample of attacks per species and (*ii*) patterns of attacks on humans over time are less sensitive to unequally biased samples of attacks than quantitative comparisons of the frequency of attacks across species (which is not the aim of the present work).

When possible, we recorded the following information for each attack: (1) species; (2) year; (3) month; (4) country; (5) time of the attack during the day (which we classified into three categories: twilight, day, night); (6) activity of the victim (15 categories: hunting, fishing, field work, camping, hiking, jogging, skiing, biking, horse riding, fruit/mushroom picking, photography, walking, dog walking, activity near the house/in the backyard, playing); (7) size of party being attacked (simplified into three categories: victim alone, child – from 0 to 16 years old– in a party of adults, adult – >16 years old – in a party of adults); (8) end of the attack, i.e. attack resulting in human injuries or death; and (9) scenario when the attack occurred, i.e. the factor that could have triggered the attack. We were able to delineate eight categories: female with young, aggressive reaction after a sudden encounter (i.e. a person surprises the large carnivore at close range), food defence (e.g. a bear close to a carcass), food conditioning (i.e. encounter with a large carnivore that consumes human-derived foods, consequently associating people with easily accessible, attractive foods, and which has lost much of its avoidance mechanisms towards humans), predatory (i.e. when the large carnivore exploited a human as prey), wounded animal (i.e. during hunting), feeding large carnivores, and presence of one or more dogs. Unleashed dogs can exacerbate the probability of a large carnivore attack, because a dog that runs away from a large carnivore towards the owner can trigger a dangerous situation when the carnivore chases it[30]. When dogs were involved, large carnivores usually focused their attention on the dog rather than on the person. However, in some instances the human was attacked as a consequence of its proximity to the dog or because of its reaction towards the large carnivore.

Below, we describe the sources used to collect data on large carnivore attacks on people for each species since 1955:

1. *North American brown and black bears*. We recorded a total of 92 and 85 attacks, respectively. Information was compiled from[28], Wikipedia List of fatal bear attacks in North America (http://en.wikipedia.org/wiki/List_of_fatal_bear_attacks_in_North_America), Fatal Bear Attack Statistics for the USA & Canada (http://www.blackbearheaven.com/bear-attack-statistics.htm) and online newspapers. Additionally, we also extracted information for the black bear from[8] and California Black Bear Public Safety Incidents, California Department of Fish and Wildlife (https://www.wildlife.ca.gov/News/Bear/Bear-Incidents).

2. *Cougar*. We recorded a total of 179 attacks. Data on attacks were collected from[1,31], the List of Mountain Lion Attacks (http://www.cougarinfo.org/attacks.htm), Mountain Lion Attacks from 1991 to 2000 (http://www.cougarinfo.org/attacks2.htm), Mountain Lion Attacks from 2001 to 2010 (http://www.cougarinfo.org/

attacks3.htm), Mountain Lion Attacks from 2011 to Now (http://www.cougarinfo.org/attacks4.htm) and on-line newspapers.

3. *Wolf*. We recorded a total of 47 attacks. Data on attacks were collected from[32,33], the Wikipedia List of wolf attacks in North America (http://en.wikipedia.org/wiki/List_of_wolf_attacks_in_North_America), Wikipedia List of wolf attacks (http://en.wikipedia.org/wiki/List_of_wolf_attacks), Wolf Attacks on Humans (http://www.aws.vcn.com/wolf_attacks_on_humans.html) and online newspapers. We did not include the wolf in Europe, because predatory attacks on people have been extremely rare during the last six decades, with the last recorded predatory attack occurring in 1974 in Spain[32].

4. *Coyote*. We recorded a total of 216 attacks. Data on attacks were collected from[4,34–36], the Wikipedia Coyote attacks on humans (http://en.wikipedia.org/wiki/Coyote_attacks_on_humans), Coyote Attacks on Children (http://www.varmintal.com/attac.htm), Coyote Attacks: An Increasing Suburban Problem (http://escholarship.org/uc/item/8qg662fb), Coyote Attacks On People in the U.S. and Canada (http://tchester.org/sgm/lists/coyote_attacks.html) and online newspapers.

5. *European brown bear*. We recorded a total of 65 attacks. Information from Spain was available from the unpublished personal database of J.N. and A.F.G., whereas Fennoscandian records were obtained from[37,38] and unpublished data from I.K., H.N. and J.F.

6. *Polar bear*. We recorded a total of 13 attacks. Information was recorded from Wikipedia List of fatal bear attacks in North America (http://en.wikipedia.org/wiki/List_of_fatal_bear_attacks_in_North_America) and online newspapers (both North American and European –some attacks have been recently recorded in the Norwegian Svalbard archipelago–).

Collection of records on outdoor human activities. Data on outdoor activities was only available for the US and Sweden. We collected the following information: (1) annual recreation visitation in American Protected Areas published by the National Park Service Visitor Use Statistics (IRMA data system), National Park Service, U.S. Department of the Interior, Natural Resource Stewardship and Science (https://irma.nps.gov/Stats/Reports/National). To reduce bias in our analyses, we only used information from the National Parks located in the 30 states where at least one large carnivore attack occurred since 1955 (Alaska, Arizona, California, Colorado, Florida, Georgia, Idaho, Illinois, Kansas, Kentucky, Massachusetts, Michigan, Minnesota, Montana, New Hampshire, New Jersey, New Mexico, New York, North Carolina, North Dakota, Ohio, Oklahoma, Pennsylvania, Tennessee, Texas, Utah, Vermont, Virginia, Washington, Wyoming); (2) statistics on number of people doing outdoor activities in the US, which were obtained from[39], the U.S. Department of the Interior, U.S. Fish and Wildlife Service, and U.S. Department of Commerce, U.S. Census Bureau[40–44]; (3) American trends in the sporting goods market related to outdoor activities associated with attacks (cross-country training shoes, jogging and running shoes, camping, optics, snow skiing, bicycles and related supplies), which were collected from the U.S. Census Bureau, Statistical Abstract of the United States[45,46]; and (4) Statistics Sweden's time series tables concerning outdoor activities, which derive from ULF surveys (Living Conditions Surveys) from 1975 onwards (http://www.scb.se/sv_/Hitta-statistik/Statistik-efter-amne/Levnadsforhallanden/Levnadsforhallanden/Undersokningarna-av-levnadsforhallanden-ULFSILC/12202/12209/#). Information on outdoor human activities was only used to support the highlighted trends and patterns of large carnivore attacks; thus, its sole function is to be supportive to the main text and it was not used in our analyses.

Collection of records on large carnivore harvest. We used data from brown bear, black bear, cougar and wolf harvests in certain US and Canadian states as examples of trends and numbers in large carnivore harvest over time. First, brown bear harvesting records for Alaska and British Columbia were obtained from the Alaska Department of Fish and Game[47,48] and M. Wolowicz unpublished data (Big Game Harvest Statistics 1976–2012, British Columbia), respectively. Second, data on black bear harvesting statistics in Alaska was obtained from the Alaska Department of Fish and Game[49–51]. Third, cougar harvesting records in Colorado, Alberta and British Columbia were obtained from[52–54], J. Apker unpublished data (Colorado Division of Wildlife) and M. Wolowicz unpublished data (Big Game Harvest Statistics 1976–2012, British Columbia). Finally, wolf harvesting statistics were extracted from the Alaska Department of Fish and Game[55–58]. Again, as we did for the information on outdoor human activities, the records on large carnivore harvest were only used to support the highlighted trends and patterns of large carnivore attacks; thus, their sole function is to be supportive to the main text and they were not used in our analyses.

Data analysis. Considering the total dataset on large carnivore attacks since 1955, we first assessed whether the number of attacks varied over time, on a yearly basis, and among species by fitting a Generalized Linear Model (GLM) with the number of attacks against year and species (Extended Data Table 1). We also included the interaction term between year and species to account for the fact that the number of attacks may vary over time heterogeneously across species. Because our data were overdispersed, we fitted the GLM using a Negative Binomial distribution instead of a Poisson distribution. Next, to assess a potential change in the behavioural temperament of large carnivores over time, we tested whether the log-transformed age of the victim and party size (three levels) varied over time and among species by fitting a linear model with a Gaussian distribution and a GLM with a multinomial distribution (three levels), respectively (Extended Data Tables 2 and 3). Party size was classified into three categories, which allows differentiating between attacks on lone individuals and groups, as well as if the victim in a group was a young person: i) the victim was alone; ii) the victim was a young person (<16 years old) in a group of adults (2 or more people); and iii) the victim was an adult (>16 years old) in a group of adults (2 or more people). We also considered the interaction term in these models to account for the fact that the surrogates of the changes in the temperament of large carnivores used may vary over time differently across species. Finally, we

analysed a subset of the dataset considering only those attacks occurring in the US and, together with information on human influx in natural areas, we tested if the number of attacks was related to the number of people involved in outdoor activities by building a GLM with a Gamma distribution, considering year, the number of visitors and their interaction term as factors in the model (Extended Data Table 4).

For each analysis, we used an information theoretic framework to rank a set of competing models based on AIC (Akaike's Information Criterion [AIC])[59]. We used a stepwise selection procedure to create a candidate set of a priori competing models starting from the simplest null model (intercept only model) to the full model (Extended Data Tables 1, 2, 3 and 4). To select the best candidate model, we used AIC value corrected for small sample sizes (AICc) and Weighted AIC, which indicates the probability that the model selected is the best among the candidates[59]. Models within $\Delta AIC < 2$ were considered to have substantial empirical support[59]. All statistical analyses were performed using R 3.0.2 statistical software[60]. GLMs were run with the "lme4"[61] and "nlme"[62] package.

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V.P., M.M.D., F.P. and J.V.L.B. initiated and conceived the study, V.P. prepared the database with the collaboration of M.M.D., J.V.L.B., J.N., A.F.-G., I.K., S.H. and H.N. M.M.D. and J.V.L.B. analysed the data, V.P. wrote the manuscript with M.M.D. and J.V.L.B. and all authors commented on the manuscript draft.

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Collapse of the world's largest herbivores

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Large wild herbivores are crucial to ecosystems and human societies. We highlight the 74 largest terrestrial herbivore species on Earth (body mass ≥ 100 kg), the threats they face, their important and often overlooked ecosystem effects, and the conservation efforts needed to save them and their predators from extinction. Large herbivores are generally facing dramatic population declines and range contractions, such that ~60% are threatened with extinction. Nearly all threatened species are in developing countries, where major threats include hunting, land-use change, and resource depression by livestock. Loss of large herbivores can have cascading effects on other species including large carnivores, scavengers, mesoherbivores, small mammals, and ecological processes involving vegetation, hydrology, nutrient cycling, and fire regimes. The rate of large herbivore decline suggests that ever-larger swaths of the world will soon lack many of the vital ecological services these animals provide, resulting in enormous ecological and social costs.

INTRODUCTION

Terrestrial mammalian herbivores, a group of ~4000 species, live in every major ecosystem on Earth except Antarctica. Here, we consider the 74 wild herbivore species with mean adult body masses ≥100 kg. These largest species represent four orders (Proboscidea, Primates, Cetartiodactyla, and Perissodactyla) and 11 families (Elephantidae, Rhinocerotidae, Hippopotamidae, Giraffidae, Bovidae, Camelidae, Tapiridae, Equidae, Cervidae, Suidae, and Hominidae). Most of these species are entirely herbivorous, but some are generalists (for example, Suidae). Herein, we provide the first comprehensive review that includes the endangerment status and key threats to the world's largest herbivores (≥100 kg), the ecological consequences of their decline, and actions needed for their conservation. We review how the combined impacts of hunting, encroachment by humans and their livestock, and habitat loss could lead to the extinction of a suite of large herbivores relatively soon. By reviewing their ecological roles, we show how the loss of large herbivores can alter ecosystems, mostly to the detriment of other species, including humans, through the loss of ecological interactions and ecosystem services. We end by outlining future directions for research

and conservation action to help diminish the imminent possibility of losing the remaining large herbivores from many ecosystems throughout the world.

STATUS

According to the International Union for the Conservation of Nature (IUCN), 44 of the 74 largest terrestrial herbivores (~60%) are listed as threatened with extinction (including 12 critically endangered or extinct in the wild), and 43 (~58%) have decreasing populations [(1); table S1]. Their current population sizes exhibit large differences among species, spanning over four orders of magnitude, with some populations estimated to comprise fewer than 100 individuals [for example, Javan rhinoceros (*Rhinoceros sondaicus*)], whereas a few others [for example, Eurasian elk/moose (*Alces alces*)] comprise more than 1 million individuals (table S1).

Most large herbivore species are found in Africa (*n* = 32), Southeast Asia (*n* = 19), India (*n* = 14), China (*n* = 14), and the rest of Asia (*n* = 19) (Fig. 1A). Fewer species are found in Europe (*n* = 7), Latin America (*n* = 5), and North America (*n* = 5) (fig. S1). Overall, 71 species occur in developing countries, whereas only 10 occur in developed countries. The highest number of threatened large herbivores occurs in Southeast Asia (*n* = 19, east of India and south of China), followed by Africa (*n* = 12), India (*n* = 9), China (*n* = 8), Latin America (*n* = 4), and Europe (*n* = 1) (Fig. 1B and fig. S1). Notably, all of the threatened species of large herbivores are found in developing countries, with the exception of European bison (*Bison bonasus*), with developed countries having already lost most of their large mammals in the ongoing megafauna extinction (2).

Ecoregions [*n* = 30, based on (3)] with the most-threatened large herbivore species (≥5) are found in southern Asia, throughout much of extreme Southeast Asia, as well as Ethiopia and Somalia of eastern Africa (Fig. 1B and tables S2 to S4). The ecoregions with seven threatened large herbivore species are the Himalayan subtropical broadleaf forests, the Sunda Shelf mangroves, and the peninsular Malaysian rain forests (table S4). Hunting for meat is the predominant threat in all ecoregions

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Fig. 1. Large herbivore total species richness (A) and threatened (B) at the ecoregion level. Ecoregion lists for each species were obtained using the IUCN Red List species range maps and (3) and are based on the ecoregions where each species is native and currently present.

including four critically endangered, and the white rhinoceros is nearly threatened with the current poaching crisis likely to alter its status downward in the near future. Ironically, this endangerment follows one of the greatest success stories in the history of modern conservation: the recovery of the southern white rhino (*C. simum simum*) from a single population of fewer than 100 individuals in the early 1900s to about 20,000 today [(7), table S1]. Even with the current crisis of rhinoceros poaching, this illustrates that, with sufficient protection, recovery is possible for relatively slow-breeding species that are highly prized by poachers.

Many of the largest herbivore species have ranges that are collapsing (8, 9). Estimates of range contractions have been made for 25 of the 74 species, and on average, these species currently occupy only 19% of their historical ranges (table S1). This is exemplified by the elephant, hippopotamus, and black rhinoceros, all of which now occupy just tiny fractions of their historical ranges in Africa (Fig. 3). Furthermore, many of these declining species are poorly known scientifically, and badly in need of basic ecological research. Scientific research effort, as measured by the number of published articles on each species, has been much greater for nonthreatened ($\bar{x} = 296$, $SE_{\bar{x}} = 129$) than threatened species ($\bar{x} = 100$, $SE_{\bar{x}} = 33$), and greater overall for species in developed countries ($\bar{x} = 790$, $SE_{\bar{x}} = 376$) than developing countries ($\bar{x} = 172$, $SE_{\bar{x}} = 33$). Indeed, those that have been most studied are primarily game species in wealthy countries, including red deer (*Cervus elephus*), reindeer (*Rangifer tarandus*), and moose/ Eurasian elk (*A. alces*) (fig. S2). In contrast, 18 of the large herbivore species from developing regions have been featured in fewer than 10 published articles each (fig. S2), which, in part, reflects negative or indifferent attitudes toward some species, or low levels of scientific funding, making it difficult to garner government and public support for scientific studies and conservation of these taxa (10). For example, although highly threatened, the six large-bodied species in the Suidae family are collectively represented by only 26 published articles ($\bar{x} = 4$ per species, range = 0 to 14) (table S5 and fig. S2).

Between 1996 and 2008, the conservation status of seven herbivore species $\geq$100 kg deteriorated, whereas only two species improved (table S1). By contrast, small herbivores are doing relatively well with just 16% of species below 5 kg in body mass classified as threatened (fig. S3). In contrast to the developing world, effective game laws and extirpation of large predators in developed countries of northern latitudes have frequently resulted in an overabundance of large herbivores. In the absence of wolves (*Canis lupus*) and other large carnivores, overabundant cervids can negatively impact biodiversity, stream morphology, carbon sequestration,

containing at least five threatened large herbivore species (table S2). These ecoregions fall mostly within the tropical and subtropical moist broadleaf forests biome (20 of 30 ecoregions), but biomes containing combinations of grasslands, shrublands, savannas, mangroves, or other forest types represent the other 10 ecoregions with at least five threatened large herbivore species (table S3).

All 10 large herbivore species within the families Elephantidae, Hippopotamidae, Hominidae, and Tapiridae are currently threatened (Fig. 2). The large herbivores of the families Suidae, Rhinocerotidae, Equidae, and Camelidae are also highly endangered, with 15 of 20 member species threatened (Fig. 2). Only eight terrestrial megafauna species ($\geq$1000 kg) exist today as opposed to more than five times that number (~42) that were present in the late Pleistocene (4–6). The eight remaining species are split between Africa (African elephant, *Loxodonta africana*, hippopotamus, *Hippopotamus amphibius*, and the white and black rhinoceros, *Ceratotherium simum* and *Diceros bicornis*, respectively) and Southeast Asia (Asian elephant, *Elephas maximus*, and the Indian, Javan, and Sumatran rhinoceros, *Rhinoceros unicornis*, *R. sondaicus*, and *Dicerorhinus sumatrensis*, respectively). Of these, seven are threatened,

Fig. 2. Proportion of large herbivore species listed as threatened by IUCN. The total number of herbivore species in each family is shown after each family name. Individual threatened species by family include Elephantidae: African elephant (VU), Asian elephant (EN); Hippopotamidae: hippopotamus (VU), pygmy hippopotamus (EN); Hominidae: eastern gorilla (EN), western gorilla (EN); Tapiridae: Malayan tapir (VU), Baird's tapir (EN), lowland tapir (VU), mountain tapir (EN); Suidae: Philippine warty pig (VU), Oliver's warty pig (EN), Visayan warty pig (CR), Palawan bearded pig (VU), bearded pig (VU); Rhinocerotidae: Indian rhinoceros (CR), Javan rhinoceros (CR), Sumatran rhinoceros (CR), black rhinoceros (CR); Equidae: Grevy's zebra (EN), mountain zebra (VU), African wild ass (CR), Przewalski's horse (EN), Asiatic wild ass (CR); Cervidae: sambar (VU), barasingha (VU), Père David's deer (EW), white-lipped deer (VU); Camelidae: bactrian camel (CR); Bovidae: Indian water buffalo (EN), gaur (VU), kouprey (CR), European bison (VU), wild yak (VU), banteng (EN), takin (VU), lowland anoa (EN), tamaraw (CR), mountain nyala (EN), scimitar-horned oryx (EW), mountain anoa (EN), Sumatran serow (VU), walia ibex (EN). Scientific names in table S1.

and ecosystem function (*11*). Confining large herbivores within fixed boundaries can also lead to overabundance as with bison (*Bison bison*) in North America (*12*) and elephants in Africa (*13*).

THREATS

The main threats to large herbivores are hunting, competition with livestock, and land-use change such as habitat loss, human encroachment, cultivation, and deforestation (Fig. 4 and fig. S4). Extensive overhunting for meat across much of the developing world is likely the most important factor in the decline of the largest terrestrial herbivores (*14–17*). Slow reproduction makes large herbivores particularly vulnerable to overhunting. The largest- and slowest-to-reproduce species typically vanish first, and as they disappear, hunters turn to smaller and more fecund species (*14*), a cascading process that has likely been repeated for thousands of years (*6, 18, 19*). In synergy with changes in land use, hunting for meat has increased in recent years due to human population growth, greater access to wildlands due to road building, use of modern firearms and wire snares, access to markets, and the rising demand for wild meat (*14, 20*). Wild meat harvests have been especially

high in tropical forests, leading to vertebrate extirpations on large spatial scales, a process originally dubbed the "empty forest" syndrome (*21*). Annual consumption of wildlife meat was estimated to be 23,500 tons in Sarawak, Malaysia (*22*), and 89,000 tons in the Brazilian Amazon (*23*). Wild meat hunting also represents an increasing threat in African savannas, resulting in widespread declines in herbivore populations (*17*). Because wildlife populations outside of protected areas wane, hunters are shifting their attention more to populations in protected areas (*17*). Demand for wild meat is intensifying, supply is declining, and protected area management budgets for protecting wildlife from overhunting are often inadequate, particularly in developing nations. This creates a "perfect storm," whereby overhunting often imparts catastrophic population declines (*17*). Between 1970 and 2005, large mammal populations in Africa's protected areas decreased by about 59% (*16*). In part due to overhunting, current ungulate biomass was recently calculated to be only 21% of estimated potential ungulate biomass in Zambia's national parks (*24*).

Hunting large herbivores for body parts is also driving down populations of some species, especially the iconic ones. Organized crime is facilitating a dramatic decline of elephants and rhinoceros in parts of Africa and southern Asia, reversing decades of conservation accomplishments. Poaching and illegal trade in elephant products are currently the top threats to elephants (*25*). Ivory poaching has surged in recent years, largely due to a rise in demand for and price of ivory in China (*26*). The number of forest elephants (*L. africana cyclotis*) in central Africa declined by 62% between 2002 and 2011 (*25*). Currently, 75% of elephant populations are declining and at risk of extirpation, and the range of elephants has drastically declined (*26*). More than 100,000 African elephants were poached during the 3-year period from 2010 to 2012 (*26*). This level of illegal kills represents 20% of the current estimated population size of 500,000 African elephants, and even populations of savanna (or bush) elephants (*L. africana africana*) are now declining (*26*). Poaching of rhinoceros for their horns has also soared in recent years because of its use in traditional Chinese medicine. The number of rhinoceros poached in South Africa grew by two orders of magnitude from 13 in 2007 to 668 in 2012 (*27*) and 1004 in 2013 (*28*). The situation is so desperate that an emergency intervention is planned in which large numbers of white rhinoceros will be translocated out of South Africa's Kruger National Park and placed in potentially more secure areas (*29*). Furthermore, at least in part due to poaching, Africa's western black rhinoceros (*D. bicornis longipes*) was declared extinct in 2011 (*1*). This slaughter is driven by the high retail price of rhinoceros horn, which exceeds, per unit weight, that of gold, diamonds, or cocaine (*27*). If accelerated poaching by organized crime syndicates continues, Africa's rhinoceroses may become extinct in the wild within 20 years (*27*). Numerous species of other large herbivores are also hunted for their body parts, including hippopotamus for their ivory teeth, bovids for horns and skulls, equids for hides, tapirs for feet and hides, cervids for antlers, giraffids for hides, and gorillas for heads, hands, and feet (*1*). Large herbivores are more vulnerable than smaller herbivores to overharvesting through a combination of the generally higher value of larger bodies or their parts, and the slow life history of the larger herbivores. Together, these increase the likelihood of large herbivores being harvested and reduce their ability to recover from such harvests.

Livestock continues to encroach on land needed for wild grazers and browsers, particularly in developing countries where livestock production tripled between 1980 and 2002 (*30*). There are an estimated 3.6
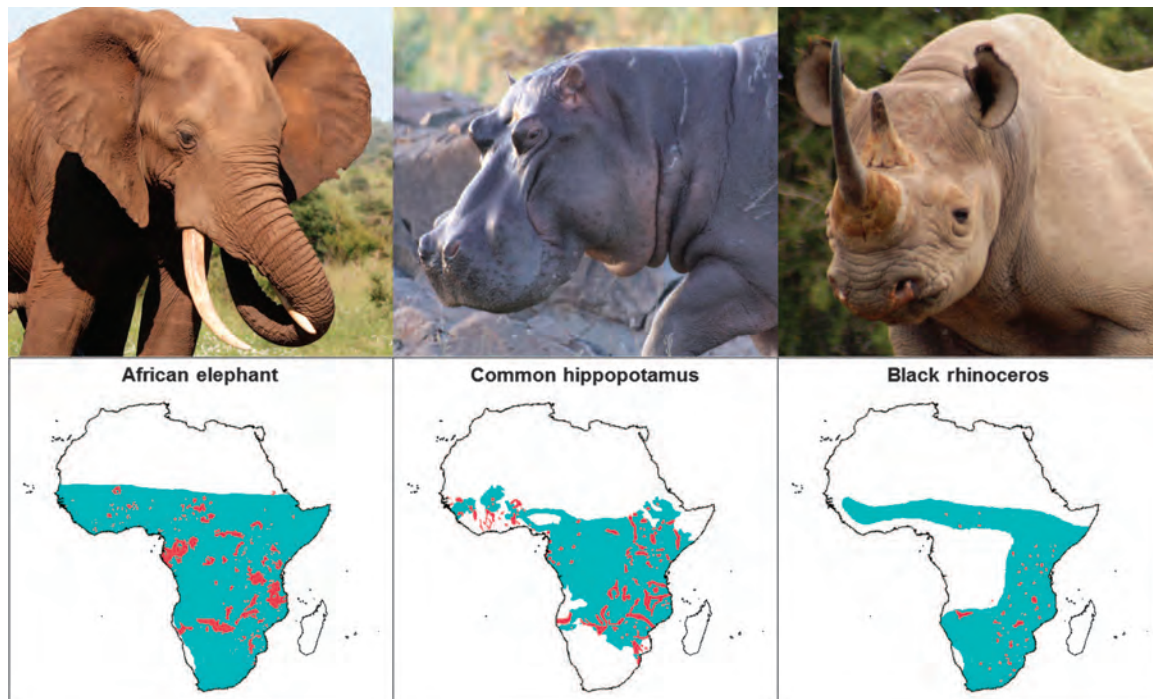
Fig. 3. Range contractions over time for three iconic African herbivores. African elephant (ca. 1600 versus 2008), common hippopotamus (ca. 1959 versus 2008), and black rhinoceros (ca. 1700 versus 1987). The historical ranges are in blue, whereas the most recent ranges are represented by darker-colored polygons. For security purposes, the most recent black rhinoceros range polygons (1987) have been moved by random directions and distances. The black rhinoceros range has continued to shrink since 1987 across most of Africa, but has expanded locally in Zambia, South Africa, and Namibia through recent reintroductions, and the most current range polygons are not shown because of the recent poaching pressure on the rhinoceros. Photo Credits: Elephant and hippopotamus (K. Everatt), rhinoceros (G. Kerley).
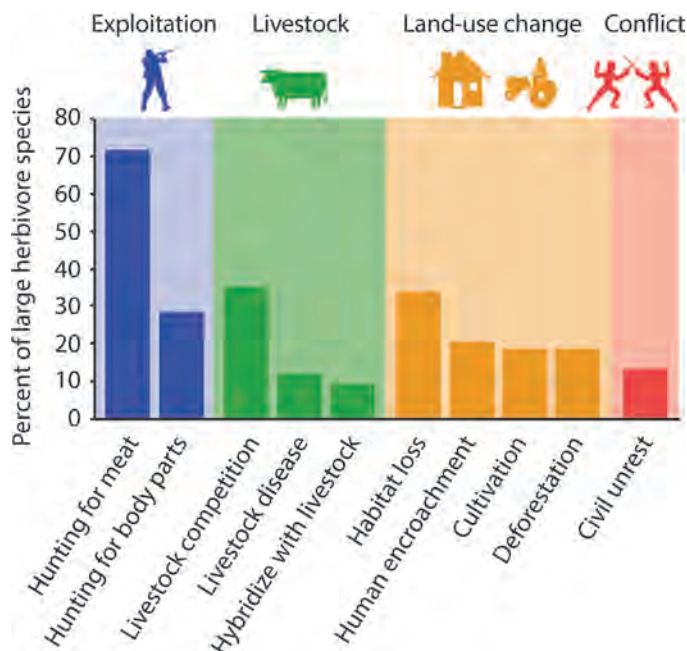
Fig. 4. Proximate threats faced by large herbivores globally. Threats faced by each species were categorized using information in the IUCN Red List species fact sheets. The total adds up to more than 100% because each large herbivore species may have more than one existing threat.

billion ruminant livestock on Earth today, and about 25 million have been added to the planet every year (~2 million/month) for the last 50 years (*31*). This upsurge in livestock has resulted in more competition for grazing, a reduction in forage and water available to wild herbivores, a greater risk of disease transmission from domestic to wild species (*32*), and increased methane emissions (*31*). In central Asia, the expansion of goat grazing for cashmere wool production for international export has reduced habitats available to large herbivores with consequent impacts on their predators including snow leopards (*Panthera uncia*) (*33*). Livestock competition is also a significant threat to large herbivores elsewhere in Asia, with multiple species jeopardized by this threat in India (*n* = 7), China (*n* = 7), and Mongolia (*n* = 4) (fig. S4). Hybridization with domestic livestock varieties is also a serious problem for some wild species such as the Indian water buffalo (*Bubalus arnee*), Bactrian camel (*Camelus ferus*), wild yak (*Bos mutus*), Przewalski's horse (*Equus ferus*), and several wild pig species (*Sus* spp.) in Southeast Asia (*1*). Ironically, in many pastoral settings in Africa, domestic livestock are abundant but not regularly consumed for subsistence, and are instead kept as a means of storing wealth, as a status symbol, or for consumption on special occasions (*14*). Livestock is a private good, and so, people invest significant energy to protect it, whereas wild herbivores are typically a public good, often resulting in weak incentives for their conservation and in many cases open access to the resource, both of which commonly result in overuse.

Habitat loss is a significant threat to large herbivores in parts of Latin America, Africa, and Southeast Asia (Fig. 4). The causes of this threat have important drivers originating in developed countries due

Fig. 5. Conceptual diagrams showing the effects of elephants, hippopotamus, and rhinoceros on ecosystems. (**A**) African elephants (*L. africana*) convert woodland to shrubland (*53*), which indirectly improves the browse availability for impala (*A. melampus*) (*53*) and black rhinoceros (*D. bicornis minor*) (*54*). By damaging trees, African elephants facilitate increased structural habitat complexity benefiting lizard communities (*100*). Predation by large predators (for example, lions) on small ungulates is facilitated when African elephants open impenetrable thickets (*48*). African elephants are also great dispersers of seeds over long distances (*13*). (**B**) Hippopotamus (*H. amphibius*) maintain pathways in swamps, leading to new channel systems (*101*). Areas grazed by hippopotamus are often more nutritious, which benefits kob (*K. kob*) (*55*). Mutualism and semiparasitism between hippopotamus and birds have also been shown, via the latter eating insects on hippopotamus (*73*). (**C**) White rhinoceros (*C. simum*) maintain short grass patches in mesic areas, which increases browse for other grazers (impalas, wildebeests, *C. taurinus*, and zebra, *Equus burchelli*) and changes fire regimes (*71*).
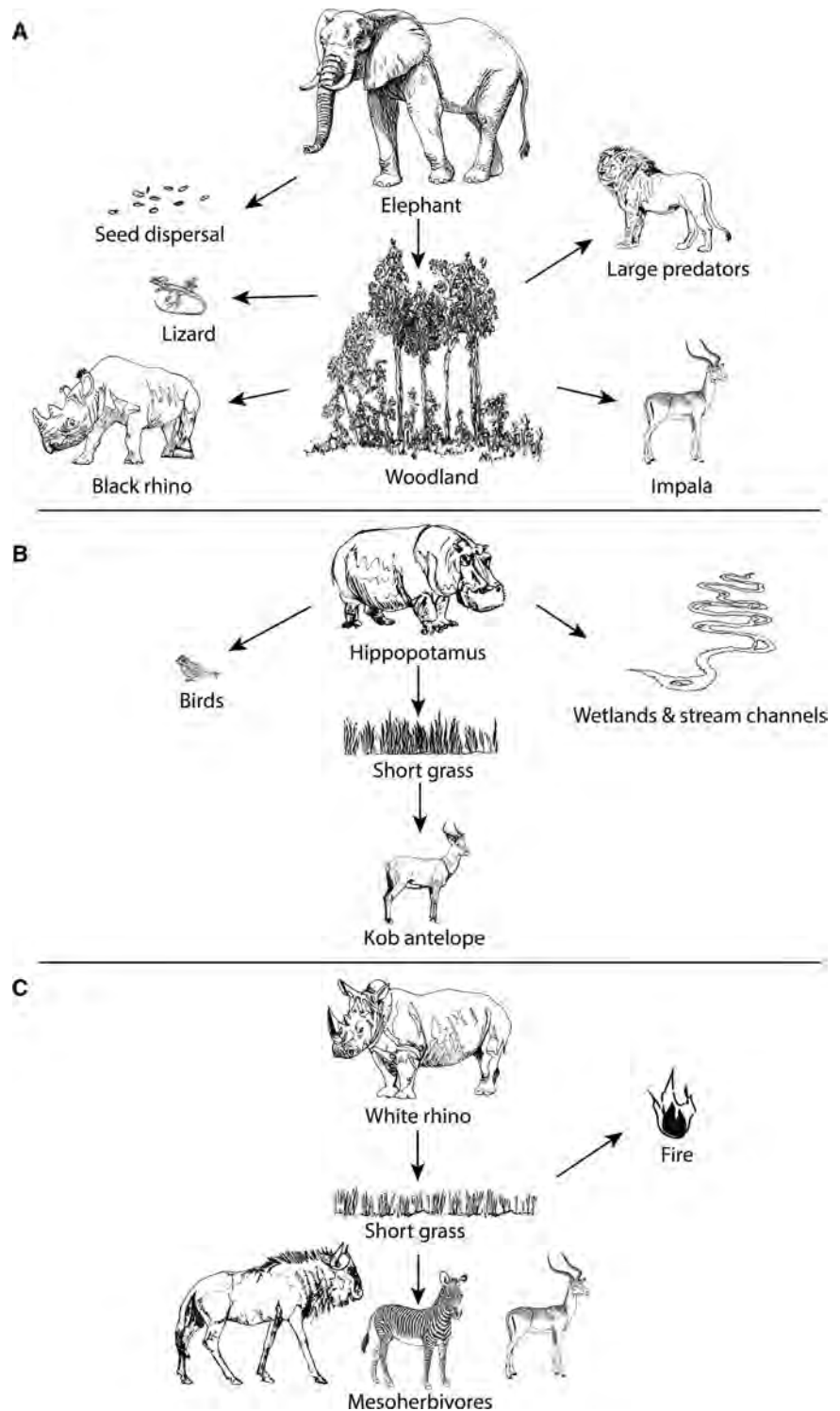
to demand for agricultural and other products. Southeast Asia has the highest rate of deforestation among tropical regions, and if trends continue, Southeast Asia could lose 75% of its original forests and nearly half of its biodiversity by the end of this century (*34*). Habitat loss is typically asymmetrical with respect to quality, with remaining habitat generally being less productive. A similar trend is found in the tendency to create protected areas in steep, rocky, or dry terrain (*35*), trapping species of conservation concern in suboptimal habitats (*36*). Additionally, the greater area requirements of larger species make them unable to persist in smaller fragments of habitat, which may still support smaller herbivores. Their larger area requirement also makes larger species that persist in fragments increasingly susceptible to conservation challenges that affect small populations. This suggests a greater likelihood of extinction among the larger rather than smaller herbivores.

Other threats to large herbivores include human encroachment (including road building), cultivation of crops, and civil unrest, all of which contribute to population decline (Fig. 4). In the future, synergies among the factors discussed here will exacerbate the dangers to large herbivores, as is the case when increased hunting results from people being given access to fragmented, isolated forest remnants within previously extensive and less accessible areas (*19*). Beyond declines in abundance, the most threatened large herbivores are further imperiled by a loss of genetic diversity. The European bison, for instance, passed through a severe genetic bottleneck in the early 20th century and now suffers from balanoposthitis, a necrotic inflammation of the prepuce that inhibits breeding (*37*).

CONSEQUENCES OF LARGE HERBIVORE DECLINE

Large herbivores shape the structure and function of landscapes and environments in which they occur (Fig. 5). They directly and indirectly affect other animal species throughout the food web, including their predators and smaller herbivores, and modify abiotic processes involving nutrient cycles, soil properties, fire regimes, and primary production. The roles of large herbivores thus cannot be taken over or compensated for by smaller herbivores. These effects of large herbivores on ecosystems are further discussed below.

Large herbivores as ecosystem engineers

Large herbivores, through their size and high biomass, exert many direct effects on vegetation via trampling and consumption of plants (38). Hence, they maintain patch heterogeneity in systems that would otherwise support continuous woody vegetation. Even in wetter climates, which favor trees over grasses, elephants can maintain open patches (39). Bison also maintain and expand grasslands, and their wallows increase habitat diversity for a variety of both plants and animals (40). Indeed, the larger herbivores consume and, hence, influence the fate of a larger variety of plant species than coexisting mesoherbivores (13). The Pleistocene megafauna extinction can be viewed as a global-scale natural experiment that highlights the continental scale of the ecological impacts that result from the loss of large herbivores. Evidence from Australia suggests that mixed rainforest was converted to sclerophyll vegetation in the aftermath of megafaunal loss (41), whereas in North America, novel plant communities formed that have no modern analogs (42), and in Europe, a heterogeneous mosaic of vegetation structures was replaced with more closed woodland communities (43) as a result of the particularly severe megafaunal declines in these regions (2).

Predators and scavengers

Large herbivores are the primary source of food for predators and scavengers that have high energetic demands, making them an integral component of the food web (11). Lions (Panthera leo) and spotted hyenas (Crocuta crocuta) prefer prey above ~90-kg body mass, and all of the world's largest terrestrial carnivores prey on large herbivores (11, 44). Indeed, even the megaherbivores (≥1000 kg) such as elephants are not immune to predation (45), because their juveniles are within the size range preferred by some large carnivores (46). Notably, large herbivores may even facilitate the hunting success of predators when their foraging activities open up dense vegetation, making small herbivores more vulnerable (47, 48). Large herbivore carcasses yield more nutrients to a wider suite of scavengers than those of smaller species because the latter are usually consumed completely, whereas large carnivores tend to consume relatively less of large carcasses, thereby leaving more for other species (49). In Yellowstone National Park, gray wolves have been shown to buffer the negative impacts of shorter winters through the food subsidies they provide for a suite of scavengers [for example, coyotes (Canis latrans), foxes (Vulpes vulpes), ravens (Corvus corax), and eagles (Haliaeetus spp.)] (50). Given the pivotal and positive role of top predators in many ecosystems, it is unfortunate that depletion of their prey is a serious threat in developing countries (11, 33, 51), particularly for obligate meat eaters such as jaguars (Panthera onca), tigers (Panthera tigris), lions, leopards (Panthera pardus), and snow leopards (P. uncia). For example, overhunting of large herbivores in West Africa has reduced the prey base, which, at least in part, has caused regional lion populations to become critically endangered (52).

Synergy between herbivores

Megaherbivores, primarily via their effects on vegetation structure, can facilitate the existence and survival of a suite of mesoherbivores. For example, in northern Botswana, browsing by African elephants helps convert woodland to shrubland, increasing the dry season browse for impalas (Aepyceros melampus) (53). In Addo Elephant National Park, South Africa, African elephants create pathways in impenetrable thickets, facilitating black rhino browsing (54). In some seasons, areas grazed by hippopotamus in Benue National Park, Cameroon, are more nutritious with regard to structure and nutrients, which is advantageous for kob (Kobus kob) (55). In contrast, high densities of large herbivores inside reserves or in the absence of their predators can be detrimental where overgrazing decreases foraging opportunities for coexisting browsers (56), particularly during periods of low rainfall (57). However, by generally promoting the replacement of tall mature woodlands or grasslands by rapidly growing shrubs or short grasses, large herbivores are more likely to have positive than negative impacts on mesoherbivores (38).

Seed dispersal

Extinct megaherbivores once played a critical role in the colonization of woody plants (58). Even today, large herbivores are irreplaceable as seed dispersers because, relative to smaller frugivores, they are able to consume larger seeds and deliver many more seeds per defecation event over longer distances. Elephants may consume more seeds from a greater number of species than any other taxon of large vertebrate (13, 59, 60). In Congo alone, forest elephants (L. africana cyclotis) disperse ca. 345 large seeds per day from 96 species, consistently more than 1 km from the parent trees (61). Indian rhinoceros (R. unicornis) move large tree seeds from forest canopies to grasslands, generally with successful germination and recruitment (62). Even smaller species, such as tapirs (Tapirus spp.) and gorillas (Gorilla gorilla) are effective seed dispersers, which helps to maintain the distribution and abundance of plant species (63, 64). For instance, in African lowland rainforests, primate-dispersed tree species were less abundant at sites with depleted primate populations due to intense hunting by humans compared with sites with low hunting pressure (65). Thus, the loss of large seed dispersers may lead to a wave of recruitment failures among animal-dispersed species (66) with potential consequences for important ecological services (67).

Nutrient cycling

Large herbivore communities consume disproportionately more plant biomass per unit area than small herbivores (68). They affect nutrient cycles via direct and indirect mechanisms that have consequences for ecosystem functioning. For example, large herbivores directly influence nutrient cycling via the consumption of plants, which indirectly causes the reallocation of carbon and nutrients within the plant, while also shifting plant species composition toward species with different rates of litter decomposition (69). Herbivores can greatly accelerate the nutrient cycle in ecosystems through consumption and subsequent defecation, returning nutrients to the soil at rates that are orders of magnitude faster than processes of leaf loss and decay. Moreover, as leaves and twigs are consumed, large herbivores excrete urine and feces and create patches of concentrated nutrients that can last for several years (69). On longer time scales, as the location of concentrated patches shifts over time, large herbivores may play a disproportionate role in diffusing nutrients across landscapes (68). Carcasses also add a variety of nutrients to the soil such as calcium, with effects that can persist several years after the death of the animal (68, 70).

Fire

By altering the quantity and distribution of fuel supplies, large herbivores can shape the frequency, intensity, and spatial distribution of fires across a landscape. There are even unique interactions among large herbivore populations that can influence fire regimes. For example, facilitative interactions between white rhinoceros and mesoherbivores result in reduced fuel loads and fuel continuity, and consequently fewer large, intense fires (71). Other factors can influence the frequency and intensity of fires, particularly in locations where the total area burned is strongly related to ungulate population size. For example, Serengeti wildebeest (*Connochaetes taurinus*) populations irrupted after the rinderpest virus was eradicated in the 1960s, and the subsequent increase in grazing pressure led to a widespread reduction in the extent of fires and delayed recovery of tree populations (72). The removal of plant biomass by browsing also reduces fire fuel loads and decreases fire susceptibility. Thus, there is scant evidence of fire in much of Australia until the megafauna disappeared after humans arrived (5).

Small animals

Despite huge differences in body size, large herbivores interact with a suite of small animals including birds, insects, rodents, lizards, and others (Fig. 5). For example, several fish species feed on flesh wounds of hippopotamus (73), and the dung of Asian elephants may be used by amphibians as daytime refuge, particularly in the dry season when leaf litter is scarce (74). Bison wallows support amphibians and birds by creating ephemeral pools, and bison grazing may facilitate habitat for prairie dogs (*Cynomys* spp.) and pocket gophers (geomyids) (40). Oxpeckers (*Buphagus* spp.) depend on the large herbivores for their diet of ectoparasites, and blood-sucking insects such as tsetse flies (*Glossina* spp.) largely depend on herbivores for food. The presence of large herbivores can also reduce the negative effects of rodent outbreaks. For example, in Kenya, the pouched mouse (*Saccostomus mearnsi*) markedly increased in density after the exclusion of large herbivores, due to an increase in the availability and quality of food (75). Thus, a reduction in large herbivore populations could have unintended consequences if rodent abundance increases, particularly if there are (i) negative effects on plant communities, (ii) increased risks of rodent-borne diseases, or (iii) increases in predators that specialize on rodents (76, 77).

Humans

The loss of large herbivores has direct effects on humans, especially for food security in developing regions. It is estimated that 1 billion people rely on wild meat for subsistence (15). Under a business-as-usual scenario, food security will continue to falter given that wild meat in African forests is expected to decline by more than 80% during the next 50 years (78). Moreover, charismatic large herbivores are important flagship fauna (Fig. 6) that draw many tourists to protected areas, especially when they are sympatric with large carnivores (79). Although the consistency of ecotourism can be interrupted by unpredictable events such as disease epidemics and civil unrest, a decline of large flagship species translates directly into reduced tourism (animal watching, photo and hunting safaris) and thereby a decline in trade balances and employment, particularly in rural parts of the developing world where most megaherbivores persist and poverty is common.

FUTURE DIRECTIONS

Saving the remaining threatened large herbivores will require concerted action. The world's wealthier populations will need to provide the

resources essential for ensuring the preservation of our global natural heritage of large herbivores. A sense of justice and development is essential to ensure that local populations can benefit fairly from large herbivore protection and thereby have a vested interest in it. The presence of a diversity of large charismatic species can yield financial benefits that flow to local communities (80). For example, with the African photo safari industry, the prospect of simply observing large carnivores, elephants, or rhinoceros can drive tourism revenue. The ultimate forces behind declining large mammal populations are a rising human population and increasing per capita resource consumption (Fig. 7). As is the case for the conservation of most taxa, programs

Fig. 6. Photos of selected threatened large herbivore species. Endangerment status and photo credits include the following: lowland tapir (*Tapirus terrestris*), vulnerable, T. Newsome; mountain nyala (*T. buxtoni*), endangered, H. Hrabar; European bison (*B. bonasus*), vulnerable, G. Kerley; eastern gorilla (*Gorilla beringei*), endangered, P. Stoel; mountain zebra (*Equus zebra*), vulnerable, H. Hrabar.
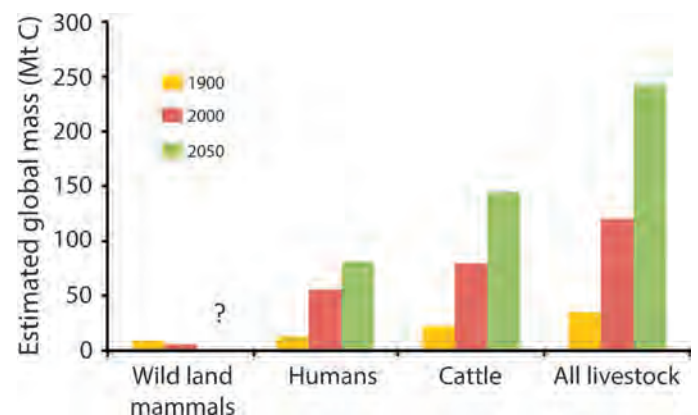
Fig. 7. Global change in the collective mass for wild mammals, humans, cattle, and all livestock for the years 1900–2050. Values for 1900 and 2000 are from (102). Human, cattle, and livestock biomass forecasts are based on projected annual growth in human population, beef production, and meat production, respectively (88, 102).

that help to lower human birth rates in rapidly growing regions such as those that enhance educational and development opportunities, particularly for young women, are a high priority. However, the reality is that strategies for conserving herbivores in the context of high human population densities are likely to be increasingly important. Increasing levels of human carnivory are at the crux of the problem. Lowering human consumption of domestic ruminants could help conserve herbivore populations by reducing demand for rangeland forage, water, and feed crops. Reducing consumption of wild herbivores can also be effective, and enforced wildlife management such as via wildlife ranching has proven to be very successful at maintaining sustainably high harvests of wild meat while providing subsistence food resources to local people. The implementation of wildlife management strategies such as male-only harvests, age-specific harvests, and quotas has the potential to improve both conservation and food security if improved governance can allow for implementation of these strategies. In the near future, urgent action is needed to prevent the extinction of species with extremely low populations, especially those with limited captive populations (for example, Bactrian camel, rhinos, and suids). Decisive steps will be required to address key threats facing threatened large herbivores including, among others, the following.

Focusing research efforts
Basic data and information on the status and ecology of a significant number of large herbivore species are still lacking. From a conservation perspective, we call for a major shift in the large herbivore research effort from the few nonthreatened species in developed countries (for example, red deer, reindeer, and moose/Eurasian elk) to the many threatened species in developing countries (43 species; fig. S2). We urgently recommend more research on the most threatened large herbivores in Southeast Asia, Africa, and Latin America. Species in need of immediate attention include the critically endangered tamaraw (*Bubalus mindorensis*), Visayan warty pig (*Sus cebifrons*), and walia ibex (*Capra walie*), as well as the endangered Oliver's warty pig (*Sus oliveri*), mountain anoa (*Tragelaphus buxtoni*), lowland anoa (*Bubalus depressicornis*), and mountain tapir (*Tapirus pinchaque*), all having fewer than 10 published articles per species (fig. S2). In particular, more research is needed to understand the various ways that rising human and livestock densities (Fig. 7), changing climate, habitat loss, and hunting, as well as different combinations of these factors, affect these large herbivores. We urge large carnivore researchers and conservation agencies to invest more money and attention on the large herbivores that comprise large carnivore prey, because depletion of prey is a significant global threat to large carnivores (*11*). In an attempt to shift the research effort from well-studied species in developed countries to highly threatened species in developing countries, we recommend the establishment of a fund to finance graduate students to conduct empirical ecological and socioeconomic research that would benefit endangered large herbivores. Examples of potential thesis topics could include (i) replicated studies of the basic ecology of large, rare herbivores that are the least studied, (ii) seed dispersal and woody flora recruitment in areas with and without large herbivores, (iii) effects of diversity of large herbivore species on financial benefits flowing to communities from tourism, (iv) success of stall-feeding livestock programs for potentially reducing competition between livestock and wild herbivores, and (v) potential for increases in traditionally grown protein-rich plant foods rather than domestic or wild meat as a primary protein source for humans.

Addressing poaching
Solving the current crisis associated with poaching for meat and body parts is an essential step, although one that is extremely challenging. Trade bans alone can sometimes succeed but can also fail because they limit supply, causing prices to rise, thereby driving more poaching for the black market (*27*). Multifaceted bold new policies are urgently needed that (i) increase the effectiveness of law enforcement both through antipoaching and strengthened penal systems related to poaching, (ii) incentivize local communities to conserve wildlife (for example, increasing tourism income), (iii) reduce demand for illegally sourced wildlife products through market mechanisms of controlled trade of products or farming animals (*17, 81*), and (iv) aid a cultural shift away from luxury wildlife products in industrializing countries such as China and Vietnam. Social marketing and environmental education programs can also be highly effective in reducing demand for wildlife. For example, shark fin sales plummeted after social media pleas by basketball celebrity Yao Ming. Likewise, other prominent Chinese celebrities have also started speaking out to reduce demand for ivory and rhinoceros horn in Southeast Asia.

Managing protected areas
Globally, only ~10% of conservation funding for protected areas is spent in developing countries (*82*). Underfunding of protected area networks, particularly in the tropics, results in failure to control key threats to herbivores. In the absence of funds for law enforcement, poaching for meat or body parts proceeds unhindered, and many protected areas are being encroached by human settlement, livestock, and logging. Large herbivores, including those that are migratory, need large areas to support viable populations. Given the global tendency for protected areas to be small (<10,000 ha), many protected areas are unable to effectively contribute to the persistence of large herbivores (*83*). Therefore, expanding protected areas and increasing connectivity between them are important. In some contexts, fencing can assist by demarcating boundaries and reducing human encroachment, while at the same time reducing edge effects and making law enforcement easier (*84*). Technological approaches such as the use of drones may help to patrol parks with limited resources, but for effectiveness, this technology will need to be low cost, easy to use, durable, and efficient. Without the cooperation of people who live near wildlife, conservation efforts are likely to fail. To ensure just outcomes, it is essential that local people be involved in and benefit from the management of protected areas. Local community participation in the management of protected areas is highly correlated with protected area policy compliance (*85*). For instance, to protect wildlife, Nepal has successfully adopted a policy of sharing of revenues from protected areas with local people who live adjacent to the reserves (*86*).

Focusing conservation efforts
In southern Asia and other developing areas, oil palm plantations, pulp and paper, and other commodity crops are rapidly replacing wet tropical forests where large herbivore populations are at risk. In this situation, it makes sense to shift agricultural expansion to abundant degraded low-carbon density lands while sparing the high carbon stock lands for climate change mitigation and animal conservation (*87*). Infrastructure and mining development are additional important factors in habitat loss. Initiatives are needed to encourage mining companies to underwrite conservation efforts. Moreover, mining sites could be used as de facto wildlife refuges by bringing security to places

that lack it, in turn providing a safe haven for large mammals away from poachers. Moreover, the move of poor rural populations to cities and towns leaves a great opportunity for restoration of large mammals in the hinterlands.

Africa has more large herbivores than any other world region and lower endangerment rates (12 of 32 are threatened) than any other region in the developing world (fig. S1). However, over the next half century, sub-Saharan Africa will have the world's highest projected growth rates of human population and livestock production (88) (fig. S5), which are potential drivers of hunting for meat, habitat loss, and livestock competition. With land use and human demographic patterns in sub-Saharan Africa becoming more similar to those in Southeast Asia, where all 19 large herbivore species are threatened with extinction, it is critical to develop a geographic approach to conservation that focuses on areas with high species diversity, and this should address both human issues (as indicated above) and conservation management. Additionally, conservation actions are dependent on available money. We advocate for a global government-funded scheme for rare large herbivores beyond elephants and rhinoceros, as well as the establishment of a nongovernmental organization that focuses exclusively on rare large herbivores, like what the Arcus Foundation does for apes or what Panthera does for large cats.

Addressing climate change

There are potential combined strategies (joined-up policies) that would mitigate climate change and at the same time benefit large herbivores. Examples include (i) curbing ruminant livestock numbers while increasing high-protein plant-based foods or nonruminant meat so as to lower greenhouse gas (for example, methane and carbon) emissions while also reducing competition with large herbivores (31), and (ii) enhancing carbon storage by preventing tropical forests from being logged while also protecting habitat for large herbivores. In addition, tropical large herbivores disperse large seeds that are typically from slow-growing and densely growing tree species important for carbon storage. By 2050, climate change has the potential to leave many of Earth's species destined for extinction (89). Additional research is urgently needed to better predict changes in large herbivore population sizes and ranges with climate change while accounting for the current threats they face.

FINAL THOUGHTS

The wave of species extinctions that obliterated 80% of the Pleistocene megaherbivores (≥1000 kg) on planet Earth appears to be continuing today in Africa and Southeast Asia. The very recent extinctions of Africa's western black rhinoceros and Vietnam's Javan rhinoceros are sober reminders of this long-term trend (1, 90). Then as now, the Pleistocene extinctions were triggered in part by human hunters (2, 91). Solving the current poaching crisis, a sinister development of organized crime, will help but will likely be insufficient to stem, much less reverse, impending declines and future extinctions among the few remaining megafauna. Megafauna remain beset by long-standing and generally escalating threats due to land-use change and ongoing parochial poaching by locals. The situation for the 66 species of large herbivores having body masses of 100 to 1000 kg is not as dire as for those ≥1000 kg, but still ominous because 55% of these herbivores are currently threatened (fig. S3). Within this body mass range, hominid, tapirid, suid, and equid species are the most highly threatened families (Fig. 2). Some

species may be slipping away even before they are discovered and described by science. Recently, two rare large herbivores were discovered: a fifth species of tapir, the kabomani tapir (*Tapirus kabomani*), in the Amazon (92) and a bovid, the saola (*Pseudoryx nghetinhensis*), in Southeast Asia (93). To jump-start protection for the saola, conservationists recently removed 27,000 snares from the forests of Vietnam and Laos (94).

The problem of large herbivore declines may not be solved by the current Convention on Biological Diversity target of protecting 17% of terrestrial land by 2020 (95). Given the substantial area requirements of large herbivores, 17% of land in isolated fragments is unlikely to provide sufficient protection to slow or reverse declines, particularly given that inadequate policing/funding can effectively reduce the size of protected areas (96). This is further exacerbated by the global tendency for protected areas to be in low-quality habitats (35), effectively reducing the densities, and hence numbers, that can be conserved in these areas (36).

The range contractions (fig. S6) and population declines of large herbivore species have ecological and evolutionary implications. Range contractions inevitably result from the loss of local populations, many of which are genetically distinct, thus representing a major and underappreciated pulse of biological extinction (97). Even if they survive in protected areas, many of these largest species might already be below the minimum numbers to be effective in generating ecological cascades (Fig. 5) or allowing evolutionary processes such as speciation (98). Furthermore, 11 of the 44 threatened species are on the Evolutionarily Distinct and Globally Endangered (EDGE) list due to their unique characteristics while being on the verge of extinction. These are the mountain, Asian, and Baird's tapirs (*Tapirus* spp.), black, Javan, and Sumatran rhinoceros, Bactrian camel, Asian elephant (*E. maximus*), pigmy hippopotamus (*Choeropsis liberiensis*), African wild ass (*Equus africanus*), and western gorilla (99). Thousands of years ago, equids were among the most abundant large grazing animals of the grasslands and steppes of Africa, Asia, and the Americas, whereas today, after many of their populations have been decimated, five of the remaining seven species are threatened and at risk of extinction (1). These are the African wild ass, Asiatic wild ass (*Equus hemionus*), Przewalski's horse, Grevy's zebra (*Equus grevyi*), and mountain zebra (*E. zebra*).

Growing human populations, unsustainable hunting, high densities of livestock, and habitat loss have devastating consequences for large, long-lived, slow-breeding, and, therefore, vulnerable herbivore species, their ecosystems, and the services they provide. Large herbivores, and their associated ecological functions and services, have already largely been lost from much of the developed world. The scale and rate of large herbivore decline suggest that without radical intervention, large herbivores (and many smaller ones) will continue to disappear from numerous regions with enormous ecological, social, and economic costs. We have progressed well beyond the empty forest to early views of the "empty landscape" in desert, grassland, savanna, and forest ecosystems across much of planet Earth. Now is the time to act boldly, because without radical changes in these trends, the extinctions that eliminated most of the world's largest herbivores 10,000 to 50,000 years ago will only have been postponed for these last few remaining giants.

SUPPLEMENTARY MATERIALS

Fig. S3. Comparison of Pleistocene extinctions by body mass with current threatened species by body mass.

Fig. S4. Global distribution of the four main threats faced by large herbivores.

Fig. S5. Human population trends and projections by region (top) and ruminant livestock trends by region (bottom).

Fig. S6. Current range maps (sorted by family) for the 72 large herbivores not classified as extinct in the wild (EW).

Table S1. Data on the 74 large terrestrial herbivores above 100 kg.

Table S2. The number of large herbivores (threatened, total, and facing each of the four main threats) found in each ecoregion.

Table S3. The number of large herbivores (threatened and total) found in each ecoregion.

Table S4. The threatened large herbivores found in each of the ecoregions with at least five threatened large herbivores.

Table S5. Summary of research effort for the period 1965 to June 2014.

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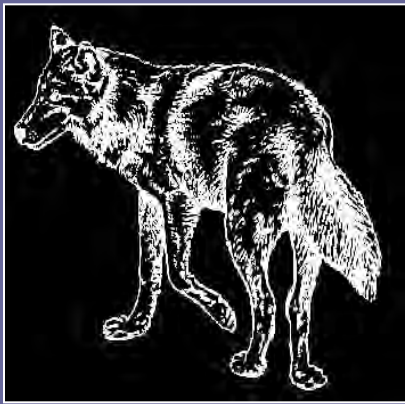
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Trophic Cascades in Great Lakes Wolves

**Tom Rooney, Ramana Callan,
Krystle Bouchard, and Nate Nibbelink**
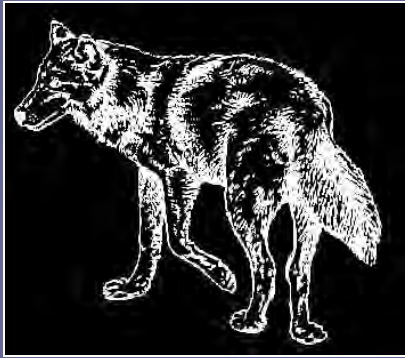
Summary of two research projects

Ramana Callan, PhD
University of Georgia
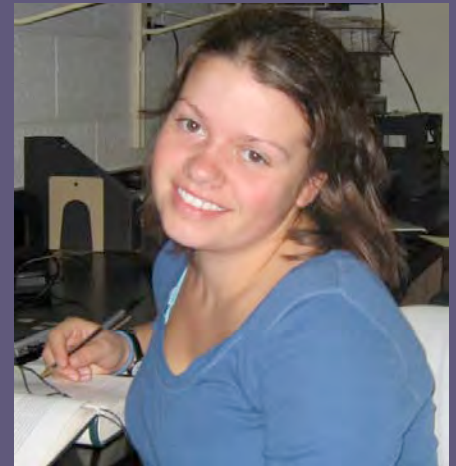
Krystle Bouchard, MS
Wright State University
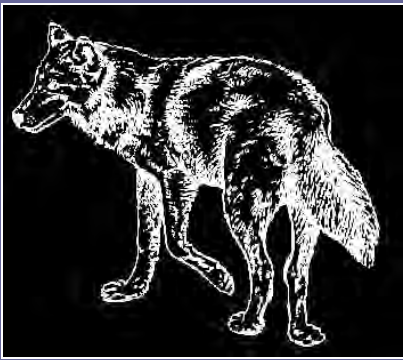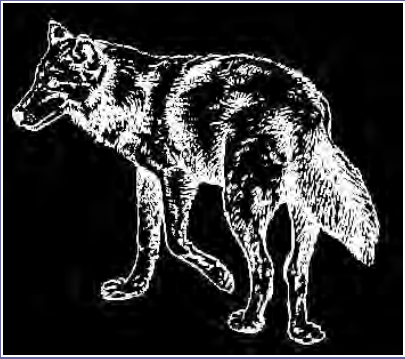
Wisconsin's Understory Plant Communities

- **Local losses in plant species diversity**

- **Regional recruitment failure of conifers**

- **N. WI White-tailed deer populations**
  - pre-settlement: < 10/mi^2
  - current: 10-40/mi^2

Wisconsin's Wolves
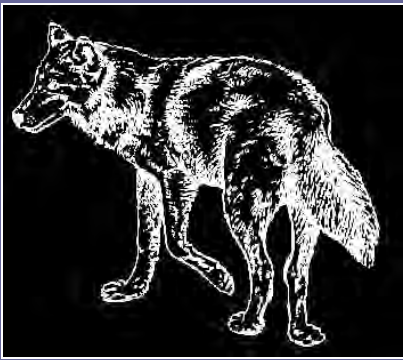
- **Predicted to contribute to the conservation of regional biodiversity**

- **Through direct impacts on white-tailed deer, wolves are predicted to trigger additional indirect impacts on plant communities**

Wolves and Trophic Cascades

Figure from Beschta and Ripple (2009)
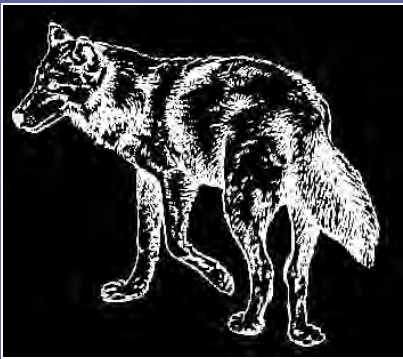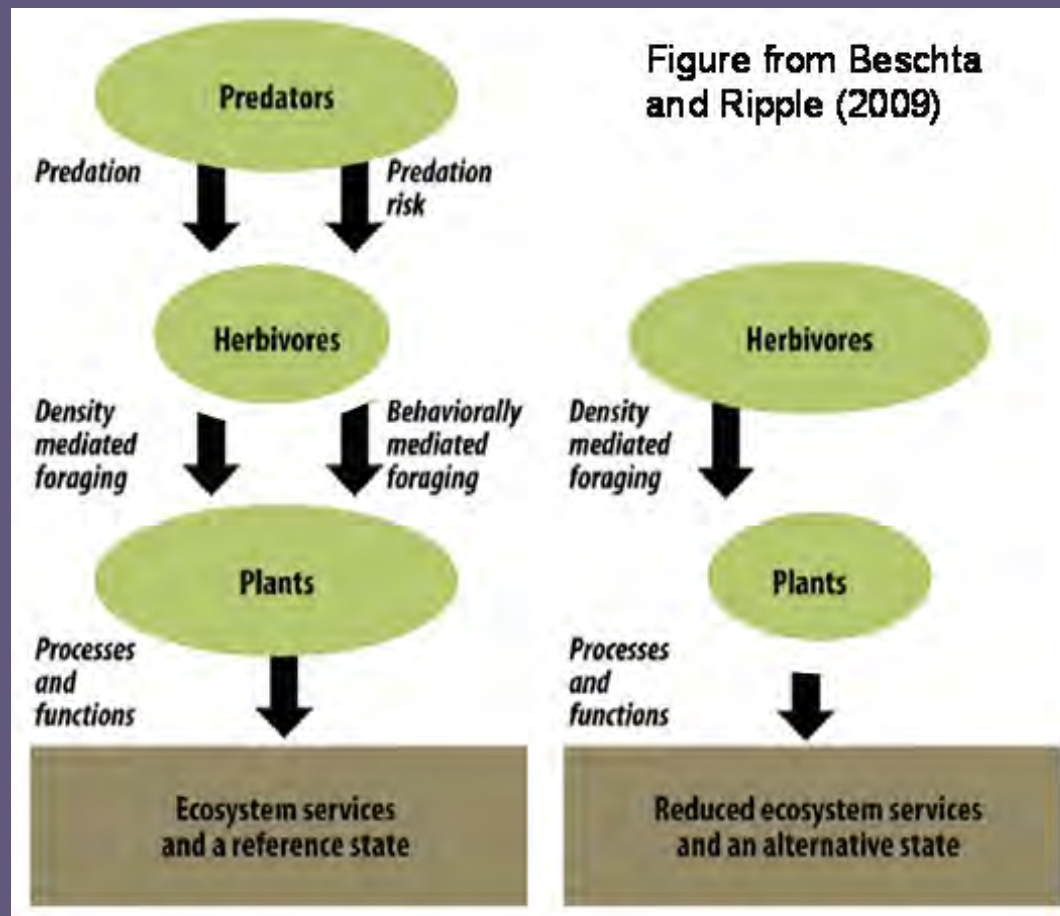
Wolves and Trophic Cascades

Predators can indirectly influence plants by:

- **Predation: Density-mediated indirect interactions (Death Effects)**

- **Predation Risk: Trait-mediated indirect interactions**

→**Behaviorally mediated trophic cascades (Fear Effects)**

Wolf-moose-balsam fir system on Isle Royale
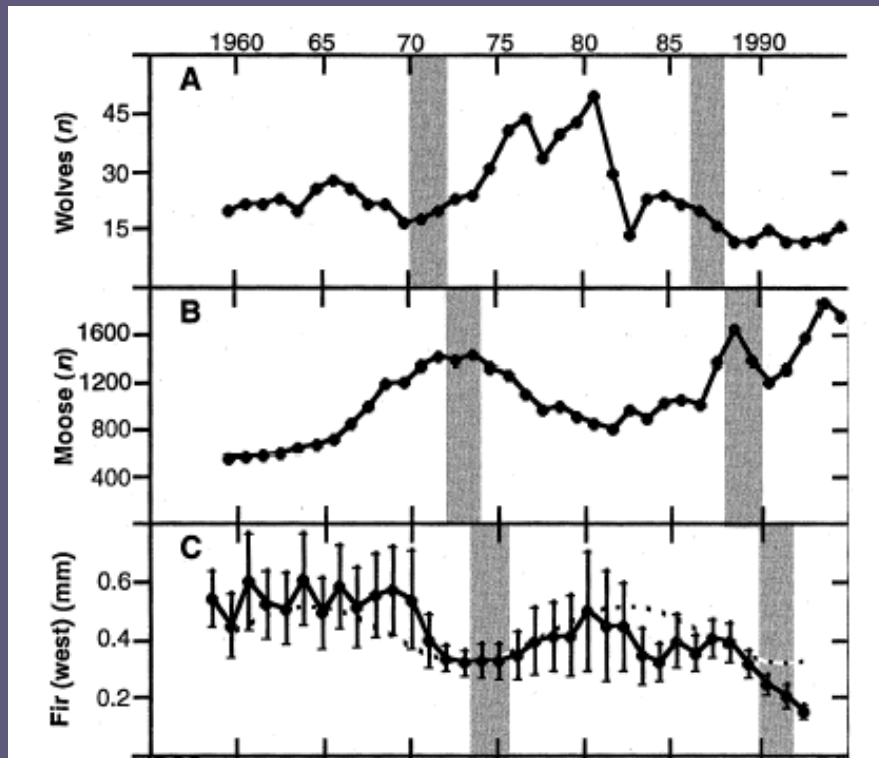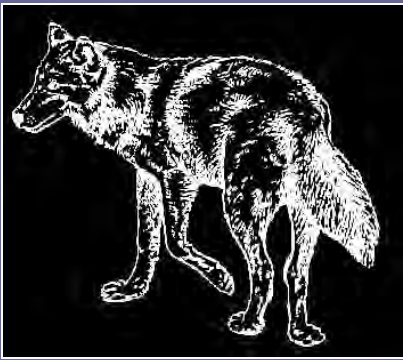
McLaren and Peterson 1994

(Photo credit: Michigan Technological University)

Trophic interactions in Wisconsin forests
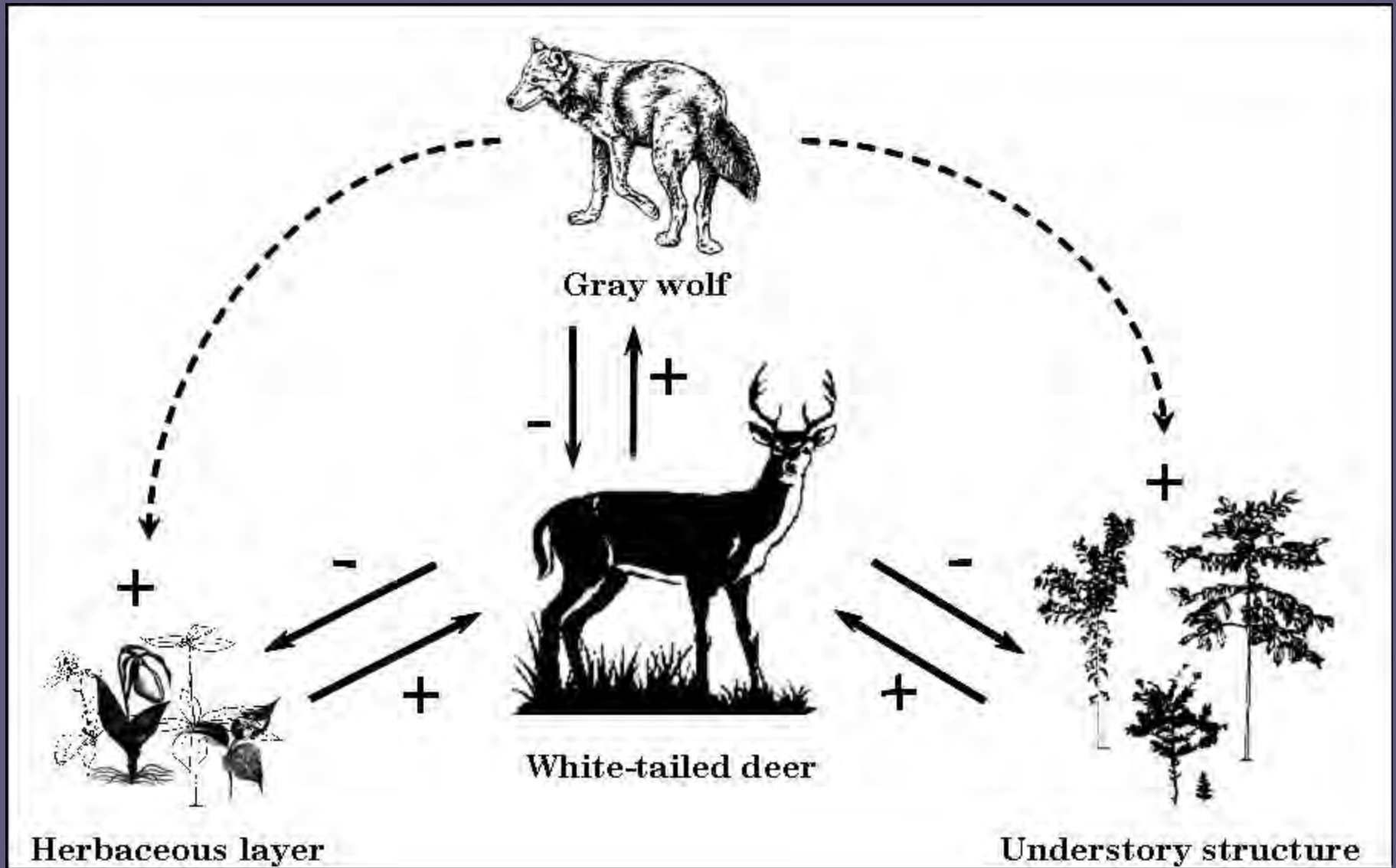
Wolves and white-tailed deer

- **400,000 deer; 690 wolves**

  regional Death Effects unlikely

- **Distribution of deer in MN found to be at margins of wolf territories → buffer zones between packs act as refugia**

  Death and Fear Effects possible

- **Wolves are predicted to alter foraging behavior by white-tailed deer (*i.e.* deer increase vigilance and movement)**

  Fear Effects possible

Deer Mortality in Wisconsin's Northern and Central Forests

Value	Category
122,000	Hunter Harvest (Gun and Bow)
5 -15%	Range of Over Winter Stress for a moderate winter *
33,000	Estimated Bear Kill (33,000 bear x 1, mostly fawns)
16,000	Estimated Coyote Kill (8,000 coyotes x 2, mostly fawns)
13,000	Estimated Wolf Kill (650 wolves x 20, fawns and adults)
13,000	Vehicle Kills
6,000	Estimated Bobcat Kill (3,000 bobcats x 2, fawns and some adults)
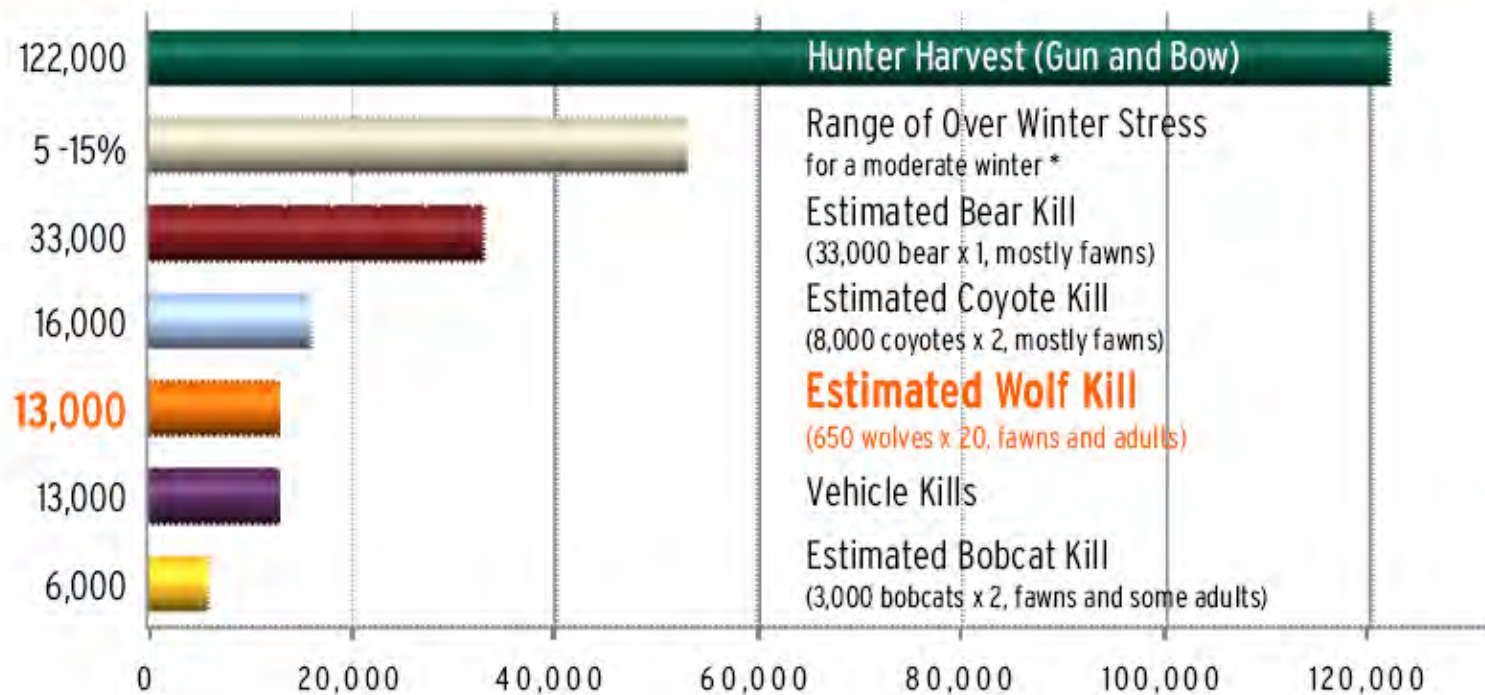
Source: Wisconsin Department of Natural Resources

* the range estimate is based on 5-15% of the 2009 winter standing deer herd for a moderate winter.

Callan: Northern white cedar wetlands

- **High Plant Species Diversity**
- **Historically used by deer as winter "yards"**

Objective

Detect and characterize differences in vegetation between areas occupied by wolves and areas unoccupied by wolves
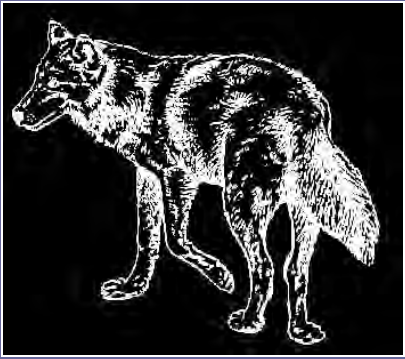
Experimental Approach

Overlay Wisconsin DNR wolf territory data

> - characterize "high wolf impact areas" (8-10 years of wolf occupancy) and "low wolf impact areas" (0-3 years of wolf occupancy)

Landscape Mosaic of Potential Wolf Impact (WI)
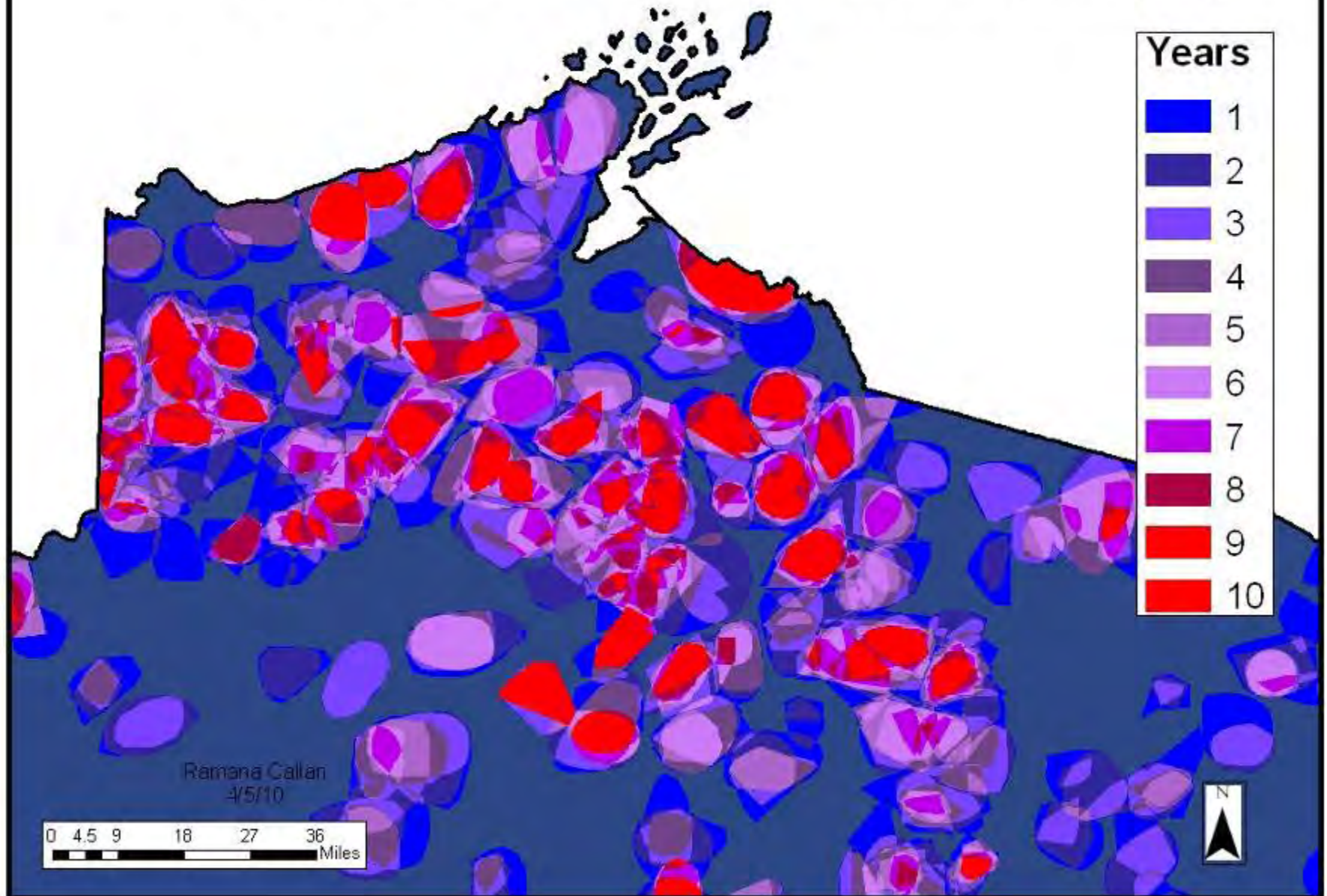
Cedar Stand Site Selection

Years
1
2
3
4
5
6
7
8
9
10

0 0.15 0.3 0.6 0.9 1.2 Miles

Ramana Callan
4/5/10.
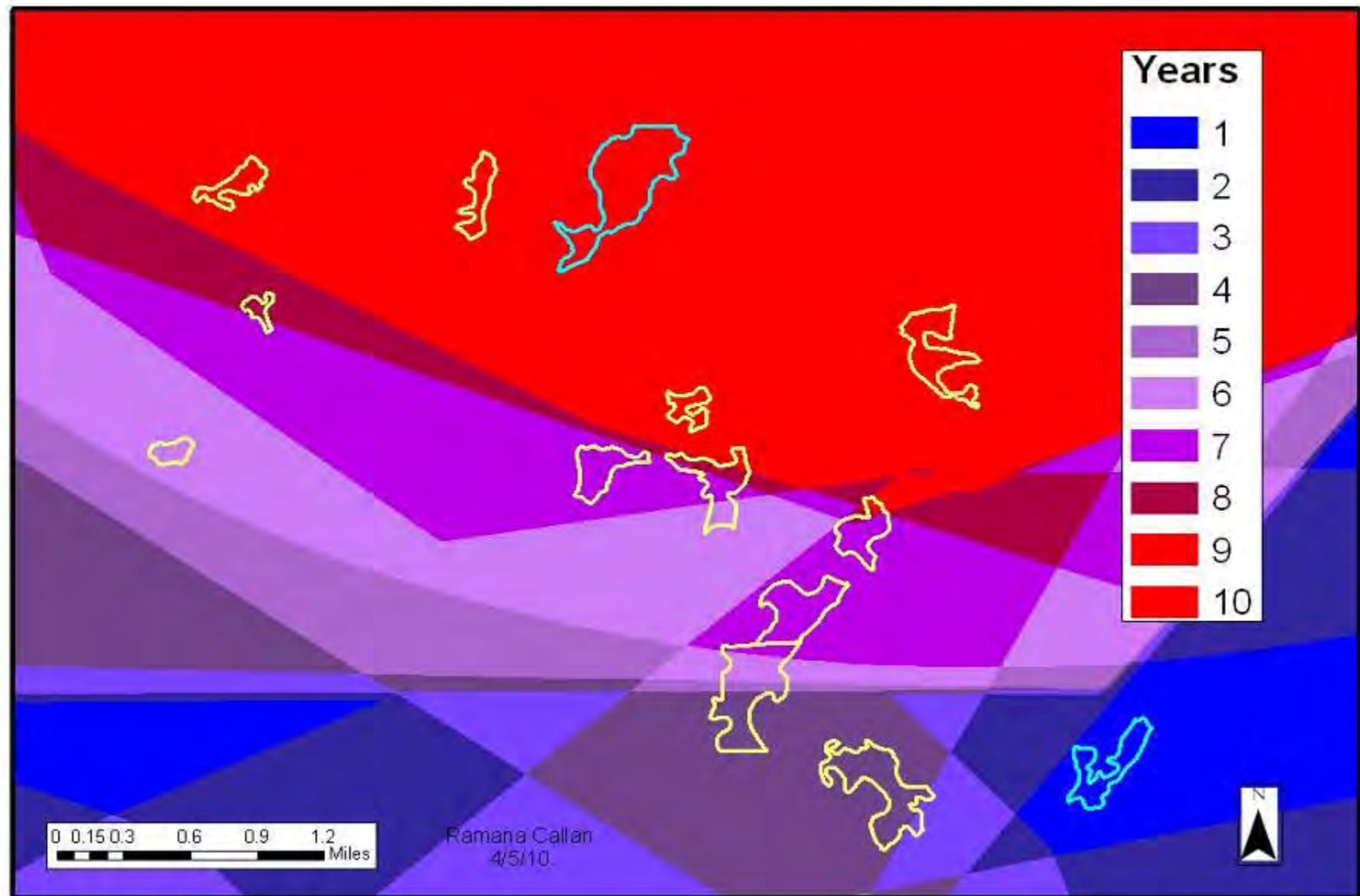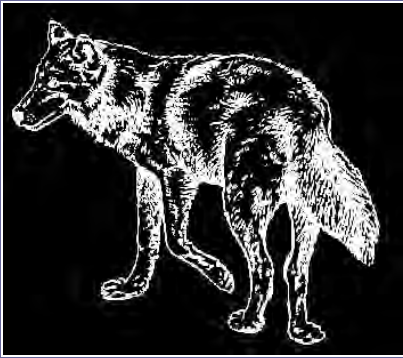
Research Questions

(1) Is plant species richness higher in white cedar wetlands occupied by wolves?

- species richness by vegetation growth form:

Tree, Shrub, Forb, Fern, Grass

(2) At what scale are these differences detectable?

- 0.01m², 0.1m², 1m², 10m², 100m², 1,000m²

Hypothesis: Spatial Scale

Species Area Curve
Indicating Higher Local Effects
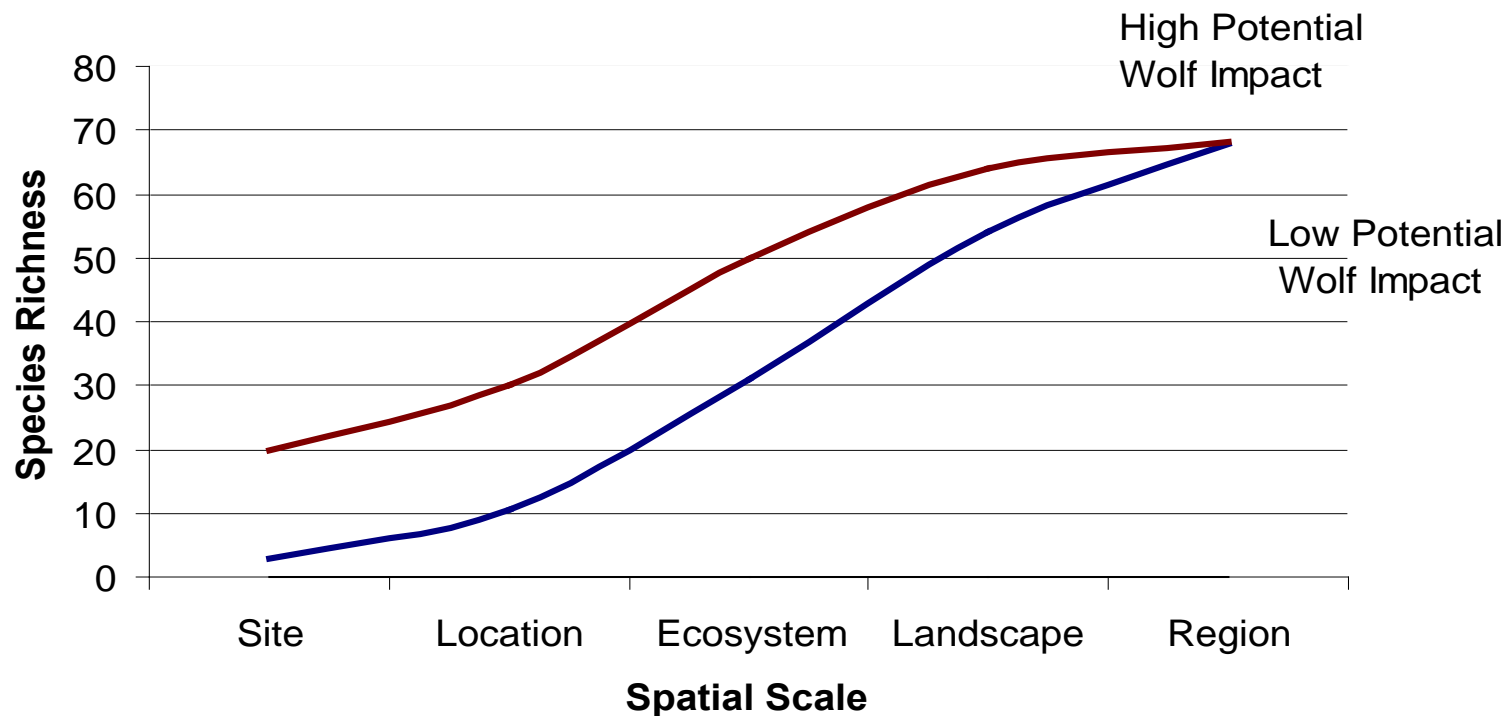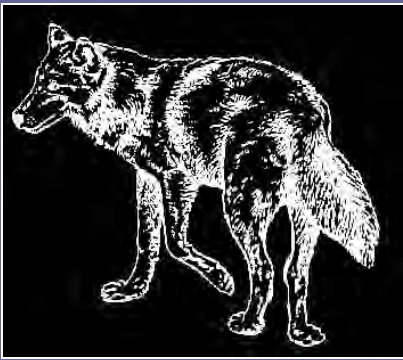
Hypotheses: Vegetation Growth Forms

High Impact Wolf Areas should display:

1) ≈ Tree species richness and % cover

2) ↑ Shrub and Forb species richness

3) ↓ Grass and Fern % cover

n=38

Legend:
- Public Forests
- Vegetation Plots
  - Low Potential Wolf Impact (0-3 years)
  - Moderate Potential Wolf Impact (5-6 years)
  - High Potential Wolf Impact (8-10 years)

Carolina Vegetation Survey (CVS) Protocol

Typical Plot:

0.01m²
0.1m²
1m²
10m²

50m

20m

3		4	3		4		
10		9		8		7	6
2		1	2		1		
1		2	1		2		
1		2		3		4	5
4		3	4		3		

KEY:
- ◎ Plot Origin
- ● Post

Module Number

Corner Number

- – – – Tape
- [2] Intensive Corner
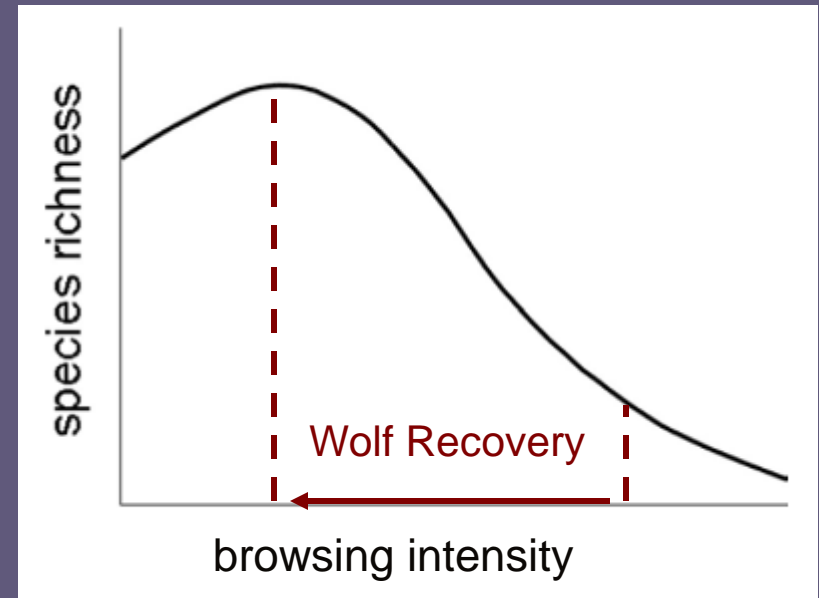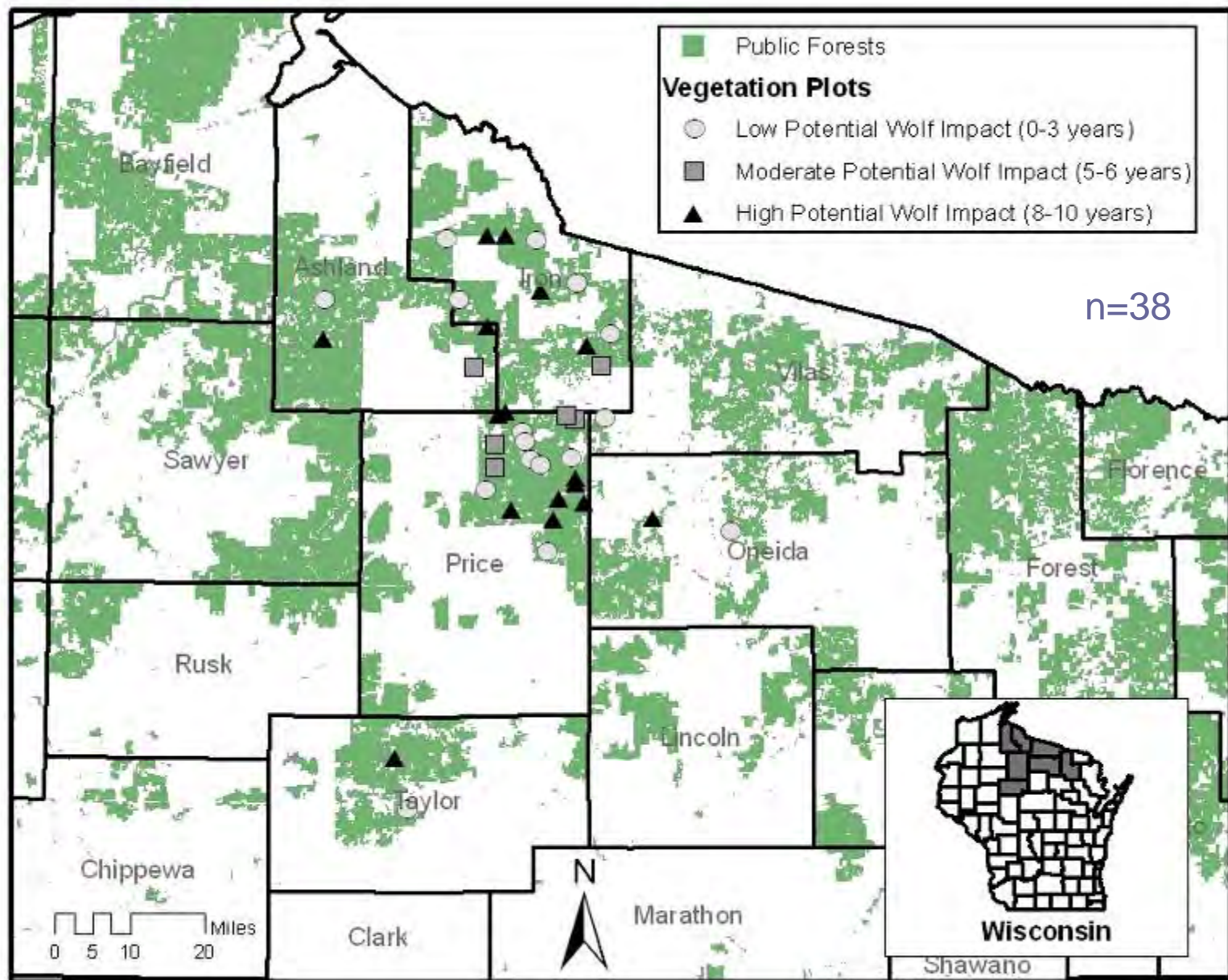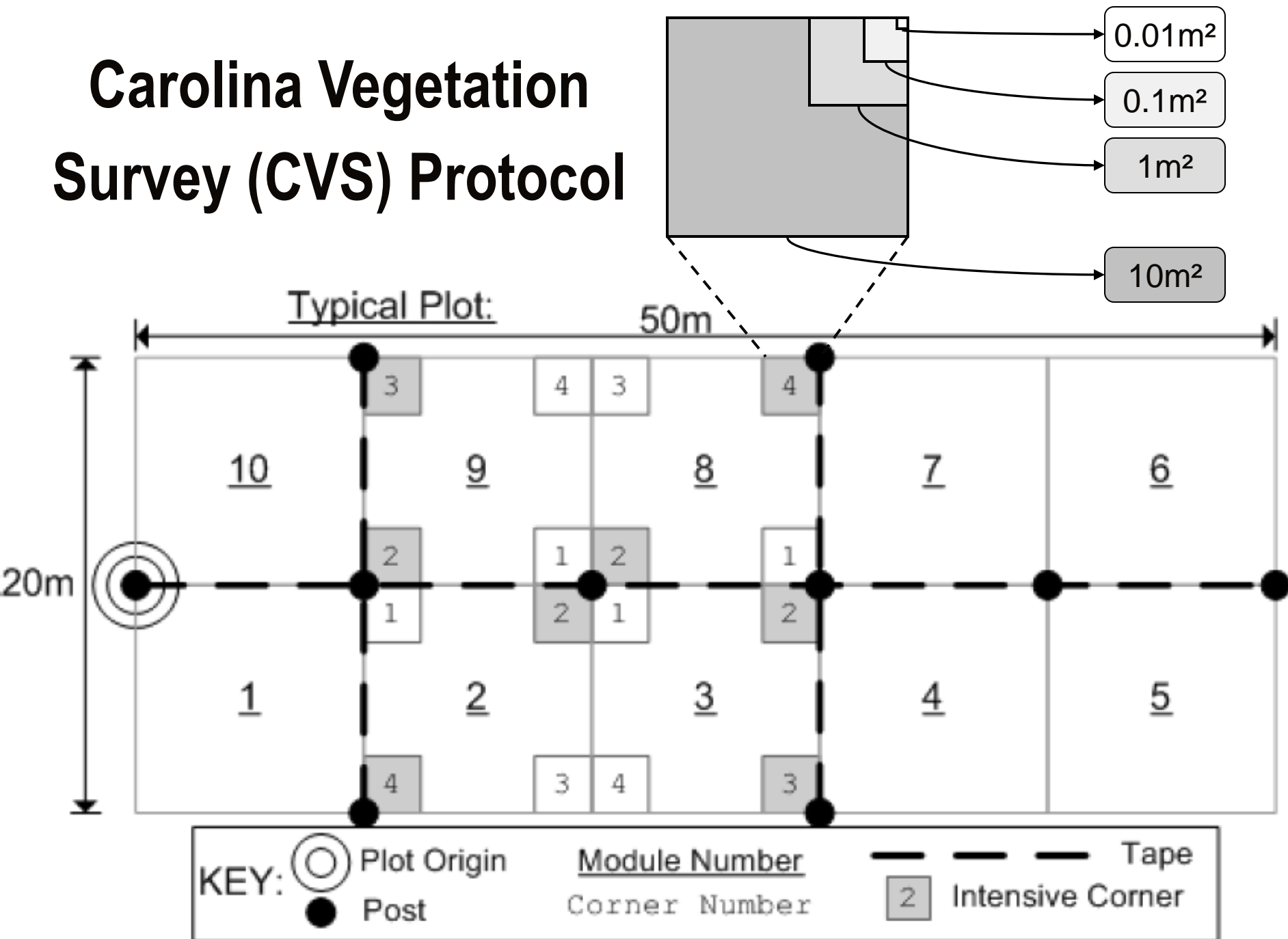
Results: Biodiversity of white cedar wetlands

Trees	23
Shrubs	31
Forbs and Vines	100
Ferns and Fern allies	17
Sedges	16
Grasses and Rushes	8
Non-natives	4
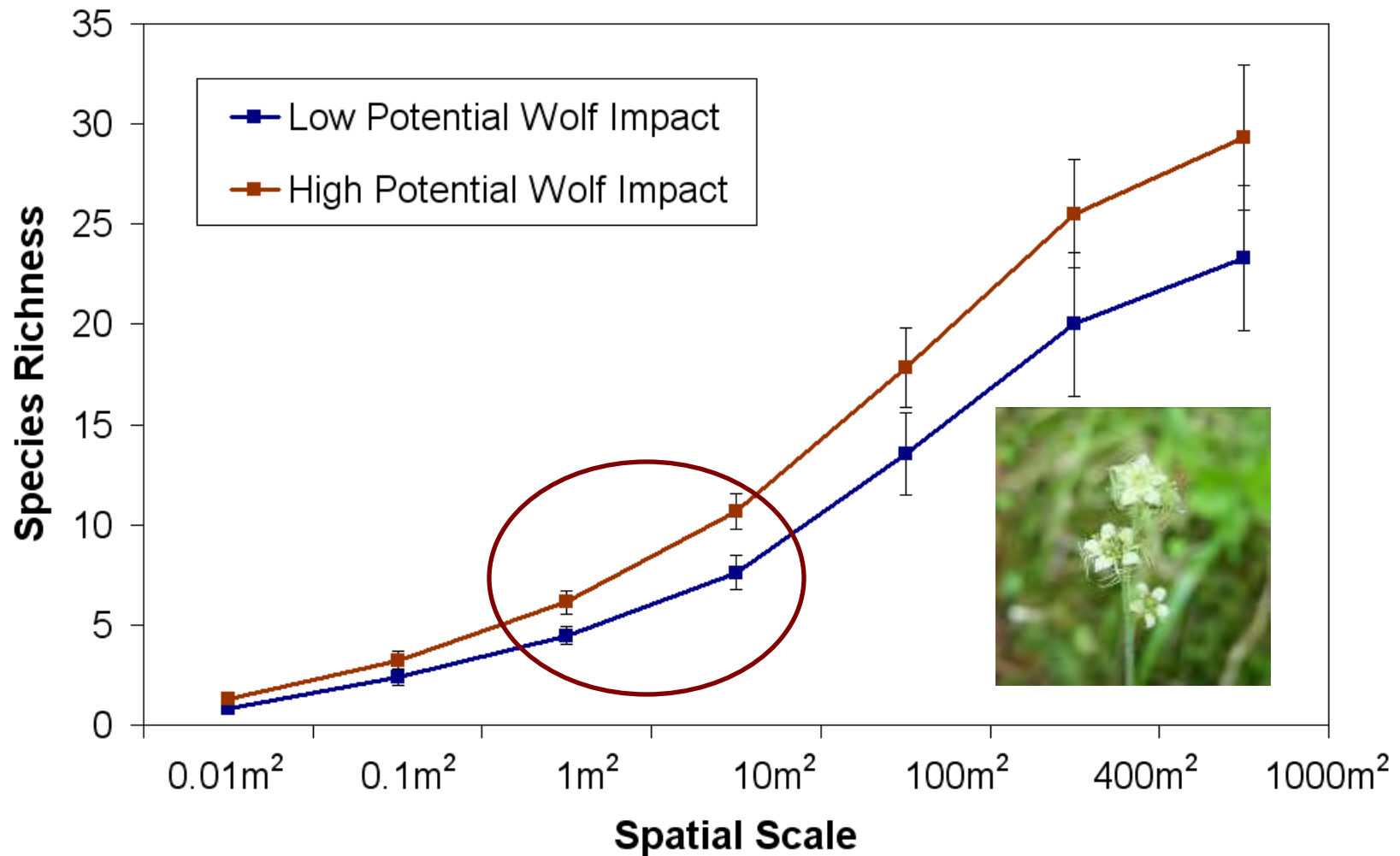
Tree Species Richness

Forb Species Richness

Shrub Species Richness
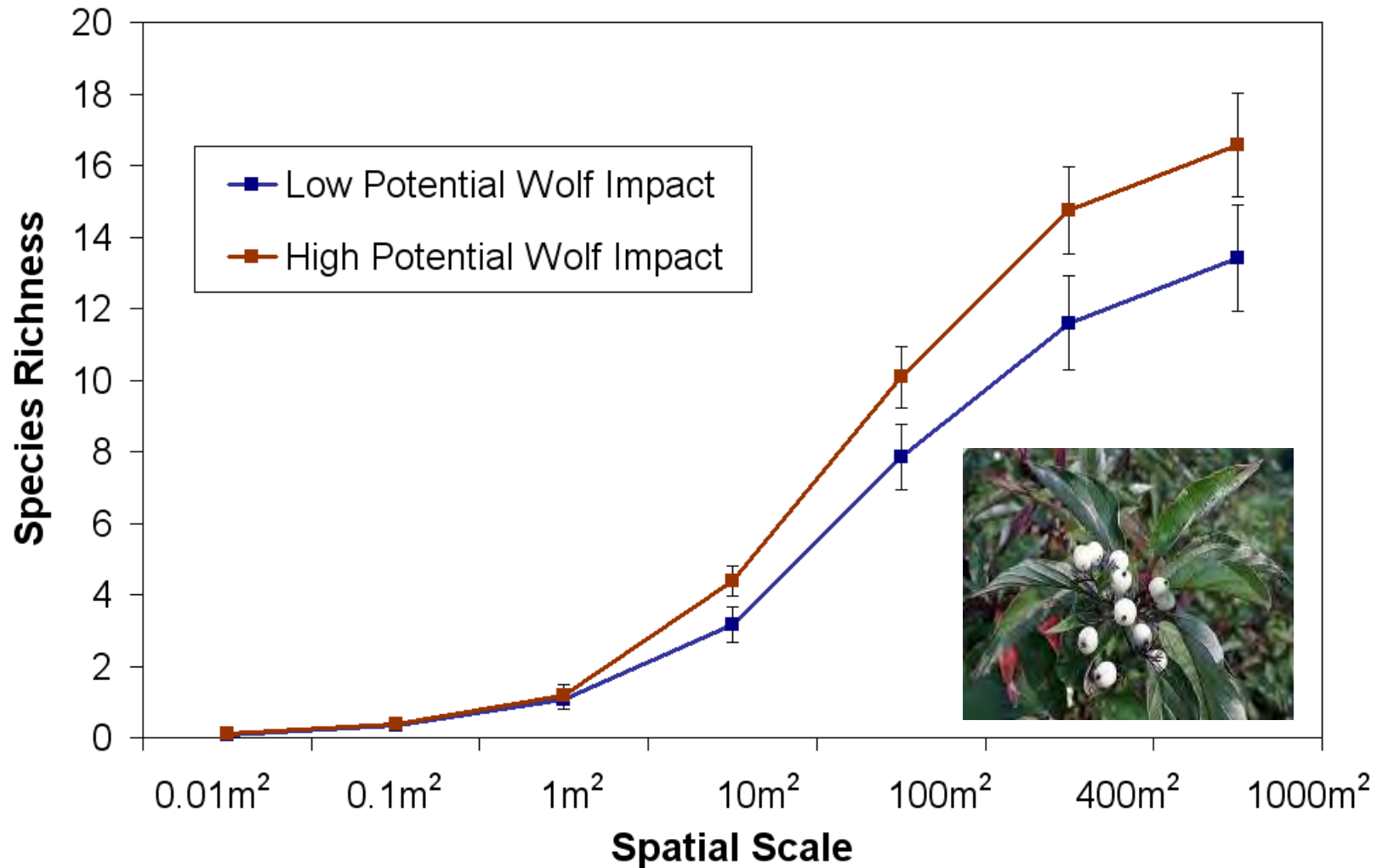
Results: Percent Cover

Hypothesis 3 Partially Supported: ↓ Grass and Fern % cover in high wolf impact areas
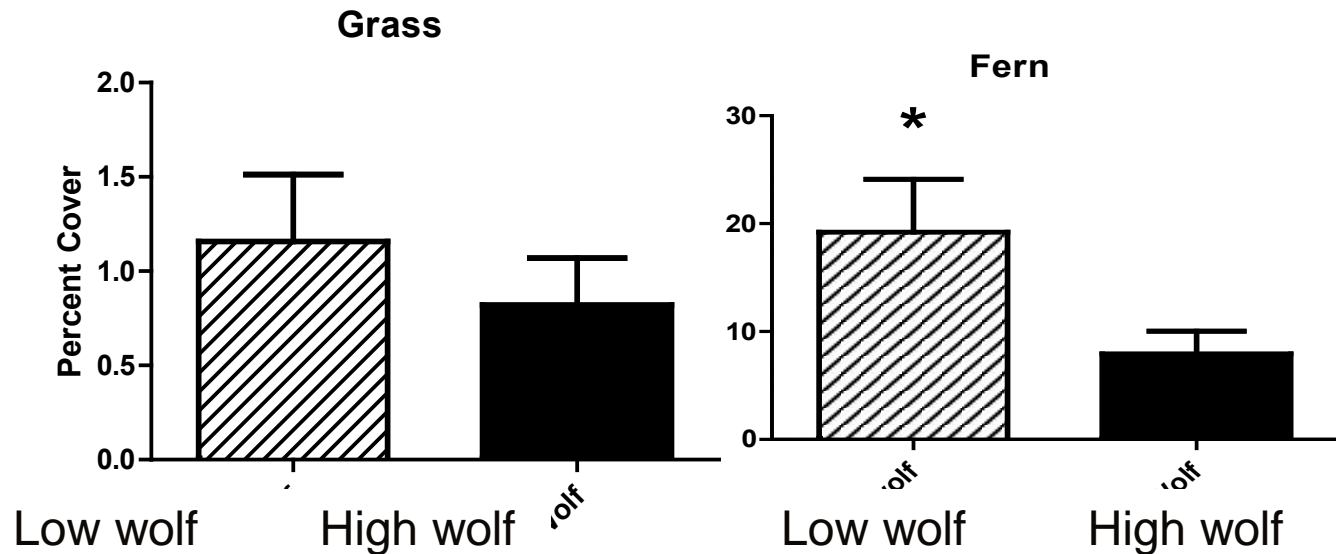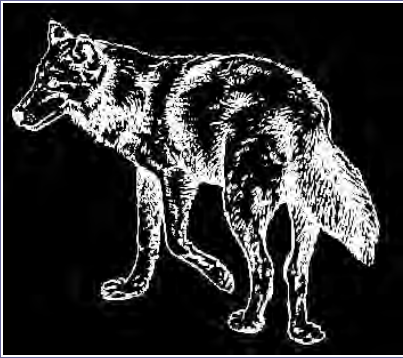
Low wolf impact area

High wolf impact area

Response of browse-sensitive species in low and high wolf impact areas

Results: Select sensitive species

Wild sarsaparilla
(Aralia nudicaulis)
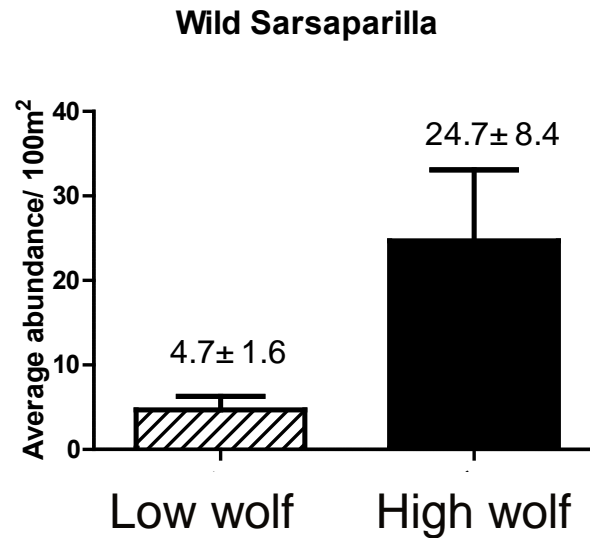
Nodding trillium
(Trillium cernuum)
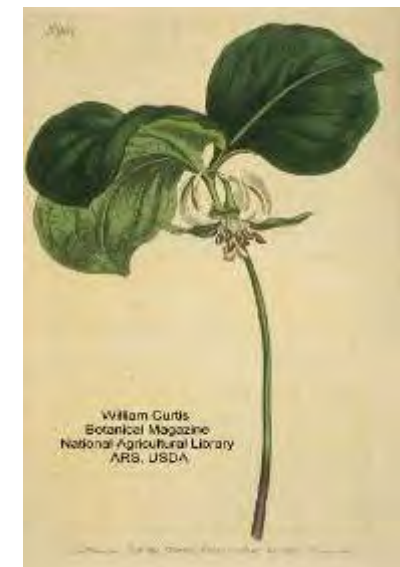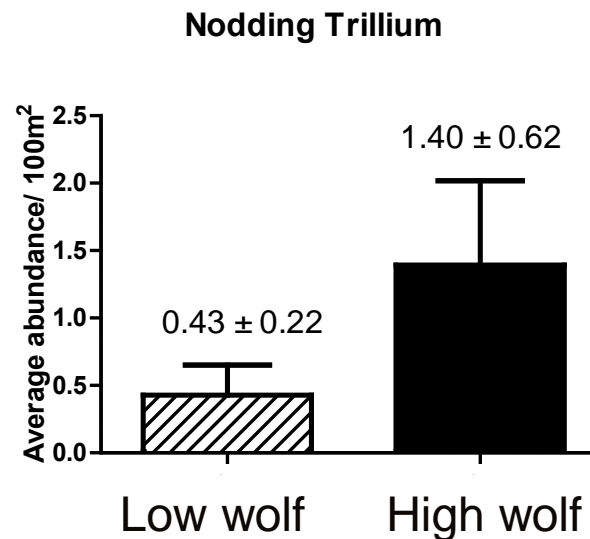
Bouchard: Upland forest wildflowers

- **Focus on 3 deer browse indicator species**

Objective

Detect and characterize differences in vegetation across a wolf recolonization gradient

Research Questions

(1) Does indicator plant size increase with time since wolf recolonization?

(2) How long does it take before wolf effects become detectable?

Experimental Approach

(1) Overlay Wisconsin DNR wolf territory data

- wolves present 12-13 years

- wolves present 4-6 years

- wolves absent

(2) Sites on national and state forest land; matched stand types (mature forest)

Landscape Mosaic of Potential Wolf Impact (WI)
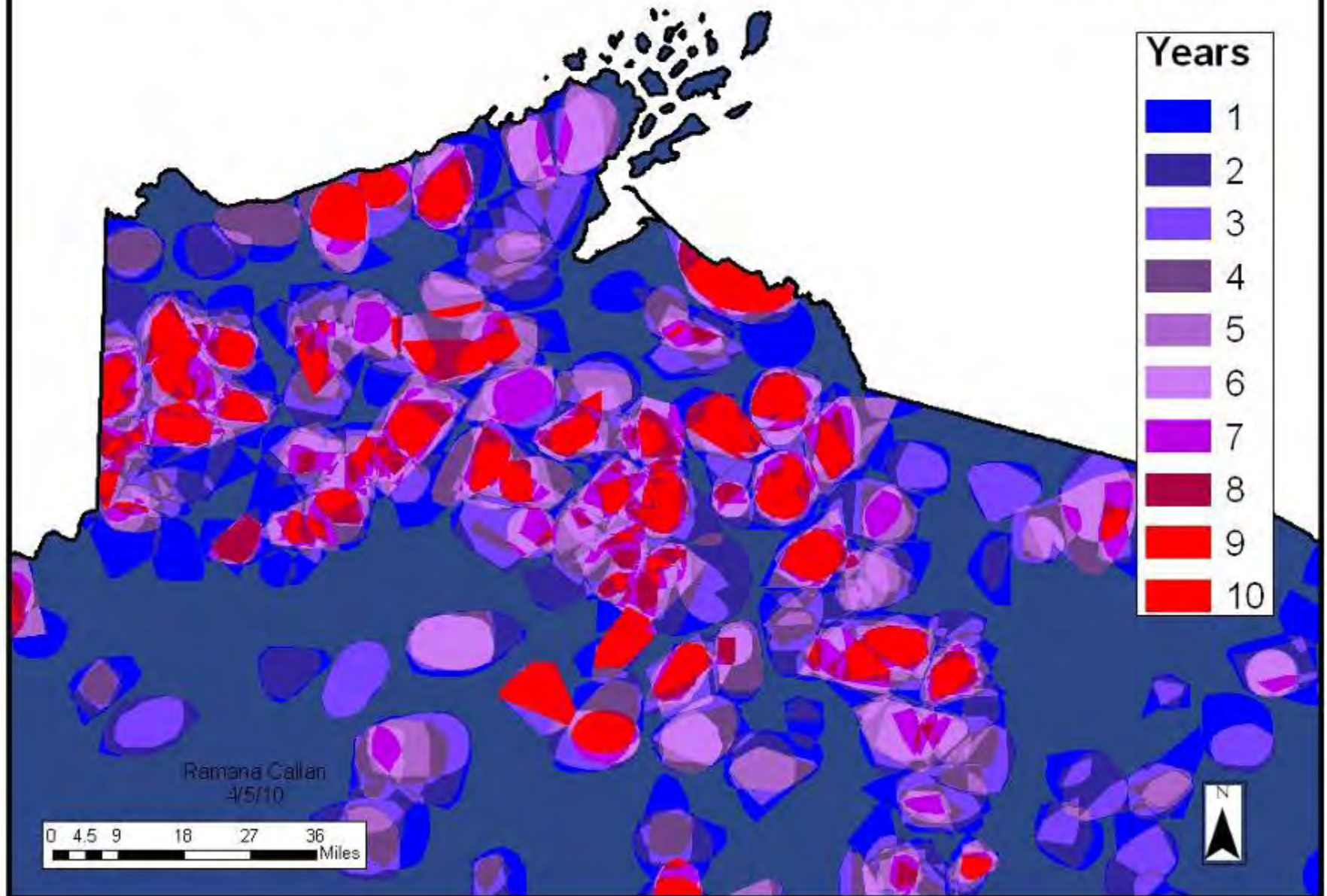
Hypothesis: Plant Size

(1) Mean indicator plant size increase with time since wolf recolonization, but does not resemble "deer-free" exclosures
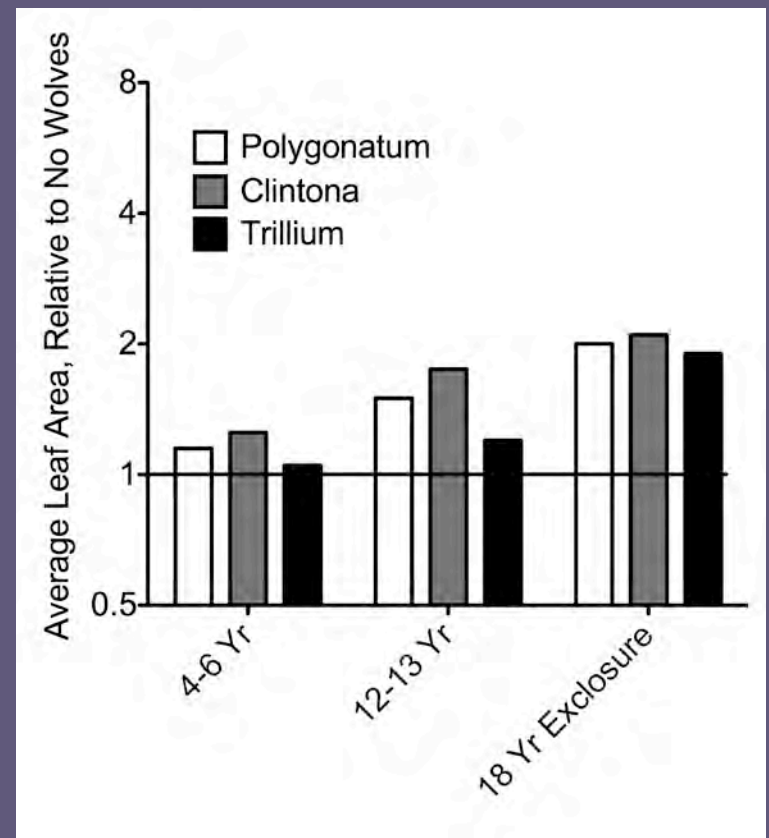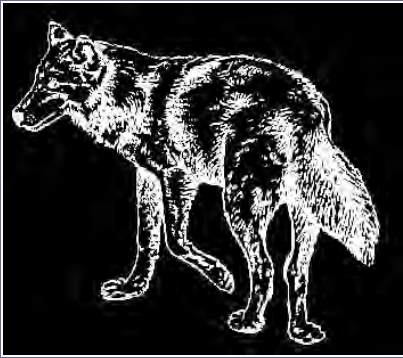
Results: Mixed Effects After 4-6 Years, Consistent Effects After 12-13 Years
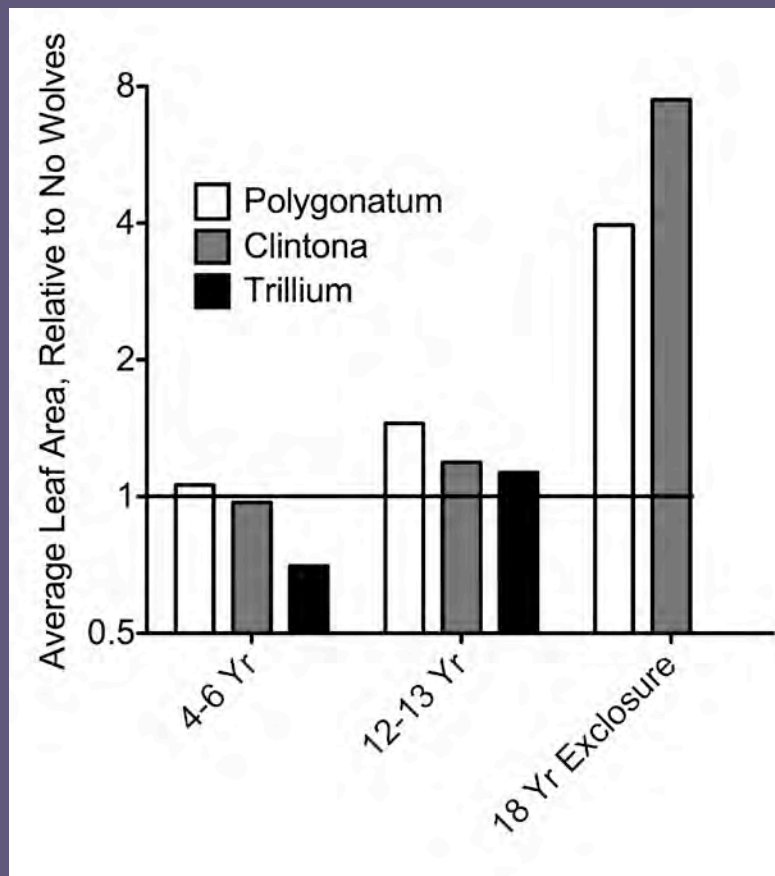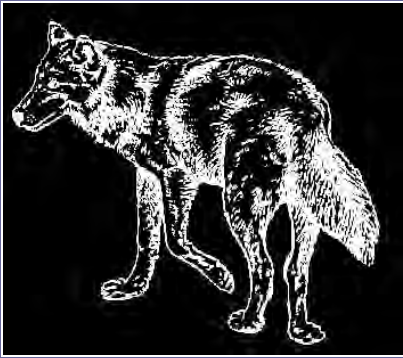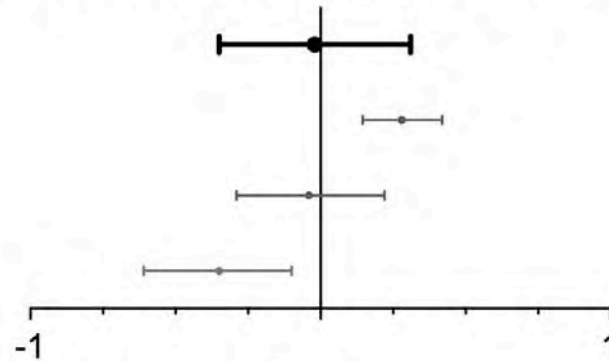
Results: Mixed Effects After 4-6 Years, Consistent Effects After 12-13 Years
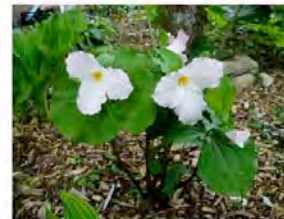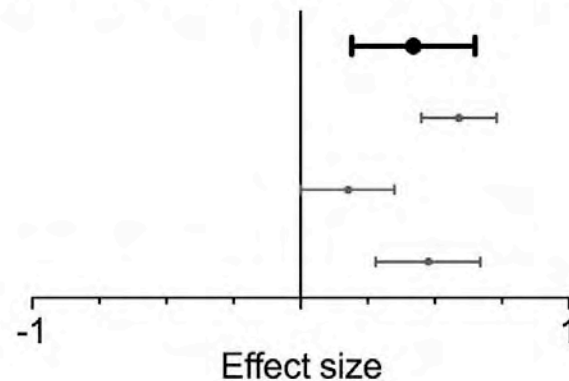
Summary of Results

- **Species richness of forbs and shrubs was greater in high wolf impact areas and evident at specific scales:**
  - » **1m²-10m² for forbs**
  - » **10m²-400m² for shrubs**
- **% cover of ferns was lower in high wolf impact areas**
- **Browse indicator species reveal reduced browsing pressure in high wolf impact areas**
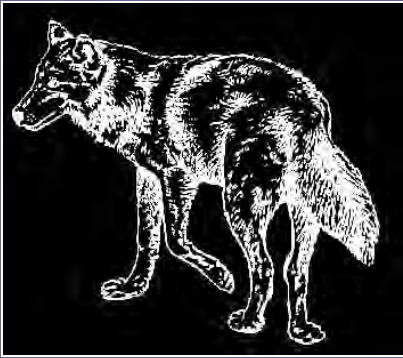
Summary of Results

- **In forests and forested wetlands, trophic cascades:**
  - Exist
  - Are subtle
  - Require about a decade before they are apparent
  - Do not resemble "deer free" conditions
  - Might become more pronounced with time

Acknowledgements

Collaborators
Adrian Wydeven, Jane Wiedenhoeft (Wisconsin DNR)
Corey Raimond and Clare Frederick (Field Assistants)
Warren Keith Moser (Forest Service)
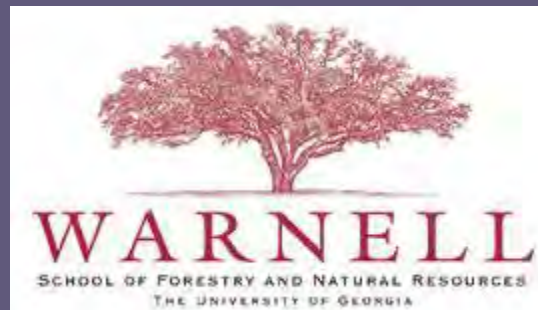
STUDY OF FEES FOR GRAZING LIVESTOCK ON FEDERAL LANDS

A Report From

The Secretary of the Interior

and

The Secretary of Agriculture

October 21, 1977

various forage improvement schemes, and a host of other management practices. The improved management practices used in the private sector are the same kinds of improvements needed to develop and manage the public rangelands.

Consideration of Predator Losses and Other Adverse Impacts on Animal Production

Permittees believe predator losses are greater on public land than on private land. Reasons are centered around Government failure to use an effective coyote control program and the nature of the range landscape which makes the land a natural habitat for predators. Predator losses are identified as resulting from coyotes, bears, bobcats, lions, and feral dogs. However, most of the comments concern the predator losses resulting from an increased coyote population. Since permittees believe predator losses are greater on public land, they feel there should be an increase In cost allowance for predation, i.e., a fee reduction.

Predator losses have been given consideration in one item of the Federal land user costs - death loss of animals. A difference was recognized in the larger number of death losses on public land and this larger loss was reflected in a lower FMV for public land. The cost difference between public and private land was the second largest, $0.23 per AUM. The only justification for a higher death loss cost allowance would be for any recent change in federal land predator losses that is significantly different from predator losses on private lands. Available data do not support arguments that predator losses have increased faster on Federal lands than on private lands, but that death losses have increased on both.

An estimate could be made of added rancher costs due to predators, with additional reduction being given in the grazing fee. This approach would require determination of predator costs on an individual rancher or limited area basis.

Credit for Wildlife Use of Private Lands

The proposal for a variable fee system for grazing on Federal lands is based in part on the presence of wildlife as well as recreational uses of associated Federal, State, and Private lands. The benefits of wildlife and recreation accrue in these areas to the individual recreationists as well as the general public. However, part of the cost for support of this wildlife may be borne disproportionately by individual landowners relative to their benefits from wildlife and recreation.
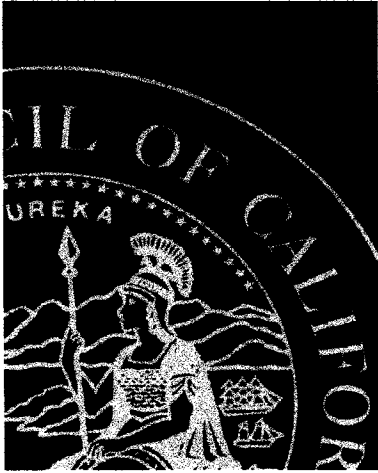
Uniform Bail and Penalty Schedules

JULY 2011 EDITION

(Cal. Rules of Court, rule 4.102)

TRAFFIC
BOATING
FORESTRY
FISH AND GAME
PUBLIC UTILITIES
PARKS AND RECREATION
BUSINESS LICENSING

JUDICIAL COUNCIL
OF CALIFORNIA

FISH AND GAME BAIL AND PENALTY SCHEDULE
(*See Preface, Section III(B)) (**See Preface, Section IV)

Section	Notes	Level	Offense	Base Fine	State PA	County PA/10	DNA PA*	Court PA*/10	Surcharge	EMS PA* /10	Total Bail**	Footnote
					10/10	7.00	4/10	5.00	20%	2.00		
			BURRO									
4600	(a)	M	Unlawful Killing or Capture of Undomesticated Burro	300	300	210.00	120	150.00	60	60	1,200.00	+
			WILD PIG									
4657		M	Wild Pig License Tag Violation	150	150	105.00	60	75.00	30	30	600.00	+
4669		M	Failure to Secure Liability Insurance Protection by For-Hire Vessel Operator	450	450	315.00	180	225.00	90	90	1,800.00	+
			FULLY PROTECTED MAMMALS									
4700	(a)(1) [7]	M	Taking or Possession of Fully Protected Mammal	5,000	5,000	3,500.00	2,000	2,500.00	1,000	1,000	20,000.00	+
			BEAR									
4753		M	Bear Tag License Violation	150	150	105.00	60	75.00	30	30	600.00	+
4758	[8]	M	Sale or Purchase of Bear Meat or Parts	3,250	3,250	2,275.00	1,300	1,625.00	650	650	13,000.00	+
4758	[9]	M	Possession of Three or More Bear Gall Bladders	10,000	10,000	7,000.00	4,000	5,000.00	2,000	2,000	40,000.00	+
			FULLY PROTECTED REPTILES AND AMPHIBIANS									
5000		M	Selling, Purchasing, Harming, Possessing, Transporting, or Shooting Desert Tortoises	300	300	210.00	120	150.00	60	60	1,200.00	+
5050	(a)	M	Taking or Possession of Fully Protected Reptile or Amphibian	500	500	350.00	200	250.00	100	100	2,000.00	+
			FISH–GENERAL PROVISIONS									
5508	[10]	M	Fish of Indeterminate Size	250	250	175.00	100	125.00	50	50	1,000.00	+
			(For Each Additional Fish)	20	20	14.00	8	10.00	4	4	80.00	+

+ $40 court security fee (reduced to $30 on 7/1/13 unless sunset repealed) and conviction assessment ($35/infraction; $30/misdemeanor) per offense.

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Opinion

OP-ED CONTRIBUTORS

T-Shirt Weather in the Arctic

By MARK URBAN and LINDA DEEGAN
FEBRUARY 5, 2016

WE crested the northern rim of Alaska's Brooks Range, and from the windows of our truck looked out across the undulating foothills toward the Arctic Ocean. Instead of seeing snow as we had in years past, we were greeted by a landscape already green with spring.

We flew by helicopter to our remote camp and shed our heavy parkas. The fish we had come to study had already disappeared downstream to spawn.

We now realize that what we saw last May was historic — the hottest May for Alaska's North Slope during what scientists recently concluded was the hottest year on record for the earth. We also saw the future.

Last year, the earth's temperature passed the mark of 1 degree Celsius above preindustrial levels. Civilization took 165 years to reach that mark, and now the increase could reach 2 degrees Celsius in just 30 more years, a point at which the risks from sea-level rise, drought and other effects could increase significantly.

Arctic Grayling
NATIONAL GEOGRAPHIC CREATIVE

Despite promises made in Paris to cut greenhouse gas emissions, we will still need to make it through the hottest years of a looming global heat age. Along with the many challenges we face, we must figure out how to protect ecosystems and the benefits they provide.

Each spring for the last 30 years, our team of biologists has traveled to remote field camps in Arctic Alaska. The Arctic is warming faster than anywhere else in the world as seawater replaces sea ice, painting the Arctic Ocean blue and fueling a dangerous feedback loop. The white sea ice reflects the sun's energy back into space through what is known as the albedo effect. But as the ice melts, the dark Arctic seawater is now absorbing that heat, turning up the earth's temperature.

With the early spring, snow melted roughly two weeks earlier than in the past and plants turned green soon after. Lakes thawed about 10 days earlier, and Arctic grayling, a fish, bred weeks earlier.

An early spring has long-term consequences. When grayling breed three weeks earlier, for instance, their offspring get a head start on feeding and grow nine times larger. This might seem like a good thing, until you consider that the same warmer temperatures dry the rivers that enable these grayling to swim to lakes where they spend the winter. As these fish wait in shallow pools for the rivers to flow, bears and birds enjoy a captive feast. If rivers do not flow before winter, the fish freeze. The drying of these rivers could threaten some grayling populations.

Last May's warmth deceived white-crowned sparrows into breeding earlier than usual. When a snowstorm roared in, the sparrows abandoned their ill-timed nests, leaving their eggs behind to perish.

Thunderstorms also raged over our camp. These storms used to be rare in the Arctic, but they strike often now. Lightning has set fire to the tundra, releasing into the atmosphere huge stores of ancient carbon from the permafrost. Sinkholes are also opening up in the thawing tundra. Walk up to one, and you will hear the trickle and clatter as heat dissolves permafrost into cascades of ice age mud and stones.

We are only just beginning to understand these changes. Ecosystems involve a complex web of connections among species and the physical environment. Climate change alters these connections in ways that can surprise and baffle us.

For example, scientists thought they understood Arctic streams until we added nutrients to one to mimic what happens when the tundra thaws. A rare moss materialized and blanketed the streambed. A new set of insects appeared, but they

sheltered in the moss instead of drifting into the waiting mouths of hungry grayling. So in a roundabout way, a more productive stream made for skinnier fish.

The surprises pose serious risks because we can't prepare for what we don't know. We can no longer be satisfied to watch and document these changes. We must predict and prevent them.

Sustaining life through the coming heat age will require tough decisions as we triage the rising number of climate casualties. We cannot hope to save all species when we haven't even figured out how many species there are.

We might focus initially on protecting those with the greatest importance to other species and ecosystems, the so-called biotic multipliers of climate change. For instance, top predators are often sensitive to climate change and magnify climate effects by yanking hard on the threads that connect them to other species in the food chain.

Our current approaches to identifying which species and ecosystems are most at risk are primitive. Most predictions rely on the correlation between a map of an animal's range and a few climate factors. As biologists, we need to develop forecasts that rely on causes, not correlations, as our colleagues studying the atmosphere did years ago. This will require an enhanced effort to comprehend how species survive, reproduce, evolve and move across landscapes, and how changes in the climate alter each of these factors.

We also need experiments that replicate a warming environment. Scientists know how to heat small plots of tundra with open-topped plastic enclosures and forests with heated cables. But the small size of these efforts limits our ability to understand consequences for larger animals and ecosystems. We need to engineer ways to warm bigger ecosystems experimentally by heating up entire lakes, streams, fields and even forests.

We plan to return to the Arctic again in May. This year is predicted to be even hotter than the last. We'll be ready this time. We understand now that we have already entered the heat age.

Mark Urban is an associate professor in ecology and evolutionary biology at the University of Connecticut in Storrs. Linda Deegan is a senior scientist at the Marine Biological Laboratory Ecosystems Center in Woods Hole, Mass.

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Making Room for Wolf Recovery:

The Case for Maintaining Endangered Species Act Protections for America's Wolves

Amaroq Weiss, Noah Greenwald, Curt Bradley

November 2014

I.   Executive Summary

In 2011 the U.S. Fish and Wildlife Service removed Endangered Species Act protections for wolves in the northern Rocky Mountains and western Great Lakes, arguing that wolves were recovered in those regions and the states could be trusted to manage them. But all of the states with substantial wolf populations have enacted aggressive hunting and trapping seasons that are intended to drastically reduce wolf populations. To date these hunts have resulted in the killing of more than 2,800 wolves. The deaths of so many wolves have contributed to declines in wolf populations of 9 percent in the northern Rockies and 25 percent in Minnesota. Given increased efforts to kill wolves in many states, these declines can be expected to continue and likely increase.

Despite the nightmare that state management of wolves has been, the Fish and Wildlife Service has proposed to remove protections for gray wolves in the remainder of the lower 48 states, excluding a small portion of Arizona and New Mexico, where the Mexican gray wolf struggles to survive. The agency argues that growth of populations in the northern Rockies and Great Lakes is sufficient to consider the species recovered and to remove Endangered Species Act protections.

In this report, we make the case that the job of recovering wolves is far from complete by:

- Identifying and mapping suitable habitat not currently occupied by wolves;
- Documenting dispersals of wolves to this habitat;
- Detailing the limitations of current management plans;
- Highlighting the important roles wolves play in ecosystems.

Gray wolves currently occupy less than 10 percent of their historic range and a fraction of currently suitable habitat. To identify and map unoccupied, suitable wolf habitat in the United States, we used 27 studies that model wolf habitat in different regions to create a single map. Based on this analysis, there is up to 530,000 square miles of suitable wolf habitat in the United States, only roughly 171,000 square miles of which is occupied, demonstrating that wolves currently occupy only about 30 percent of existing suitable habitat. The southern Rocky Mountains, Grand Canyon, Cascade Mountains in Washington, Oregon and California, the Sierra Nevada and the Adirondacks are all places that could support wolf populations. According to the studies, these areas are capable of supporting a minimum of 5,000 wolves, which would nearly double the existing wolf population.

Recovering wolves to these additional areas is necessary to ensure the long-term survival of gray wolves in the lower 48 states and enrich the diversity of U.S. ecosystems that have lacked the gray wolf as a top predator for decades. At last count the three existing wolf populations combined include only roughly 5,400 wolves, which is below what scientists have identified as the minimum viable population size necessary to avoid extinction. Considering that populations are now declining and isolated at several scales, doubling the population by facilitating wolf recovery in additional areas is needed to secure the future of gray wolves in the U.S.

Studies following reintroduction of wolves to Yellowstone National Park have documented that wolves as top predators play pivotal roles in shaping the structure and function of ecosystems, benefitting a wide range of species, including beavers, songbirds, grizzly bears, foxes, bison, pronghorn and more.

Gray wolves are also a substantial draw for people from around the world. Millions of people have traveled to Yellowstone from around the world to see the gray wolves reintroduced in 1995 and 1996, and polls consistently show that a broad majority of the American public supports the recovery of gray wolves, including to new areas where they don't currently occur.

Wenaha pack male courtesy ODFW
Cover photo by Chris Smith / Flickr

1

II.   **Introduction**

Gray wolves once occupied the majority of North America, excluding perhaps only the driest deserts and the southeastern United States, where the red wolf occurs (FWS 2013). Scientists estimate that pre-European settlement there may have been as many as 2 million wolves in North America (Leonard et al., 2005). During the late 19th century and early 20th century, state and local bounties reduced wolf numbers. From 1915 through mid-century, the U.S. government exterminated wolves from the United States and Mexico (Seton, 1929; Young and Goldman, 1944). By 1967, when wolves were protected under a precursor to the Endangered Species Act, they had been reduced to fewer than 1,000 wolves in northeastern Minnesota (FWS 2009).

With protection, wolves began to see some recovery, but only in portions of their former range where the U.S. Fish and Wildlife Service (FWS) developed recovery programs. Wolves were originally protected as four subspecies -- the northern Rockies wolf, eastern wolf, Mexican wolf and Texas wolf (FWS 1978). Recognizing that these subspecific designations were potentially invalid, FWS consolidated protection for gray wolves to the species level in 1978, including the entire lower 48 states (Ibid.) The agency, however, never developed a national strategy to recover wolves in the lower 48 in line with expanded protection. Instead it completed recovery plans that had already been started in 1978 for three of the four purported subspecies, excluding the Texas wolf.

With recovery programs in place, including reintroduction of wolves in portions of the northern Rocky Mountains, wolves began to grow in number and expand their range in the northern Rockies and western Great Lakes states. Mexican wolves were also reintroduced to a portion of the Southwest, but their numbers have grown slowly. In 2003 FWS began moving to delist wolves in the northern Rockies and western Great Lakes, and after multiple rounds of litigation in which the agency was repeatedly found not to have followed best science, were successful in removing protections in both regions in 2011 (FWS 2011ab). Since delisting, all states in the northern Rockies and western Great Lakes have instituted aggressive hunting and trapping seasons intended to drastically reduce wolf populations.

The agency is now proposing to remove protections for wolves across the lower 48 excluding a portion of the range of the Mexican gray wolf in Arizona and New Mexico (FWS 2013). This proposal disregards that there are only roughly 5,400 wolves in portions of the Midwest (~3,700 wolves), northern Rockies (~1,670) and Southwest (~80) (FWS 2013), and the states are actively working to reduce populations. Moreover, wolves occupy just a fraction of their historic range, less than 10 percent, and only a small portion of existing suitable habitat. Indeed, multiple researchers have modeled extensive suitable habitat for wolves in the Northeast, Pacific Northwest, southern Rocky Mountains, California and elsewhere. To describe the full extent of suitable habitat available for further recovery of wolves, we reviewed literature estimating existing wolf habitat, created composite maps of all known wolf habitat in the lower 48, quantified unoccupied habitat, and estimated the minimum number of wolves that could occur in this habitat. We also quantified and mapped wolf dispersal events over the past 30 years. In the following discussion, we present the results of these analyses, further discuss the history of efforts to remove protections for wolves, including discussion of the current proposal, and provide a rationale for not walking away from wolf recovery now.

III.   **Studies Estimating Wolf Habitat in the United States**

We reviewed 27 studies that modeled potential wolf habitat in the lower 48 states and used the composite results to estimate and map the full range of potential unoccupied wolf habitat and the number of wolves that could be supported in the lower 48 (Appendix A). The studies modeled wolf habitat across the western United States, the upper Midwest and the Northeast (Appendix B). This likely encapsulates a majority of existing wolf habitat in the United States excluding the range of the red wolf in the Southeast. But there may be additional habitat in North and South Dakota and other areas that should be the subject of additional modeling.

Predictive modeling parameters used in the studies consisted of road density (26 studies), human population density (20 studies), prey density (20 studies) and land cover/use (16 studies). Some studies used additional parameters including

land ownership (11 studies), livestock density (7 studies), slope or elevation (5 studies), climate or snowfall (4 studies), surface water availability (4 studies), and prey accessibility or availability (3 studies). Two studies used soil depth or hydrology (Appendix C).

and the Sierra Nevada in California. In the northeastern United States, thousands of square miles of terrain spanning upstate New York and portions of Vermont, New Hampshire and Maine were identified as capable of supporting a wolf population. And some studies indicate the lower peninsula of Michigan could support wolves.
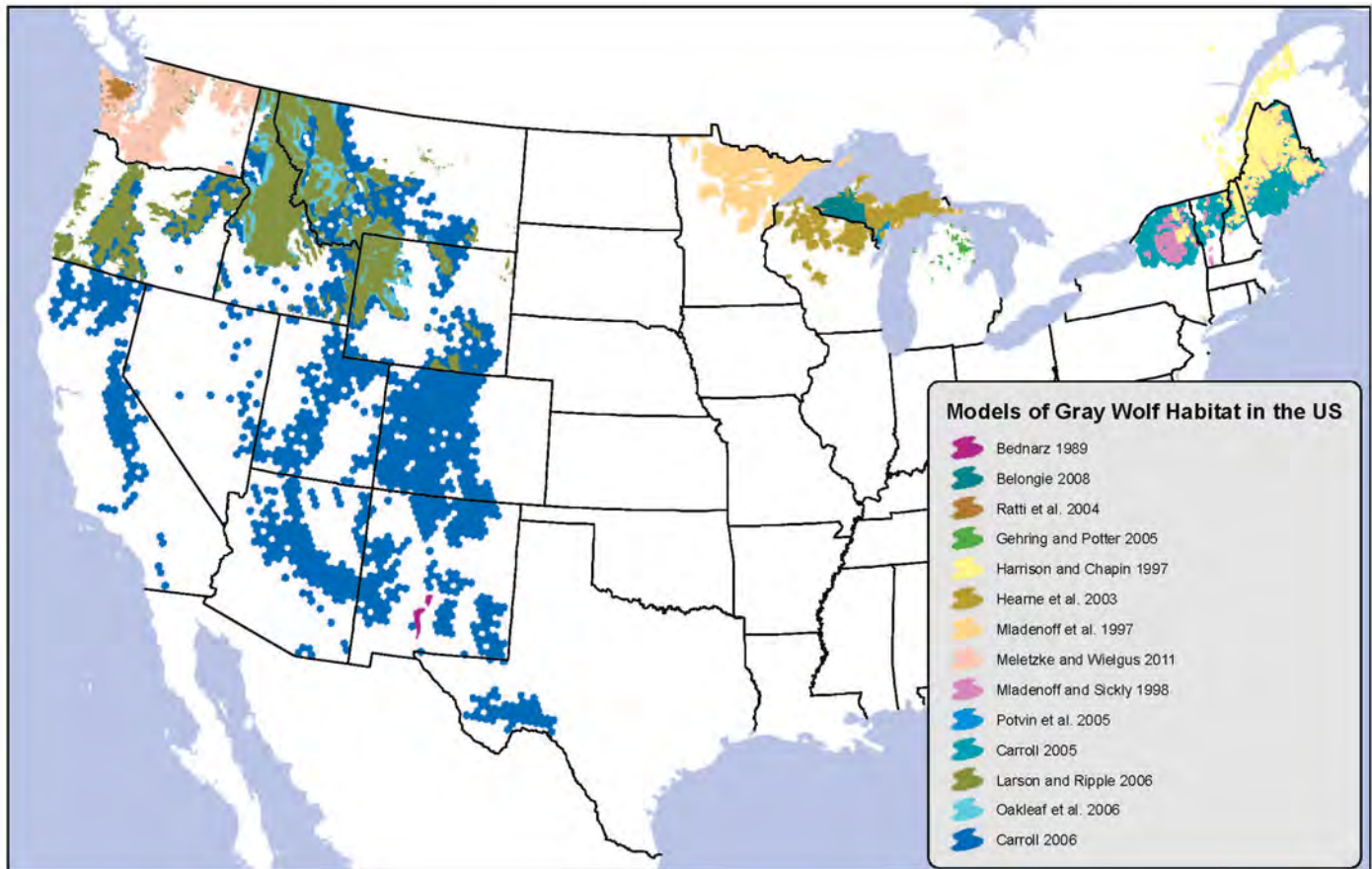
Figure 1. Suitable gray wolf habitat in the contiguous United States as identified in 14 modeling studies.

Past modeling of wolf habitat has accurately predicted wolf occupancy in both the northern Rockies and Midwest, suggesting modeling can accurately convey potential wolf habitat. We used 14 of the 27 studies to create a composite map of wolf habitat for the lower 48 states (Figure 1). We did not use all of the studies because in some cases they represented different modeling iterations for the same areas by the same authors, and in others there was insufficient spatial information to allow mapping.

Reviewed studies identified extensive wolf habitat in regions where wolves have not yet recovered. In the western United States, this includes the central and southern Rocky Mountains in both Colorado and Utah, the Grand Canyon and surrounding areas in northern Arizona, the Olympic Peninsula in Washington, the Cascade Mountains in Washington, Oregon and California

According to our mapping, there are approximately 530,000 square miles of suitable wolf habitat in the lower 48, of which roughly 171,000 square miles are currently occupied, meaning wolves have recovered to only roughly 30 percent of known suitable habitat. Although not all studies estimated the number of wolves that could be supported, those that did suggest that at least another 5,000 wolves could populate the Northeast, southern Rockies, West Coast and Southwest, nearly doubling the existing population and creating a network of interconnected populations bolstering genetic security.
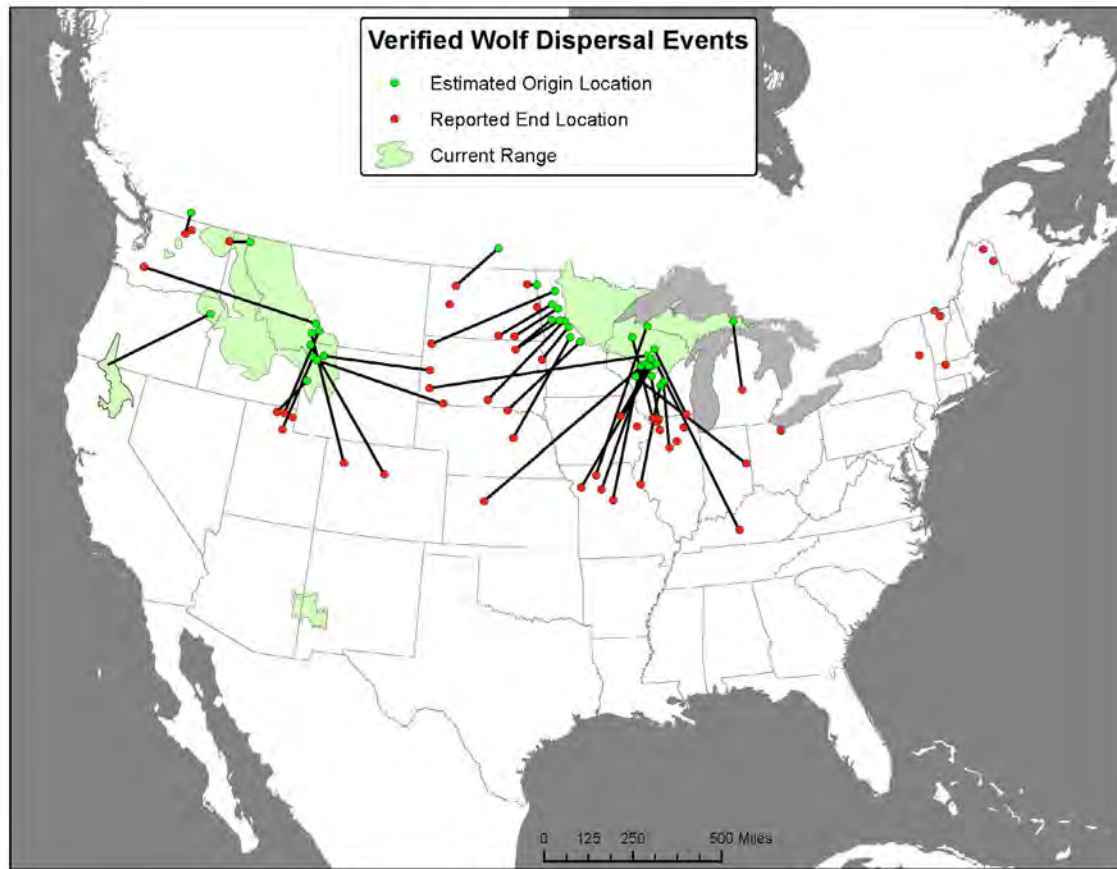
IV. **Wolves Are Dispersing Into Areas of Suitable Habitat and Need Endangered Species Act Protections to Survive**

Not only is there extensive suitable habitat in other

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regions of the country, but wolves are dispersing into this habitat. Wolves can travel substantial distances traversing diverse landscapes when leaving their birth-packs to seek mates and territory of their own (Mech and Boitani, 2003). The most-recent and well-known example is that of wolf OR-7, who traveled more than 4,000 miles after dispersing from his birth pack in northeastern Oregon to travel to California and back into Oregon repeatedly during 2011-2014. He recently found a mate, with whom he has denned and produced pups in southwestern Oregon just north of the California border. In order to quantify and visually display these

Figure 2. Dispersals by wolves to locations outside of core federal recovery areas, 1981-2014.

dispersal events, we tabulated all known wolf dispersals between 1981 and 2014 in which wolves dispersed to areas and states outside of existing core recovery areas (Appendix D). The dispersals we tabulated were reported in newspaper stories, agency reports and other sources, and for each dispersal event we attempted to obtain a point of origin and endpoint. We identified 56 dispersal events in total, with an average dispersal distance of 264 miles. This data shows that wolves have and will continue to move into suitable habitat on the West Coast, southern Rocky Mountains and Northeast, where they need protection if they are going to survive and establish populations (Figure 2). Indeed, with protections under the Endangered Species Act, wolves were able to move into Oregon and Washington from both the northern Rockies and British Columbia and form fledgling populations.

Our data also shows dispersal events steadily increased from 2000 to 2011, when populations were steadily growing with endangered species protections in place, and appear to have since declined now that all states with substantial wolf populations have enacted aggressive hunting and trapping seasons, leading to population declines (Figure 3). This further highlights the need for continued protection both in

areas that support source populations and in areas to which wolves are dispersing.

V.   **Recovery of Wolves to Additional Areas is Required by the Endangered Species Act**

Unlike previous endangered species statutes, the Endangered Species Act does not simply require recovery of species to the point that they are not at risk of global extinction. Indeed, the primary purpose of the Act is to conserve the ecosystems upon which endangered species depend (16 U.S.C. § 1531(b)). Significantly, the Act defines an endangered species as any species in danger of extinction in all or a *significant portion of its range* (16 U.S.C § 1532(6)). This means that a species need not be at risk of extinction everywhere to qualify for protection, but rather only in a significant portion of range. Accordingly, it also means that species cannot be considered recovered until no longer endangered in any significant portion of range. As demonstrated by the 27 studies we reviewed, wolves remain absent or at very low numbers over significant portions of their historic range where there

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Gray Wolf Dispersal Timeline
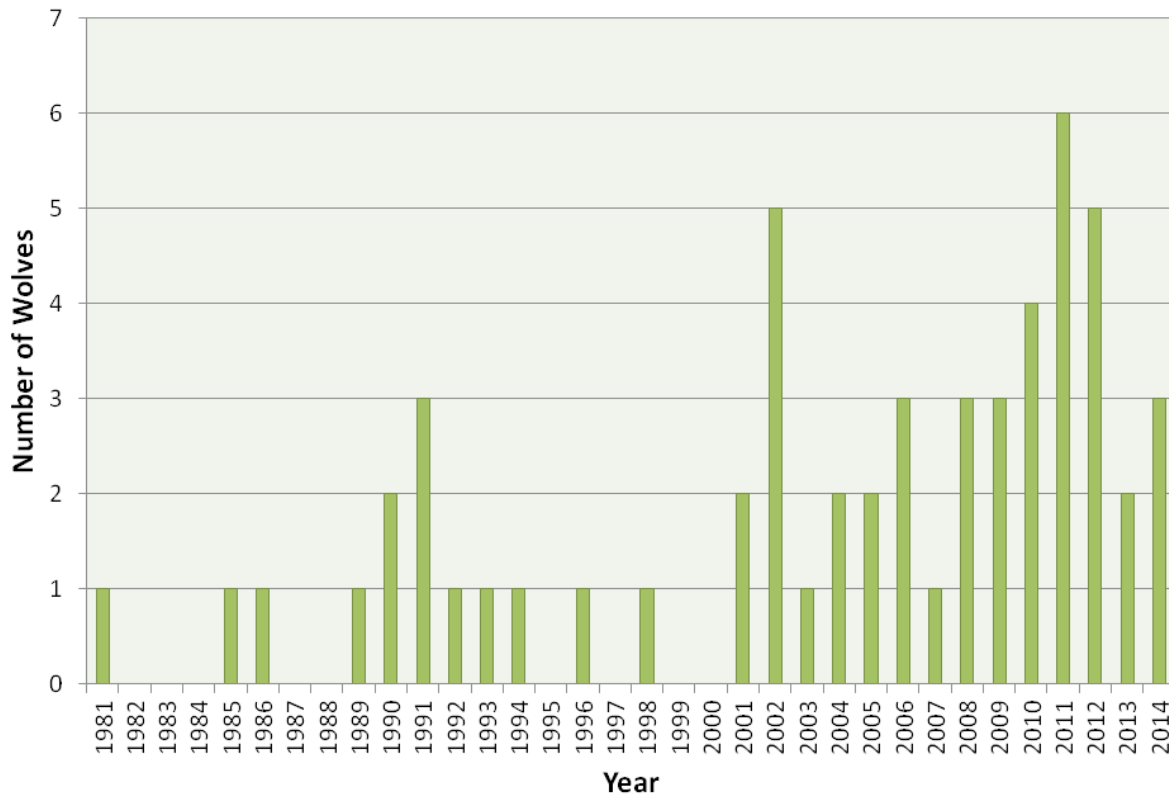
Figure 3. Annual gray wolf dispersal events to areas and states outside of federal core recovery areas.

is extensive remaining habitat, including the Northeast, southern Rocky Mountains, West Coast and elsewhere. For this reason alone, wolves remain an endangered species that continues to need the protections of the Endangered Species Act.

VI. **Existing Wolf Populations Are Not Viable in the Absence of Additional Population Expansion**

The existing wolf populations in the northern Rocky Mountains, western Great Lakes and Southwest are below minimum viable population sizes sufficient to ensure their survival (Shaffer, 1981; Reed et. al., 2003, Traill et al. 2007). In an analysis of 102 species including the gray wolf, Reed et al., (2003) estimated a mean and median minimum viable population of 7,316 and 5,816 individuals respectively, concluding that long-term persistence of wild populations of animals, such as wolves, requires 7,000 adult individuals. Likewise, Traill et al., (2007) combined results from studies on 212 species, including the gray wolf, finding that the median minimum viable population was 4,169 individuals.

As of the end of 2013, the existing wolf populations

numbered 1,691 in the northern Rockies, 3,669 in the western Great Lakes, and 83 in the Southwest.[i] According to the above studies, which collectively examined hundreds of species, all existing wolf populations are below minimum population sizes considered necessary to ensure long-term survival.

Of further concern, wolf populations in both the northern Rockies and Great Lakes are declining in response to aggressive hunting and trapping seasons enacted by individual states. In the northern Rockies, the last population count showed a 9 percent decline since federal delisting and in Minnesota, the population declined by an estimated 25 percent between 2008 and 2012.[ii] If these population declines continue, risk to wolf populations will only increase.

Existing wolf populations are also below levels considered necessary to avoid genetic inbreeding. A number of studies have concluded that an "effective" population size of 500 individuals is necessary to avoid

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[i] For northern Rockies see: http://www.fws.gov/mountain-prairie/species/mammals/wolf/annualrpt12/; for western Great Lakes see http://www.fws.gov/midwest/wolf/aboutwolves/WolfPopUS.htm.

[ii] See: *Ibid.* and www.mndnr.gov/wolves

the effects of genetic inbreeding (Soule and Wilcox, 1980; Frankel and Soule, 1981; Soule, 1986; Franklin and Frankham, 1998). Effective population size is defined as the number of breeding individuals, rather than total individuals, translating into a total population of 2,500-5,000 individuals to maintain a total of 500 breeding individuals (Frankham, 1995). Gray wolves in North America have already lost substantial genetic diversity because of the severe reduction in their overall historical numbers and range and further losses could lower survival and reproduction further endangering wolves (Leonard et al., 2005).

Loss of genetic diversity due to small population size and historic declines is compounded by the isolation of existing wolf populations (Soule, 1980). The Mexican gray wolf, for example, is isolated from all other wolf populations and the population in the Greater Yellowstone ecosystem is largely isolated from other wolves in the northern Rockies. This lack of connectivity further increases the potential for loss of genetic variation over time. Restoring wolves to additional suitable habitat would create more opportunity for connectivity between populations. It would also increase the likelihood that wolves dispersing from currently existing wolf populations would be able to find other wolves with whom to mate, and thus contribute genetically to the health of adjacent populations.

VII.   Recovering Wolves to Additional Areas Is Necessary for Healthy, Functioning Ecosystems

The loss of large carnivores is a global problem with broad ecological consequences. Because of their position at the top of food chains, large carnivores play an inordinate role in shaping the structure and function of diverse ecosystems (Estes et al. 2011, Ripple et al., 2014). According to Ripple et al. (2014), nearly two-thirds (61 percent) of large carnivore species are considered threatened by the IUCN and most (77 percent) are declining. The extirpation of the gray wolf across most of the American landscape is no exception to this pattern and as elsewhere around the world, loss of a top predator like the gray wolf has resulted in a number of rippling ecological consequences that have negatively impacted a broad range of species. This can be inferred largely by studies showing positive trends in a broad range of species following reintroduction of wolves in the northern Rockies.

Studies following reintroduction of wolves to Yellowstone National Park documented that wolves had a profound and transformative impact on the landscape that benefitted a wide variety of species. In particular, the reintroduction of wolves resulted in a dramatic decrease in elk numbers and also potentially forced them to move more (Barber-Meyer et al., 2008,

Ripple and Beschta, 2012). Reduced elk browse in turn has led to recovery of woody species, such as cottonwood, aspen, willow and serviceberry (Ripple and Beschta, 2012). This has fostered many beneficial ecosystem changes, from providing crucial nesting and roosting sites for songbirds, to enhancing root strength and thereby protecting streams from soil erosion, to providing food and building sources for beavers whose dams then create cool, deep ponds needed by juvenile fish, and finally to facilitating growth of berry-producing shrubs that provide food for grizzly bears and other animals (Ripple and Beschta, 2004; Hebblewhite et al., 2005; Weiss et al., 2007; Eisenberg et al., 2013, Hollenbeck and Ripple, 2008, Ripple et al., 2013).

Wolves prey on wild ungulates which are the most vulnerable due to factors such as age, injury or ill-health, allowing greater numbers of healthier, more robust, and more alert animals to survive and pass on their genes (Stahler et al, 2006). Wolves may also prevent the spread of diseases among prey species by culling sick animals before they infect others (Wild et al., 2005). Wolves view coyotes as territorial competitors and in some parts of Yellowstone wolves have greatly decreased the coyote density. This has led to increases in numbers of foxes and increased

survival of pronghorn antelope fawns due to reduced predation by coyotes (Berger et al., 2008). Carcasses of elk killed by wolves provide food for a host of other scavenger species, including but not limited to grizzly bears, black bears, coyotes, eagles, ravens, magpies and hundreds of species of beetles (Smith et al., 2003). Wolf-kills may also provide a buffering effect against climate change for carrion-feeders that depend on carcasses for food. As warming temperatures result in decreased winter severity, and thus a decreased die-off of vulnerable animals that would otherwise succumb to harsh weather, wolf-kills will provide the carcasses scavengers need to survive (Wilmers and Getz, 2005).

The ecosystems of the southern Rocky Mountains, Colorado Plateau, Grand Canyon, Cascade Mountains, Adirondack Mountains, Sierra Nevada and elsewhere would all benefit from the return and recovery of the gray wolf. It is not enough to restore the wolf to small fragments of its historic range. Instead, large carnivores like wolves should be restored to population levels allowing them to once again be "ecologically effective" – that is, a population that has enough individuals and a wide enough geographic distribution so that not just the species' existence has been reestablished but, also, its essential role in nature (Soule et al., 2003; Carroll et al., 2006.)

VIII. __Maintaining Federal Protections for Wolves Is Essential Because States Cannot Be Trusted to Conserve Existing Wolf Populations or Protect Wolves Dispersing to Other Areas__

Following removal of Endangered Species Act protections in the northern Rockies and western Great Lakes, all of the states with substantial wolf populations enacted aggressive hunting and trapping seasons designed to drastically lower populations, and indeed population declines are occurring. In the three years since protections were removed, nearly 3,000 wolves have been killed through state-sanctioned "harvest" seasons. The killing of so many wolves in such a short time directly reflects the negative prejudices towards wolves held by powerful minorities in all of these states. These prejudices were the primary cause of the extirpation of the wolf across significant portions of its range and highlight why wolves continue to need federal protections and a national recovery plan.

Worse still, anti-wolf policies appear to be getting more severe in most states where protections have been removed. In Idaho, for example, wolf hunting is allowed year round, including during breeding season and has resulted in the death of at least 1,000 wolves and reduced the state's wolf population by around 23 percent from its 2008 peak. This not being enough, the Idaho Department of Fish and Game in January 2014 hired a bounty hunter to pack into the Frank Church-River-of-No-Return Wilderness where he killed nine wolves; has sent U.S. Department of Agriculture/Wildlife Services' airborne sharpshooters into the Clearwater National Forest where 48 wolves have been killed in six operations; and Gov. Butch Otter this spring signed into law a bill that establishes a wolf-control board and provides over $600,000 annually to kill most of Idaho's remaining wolves.[iii] In Montana, the state wildlife commission nearly doubled the number of wolves that can be killed by an individual hunter or trapper in 2013 compared to 2012, and extended the wolf-killing season through the middle of March (when wolves would

be pregnant.) In Wyoming, wolves were designated a predatory animal that can be killed at anytime by nearly any means, including killing pups in dens, in nearly 85 percent of the state and designated the rest of the state outside of Yellowstone and Grand Teton National Parks, a trophy game area, where hunting of wolves was permitted. This management was found to be inadequate by a federal court in September, 2014 and Endangered Species Act protections were reestablished, stopping the 2014-2015 hunt and killing of wolves in the predatory zone.

In Minnesota, the state had promised in its state wolf plan that there would be no hunting or trapping of wolves for five years post delisting, but instead instituted wolf hunting and trapping immediately following delisting. To date, at least 650 wolves have been killed and the population declined by 25 percent between 2008-2012. Starting in 2012, Wisconsin authorized wolf-hunting and trapping that has to date resulted in killing of 374 wolves with a goal of reducing the population by more than half to 350 wolves from over 800. Wolves are allowed to be hunted and trapped with the use of hounds, night-hunting by artificial lights, and baiting, despite overwhelming public opposition to any of these practices.[iv] Michigan's governor in 2013 signed a bill allowing its state department of natural resources to institute hunting of wolves despite citizens having collected over a quarter of a million signatures to place a no-wolf-hunting measure on the election-season ballot; a second signature-collecting effort has resulted in a second ballot measure to overturn the newly-signed wolf-hunting law, but a pro-hunting ballot measure was just passed by the legislature. Because the no-wolf hunting ballot measure must be decided by the voters in the November election, Michigan wolves have received a temporary reprieve and there will be no wolf-hunting season in Michigan this year. But if the no-hunting measure does not pass, the legislative bill will go into effect in March meaning Michigan's wolves will once again be facing legal harvest and certain death. Finally, in South Dakota, the state passed a law that classifies wolves in the eastern half of the state as "varmints" that can be shot on sight.

[iii] See: http://gazers.com/previously-endangered-wolves-can-now-exterminated-idaho/

[iv] Wisconsin Department of Natural Resources 2013 wolf hunting and trapping regulations; The Political Environment, April 12, 2013

IX.   **Conclusion**

In its rush to remove federal protections for gray wolves in most of the lower 48, the U.S. Fish and Wildlife Service relied on the states to adequately manage and conserve the species. As these examples above demonstrate, however, state management of wolves has been a political, rather than a science-based, endeavor. In the three years states have had wolf-management authority, nearly 3,000 wolves have been killed from hunting and trapping, sanctioned by state policies that fail to adequately consider the long-term viability or need for further recovery of wolves.

The Service's plan to now remove federal protections throughout most of the remaining lower 48 states and allow states to fully manage wolves not only jeopardizes the future of existing wolf populations it also makes it nearly impossible for dispersing wolves to make their way to adjacent states to establish new populations of wolves.

To achieve true, long-term, sustainable, recovery of the gray wolf, federal wolf protections should be maintained and recovery plans developed, with the goal of restoring connected, resilient, ecologically-effective wolf populations wherever suitable wolf habitat exists. Formation of a recovery team made up of the many highly-qualified wolf biologists and other scientists could ensure that considerable recent science is brought to bear and ultimately produces a scientifically and legally defensible recovery strategy that specifies the conditions under which wolves are downlisted and ultimately delisted in all or portions of the species' range. Restoring wolves to these areas would fulfill the ESA's mandate to recover threatened or endangered species throughout all significant portions of their ranges and to conserve the ecosystems upon which they depend.

Yellowstone wolf by doublejwebers / Flickr

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APPENDIX A: Wolf Habitat Modeling Literature Reviewed

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APPENDIX B: Predicted Wolf Habitat Area and Wolf Populations

Reference	Study Region	Method	Study Location	Suitable Wolf Habitat (mi2)	# of Wolves Region Could Support
Bednarz 1989	Southwest	LANDSAT	White Sands Missile Range, NM	996	32-40
Belongie 2008	Midwest	GIS Overlay, Expert Ranking	MI's Upper Peninsula	4,846	-
Bennett 1994	S. Rockies	Unweighted Ranking	CO	12,000 - 25,000	407 – 814
Carroll 2003	Northeast	PATCH	ME (2025)	-	1,030
			NH (2025)	-	68
			NY (2025)	-	338
			VT (2025)	-	50
Carroll et al. 2001	West Coast	GIS Index	OR & CA	48,494	-
			Northeast OR		100
			Southwest OR and Northern CA		190 – 470
Carroll et al. 2003	S. Rockies		-	-	>1,000
Carroll et al. 2004	Southwest	PATCH	Blue Range AZ/NM, Grand Canyon, AZ, Mogollon Rim, AZ, San Juans, CO, Vermejo/Carson, NM, UT	17,390 - 24,131	3,166
Carroll et al. 2006	Western U.S.		-	233,081	-
Gehring and Potter 2005	Midwest	Per Mladenoff et al. 1995	MI	849-1,634	40 – 105
Harrison and Chapin 1997	Northeast	ARC Info and GIS	ME	17,064	-
			NY	5,644	-
			NH	1,773	-
			VT	954	-
			MA	20	-
			ME & NH	-	488
			Adirondacks, NY	-	146
Hearne et al. 2003	Midwest	Logistic Regression	MI & WI	-	>1,000
Houts 2001	N. Rockies	Logistic Regression	Central ID, GYE, Western MT	27,751	-
Houts 2003	West Coast	Logistic Regression	OR & WA	9,730	-
	N. Rockies		Central ID, GYE, Western MT	117,000	-
Johnson et al. 1992	Southwest		AZ	14,099	-
Larsen and Ripple 2006	N. Rockies	Logistic Regression	OR, ID, MT, WY	26,448	1,450

APPENDIX C: Predictive Modeling Parameters Used in 27 Wolf Habitat Suitability Models for the Lower 48 United States

Reference	Road density	Human density or disturbance	Land cover/use	Land use/owner	Prey density	Prey accessability	Prey availability	Livestock density	Climate or snowfall	Slope or elevation	Soil depth / hydrology	Surface water availability
Bednarz 1989												
Belongie 2008	x	x	x		x							
Bennett 1994												
Carroll et al. 2001	x	x		x	x	x						
Carroll et al. 2003	x	x			x		x					
Carroll et al. 2004	x	x	x		x			x				
Carroll et al. 2006	x	x										
Carroll 2003	x	x			x							
Carroll 2005	x	x	x		x				x	x		
Gerhing and Potter 2005	x	x										
Harrison and Chapin 1997	x	x	x									
Hearne et al. 2003	x	x		x								
Houts 2001	x		x	x	x							
Houts 2003	x		x									
Johnson et al. 1992	x	x	x	x	x			x	x			x
Larsen and Ripple 2006	x	x	x	x	x		x		x			
Maletzke and Wielgus 2011												
Mladenoff and Sickly 1998	x	x			x							
Mladenoff et al. 1995	x	x	x	x	x							
Mladenoff et al. 1997	x	x	x	x	x							
Mladenoff et al. 1999	x	x										
Oakleaf et al. 2006	x	x	x	x	x			x		x		
Paquet et al. 1999	x	x	x		x					x	x	
Potvin et al. 2005	x	x			x							
Ratti et al. 2004	x	x	x	x	x			x		x		
Sneed 2001	x	x		x	x							x
Wydevan et al. 1998	x	x	x		x							

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APPENDIX D: Tabulation of Dispersing Wolves, 1981-2014

Date	Reported End Location	Estimated Origin Location	Estimated Dispersal Distance (mi)	Outcome	Source
3/15/81	Brown County, South Dakota	Minnesota	139	Shot and killed	Licht, D.S. and S.H. Fritts. 1998. Gray Wolf (Canis lupus) occurrences in the Dakotas. U.S. Fish and Wildlife Service. Jamestown, ND: Northern Prairie Wildlife Research Center Online. Accessed at: http://www.npwrc.usgs.gov/resource/mammals/wolves/index.htm
10/13/85	Dickey County, North Dakota	Minnesota	154	Shot and killed	Licht, D.S. and S.H. Fritts. 1998. Gray Wolf (Canis lupus) occurrences in the Dakotas. U.S. Fish and Wildlife Service. Jamestown, ND: Northern Prairie Wildlife Research Center Online. Accessed at: http://www.npwrc.usgs.gov/resource/mammals/wolves/index.htm
6/4/86	Harding County, South Dakota	Unknown	349	Shot and killed	Licht, D.S. and S.H. Fritts. 1998. Gray Wolf (Canis lupus) occurrences in the Dakotas. U.S. Fish and Wildlife Service. Jamestown, ND: Northern Prairie Wildlife Research Center Online. Accessed at: http://www.npwrc.usgs.gov/resource/mammals/wolves/index.htm
11/10/89	Brown County, South Dakota	Minnesota	158	Shot and killed	Licht, D.S. and S.H. Fritts. 1998. Gray Wolf (Canis lupus) occurrences in the Dakotas. U.S. Fish and Wildlife Service. Jamestown, ND: Northern Prairie Wildlife Research Center Online. Accessed at: http://www.npwrc.usgs.gov/resource/mammals/wolves/index.htm
2/27/90	McIntosh County, North Dakota	Minnesota	185	Shot and killed	Licht, D.S. and S.H. Fritts. 1998. Gray Wolf (Canis lupus) occurrences in the Dakotas. U.S. Fish and Wildlife Service. Jamestown, ND: Northern Prairie Wildlife Research Center Online. Accessed at: http://www.npwrc.usgs.gov/resource/mammals/wolves/index.htm
2/2/90	Walsh County, North Dakota	Minnesota	29	Shot and killed	Licht, D.S. and S.H. Fritts. 1998. Gray Wolf (Canis lupus) occurrences in the Dakotas. U.S. Fish and Wildlife Service. Jamestown, ND: Northern Prairie Wildlife Research Center Online. Accessed at: http://www.npwrc.usgs.gov/resource/mammals/wolves/index.htm
2/27/91	Mountrail County, North Dakota	Manitoba, Canada	167	Shot and killed	Licht, D.S. and S.H. Fritts. 1998. Gray Wolf (Canis lupus) occurrences in the Dakotas. U.S. Fish and Wildlife Service. Jamestown, ND: Northern Prairie Wildlife Research Center Online. Accessed at: http://www.npwrc.usgs.gov/resource/mammals/wolves/index.htm
12/1/91	Grant County, South Dakota	Minnesota	126	Shot and killed	Licht, D.S. and S.H. Fritts. 1998. Gray Wolf (Canis lupus) occurrences in the Dakotas. U.S. Fish and Wildlife Service. Jamestown, ND: Northern Prairie Wildlife Research Center Online. Accessed at: http://www.npwrc.usgs.gov/resource/mammals/wolves/index.htm

Date	Location		Status	Reference
12/22/91	Tripp County, South Dakota	329	Shot and killed	Licht, D.S. and S.H. Fritts. 1998. Gray Wolf (Canis lupus) occurrences in the Dakotas. U.S. Fish and Wildlife Service. Jamestown, ND: Northern Prairie Wildlife Research Center Online. Accessed at: http://www.npwrc.usgs.gov/resource/mammals/wolves/index.htm
1/6/1992	Dunn County, North Dakota	213	Shot and killed	Licht, D.S. and S.H. Fritts. 1998. Gray Wolf (Canis lupus) occurrences in the Dakotas. U.S. Fish and Wildlife Service. Jamestown, ND: Northern Prairie Wildlife Research Center Online. Accessed at: http://www.npwrc.usgs.gov/resource/mammals/wolves/index.htm
Aug-93	Northeast Maine	Unknown	Shot and killed[1]	Maine Wolf Coalition. Wolves in the Northeast. Accessed at: http://mainewolfcoalition.org/wolves-in-the-northeast/; New York Times. 1996. Signs Suggest a Return Of Timber Wolf to Maine. Accessed at: http://www.nytimes.com/1996/12/22/us/signs-suggest-a-return-of-timber-wolf-to-maine.html
1994/95	Boyd County, Nebraska	300	Shot and killed	U.S. Fish and Wildlife Service. 2011. Revisiting the Listing of the Gray Wolf in the Western Great Lakes. Federal Register, Vol. 76, No. 249.
Nov-96	Eastern Maine	Unknown	Shot and killed	Maine Wolf Coalition. Wolves in the Northeast. Accessed at: http://mainewolfcoalition.org/wolves-in-the-northeast/; New York Times. 1996. Signs Suggest a Return Of Timber Wolf to Maine. Accessed at: http://www.nytimes.com/1996/12/22/us/signs-suggest-a-return-of-timber-wolf-to-maine.html
Nov-98	Glover, Vermont	Unknown	Shot and killed	Maine Wolf Coalition. Wolves in the Northeast. Accessed at: http://mainewolfcoalition.org/wolves-in-the-northeast/; Urbigkit, C. 2007. Wolf killed in Vermont. Pinedale Online! Accessed at: http://www.pinedaleonline.com/news/2007/10/WolfkilledinVermont.htm
2001	Harding County, South Dakota	400	Killed	U.S. Fish and Wildlife Service. 2011. Revisiting the Listing of the Gray Wolf in the Western Great Lakes. Federal Register, Vol. 76, No. 249.
Dec-01	Day, New York	Unknown	Shot and killed (MC)	Maine Wolf Coalition. Wolves in the Northeast. Accessed at: http://mainewolfcoalition.org/wolves-in-the-northeast/; Nearing, B. 2011. A century later, the wild wolf returns: Animal shot a decade ago hints at the arrival of predator in New York. Times Union. Accessed at: http://www.timesunion.com/local/article/A-century-later-the-wild-wolf-returns-2222681.php
Feb-02	Pend Oreille County, Washington	Unknown	Moved into B.C.	Wiles, G.J., H.L. Allen, and G.E. Hayes. 2011. Wolf conservation and management plan for Washington. Washington Department of Fish and Wildlife, Olympia, Washington. 297 pp.

Date	Location	Origin	Distance (mi)	Fate	Reference
10/23/02	Outside of Trenton, Grundy County, Missouri	Ironwood, Gogebic County, Michigan	470	Shot and killed	Michigan Department of Natural Resources. 2008. Michigan Wolf Management Plan. Wildlife Division Report No. 3484. Accessed at: http://www.michigan.gov/documents/dnr/Draft_Wolf_Management_Plan_030708_227742_7.pdf; Beringer, J. Personal communication with Jeff Beringer, Resource Scientist, Missouri Department of Conservation. May 9, 2013.
Dec-02	Henry, Marshall County, Illinois	Wisconsin	200	Shot and killed (MC)	University of Illinois. 2013. Wildlife Directory: Gray Wolf (Canis lupus). Accessed at: http://web.extension.illinois.edu/wildlife/directory_show.cfm?species=wolf; Kath, J.A. 2013. Personal Communication with Joseph A. Kath, Endangered Species Manager, Illinois Department of Natural Resources. May 15, 2013.
12/15/02	Spalding, Greeley County, Nebraska	Western Great Lakes DPS	350	Shot and killed	U.S. Fish and Wildlife Service. 2003. Status of Gray Wolf Recovery, Weeks of 3/28 to 4/04, 2003. Weekly Report, Gray Wolves in the Northern Rocky Mountains. Accessed at: http://www.fws.gov/mountain-prairie/species/mammals/wolf/WeeklyRpt03/wk04042003.htm
2002	Morgan, Utah	Yellowstone NP	240	Trapped and released in Yellowstone	Hollenhorst, J. 2002. Wolf Capture in Utah Ignites Controversy. KSL-TV. Accessed at: http://web.ksl.com/dump/news/cc/local/wolf_return.php
2003	Southwest (SW 1/4 Sec. 10, T19N, R13E) Randolph County, Indiana	Jackson County, Wisconsin	428	Found dead	Wisconsin Department of Natural Resources. 1999. Wisconsin Wolf Management Plan. Madison, Wisconsin. Accessed at: http://dnr.wi.gov/files/pdf/pubs/er/er0099.pdf; http://www.predatormastersforums.com/forums/ubbthreads.php?ubb=showflat&Number=8926 1
6/7/04	I-70, 30 mi west of Denver, Colorado	Northwest corner of Yellowstone NP	446	Killed by motor vehicle	U.S. Fish and Wildlife Service. 2004. News Release: Preliminary Necropsy Results For Gray Wolf Found Dead Near Denver, Colorado. U.S. Fish and Wildlife Mountain-Prairie Region, Lakewood, Colorado. Accessed at: http://www.fws.gov/mountain-prairie/pressrel/04-43.htm
Oct-04	Lower Peninsula, Michigan	Upper Peninsula, Michigan	Unknown	Killed	U.S. Fish and Wildlife Service. 2011. Revisiting the Listing of the Gray Wolf in the Western Great Lakes. Federal Register, Vol. 76, No. 249.
2/17/05	Chain O'Lakes State Park, Lake County, Illinois	Wisconsin	Unknown	Killed by motor vehicle	University of Illinois. 2013. Wildlife Directory: Gray Wolf (Canis lupus). Accessed at: http://web.extension.illinois.edu/wildlife/directory_show.cfm?species=wolf; Kath, J.A. 2013. Personal Communication with Joseph A. Kath, Endangered Species Manager, Illinois Department of Natural Resources. May 15, 2013.
Dec-05	New Canton, Pike County, Illinois	Central Wisconsin	300	Shot and killed	U.S. Fish and Wildlife Service. 2011. Revisiting the Listing of the Gray Wolf in the Western Great Lakes. Federal Register, Vol. 76, No. 249; University of Illinois. 2013. Wildlife Directory: Gray Wolf (Canis lupus). Accessed at: http://web.extension.illinois.edu/wildlife/directory_show.cfm?species=wolf; Young, C. 2006. Wild wolf killed in Pike County Illinois. Wolf Saga. Accessed at: http://wolfsaga.blogspot.com/2006/02/wild-wolf-killed-in-pike-county.html; Kath, J.A. 2013. Personal Communication with Joseph A. Kath, Endangered Species Manager, Illinois Department of Natural Resources. May 15, 2013.

Date	Location	Origin/Region	Number	Cause of death	References
Apr-06	Sturgis, South Dakota	Yellowstone NP	300	Killed by motor vehicle	Maughan, R. 2006. Wolf hit on I-90 near Sturgis, SD last April was a Yellowstone area wolf. Wolf Report 8-15-2006. Accessed at: http://www.forwolves.org/ralph/sturgis-wolf.htm; Stark, M. 2007. Yellowstone wolf hit near Sturgis. The Billings Gazette. Accessed at: http://helenair.com/news/article_cee1229e-ec91-575c-a7ea-30287aac9b33.html
Oct-06	North Troy, Vermont	Unknown	Unknown	Shot and killed	Maine Wolf Coalition. Wolves in the Northeast. Accessed at: http://mainewolfcoalition.org/wolves-in-the-northeast/; Urbigkit, C. 2007. Wolf killed in Vermont. Pinedale Online! Accessed at: http://www.pinedaleonline.com/news/2007/10/WolfkilledinVermont.htm
2006	Tremonton, Utah	Northern Rocky Mountain DPS	Unknown	Killed	U.S. Fish and Wildlife Service. 2007. Rocky Mountain Wolf Recovery 2006 Annual Report. C.A. Sime and E.E. Gangs, eds. USFWS, Ecological Services, 585 Shepard Way, Helena, Montana. 59601. 235 pp.
Oct-07	Shelburne, Massachusetts	Unknown	Unknown	Shot and killed	Maine Wolf Coalition. Wolves in the Northeast. Accessed at: http://mainewolfcoalition.org/wolves-in-the-northeast/; Reitz, S. 2008. Rare Gray Wolf Appears in Western Massachusetts. National Geographic News. Accessed at: http://news.nationalgeographic.com/news/2008/03/080305-AP-wolf-return.html
2/19/08	Lena, Illinois	Western Great Lakes DPS	Unknown	Shot and killed (MC)	University of Illinois. 2013. Wildlife Directory: Gray Wolf (Canis lupus). Accessed at: http://web.extension.illinois.edu/wildlife/directory_show.cfm?species=wolf; Kath, J.A. 2013. Personal Communication with Joseph A. Kath, Endangered Species Manager, Illinois Department of Natural Resources. May 15, 2013.
2008	Okanogan County, Washington	"Coastal B.C. and NE B.C., NW Alberta, or reintroduced populations in central ID and GYE"	Unknown	Unknown	Wiles, G.J., H.L. Allen, and G.E. Hayes. 2011. Wolf conservation and management plan for Washington. Washington Department of Fish and Wildlife, Olympia, Washington. 297 pp.
Jul-08	Twisp, Washington	Coastal/Southern British Columbia	Unknown	Unknown	U.S. Fish and Wildlife Service. 2011. Rocky Mountain Wolf Recovery 2010 Interagency Annual Report. C.A. Sime and E.E. Bangs, eds. USFWS, Ecological Services, 585 Shepard Way, Helena, Montana, 59601.
2009	Kane County, Illinois	Unknown	Unknown	Shot and killed (MC)	University of Illinois. 2013. Wildlife Directory: Gray Wolf (Canis lupus). Accessed at: http://web.extension.illinois.edu/wildlife/directory_show.cfm?species=wolf; Kath, J.A. 2013. Personal Communication with Joseph A. Kath, Endangered Species Manager, Illinois Department of Natural Resources. May 15, 2013.
Apr-09	South of Meeker, Colorado	South of Bozeman, Montana	400	Killed by Compound 1080	The Southwest Environmental Center. 2011. Lone wolf travels 3,000 miles before being poisoned. Accessed at: http://www.wildmesquite.org/news/lone-wolf-travels-3000-miles-being-poisoned/071511

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Date	Location		Region/DPS	Fate	Reference
May-09	Pend Oreille County, Washington	Unknown	Northwestern Montana/northern Idaho	Unknown	Wiles, G.J., H.L. Allen, and G.E. Hayes. 2011. Wolf conservation and management plan for Washington. Washington Department of Fish and Wildlife, Olympia, Washington. 297 pp.
Mar-10	Bellevue, Sandusky County, Ohio	Unknown	Unknown	Shot and killed	Butterworth, S. 2013. Personal communication with Scott Butterworth, District Manager, Wildlife District Two, Ohio Department of Natural Resources. May 14, 2013.; http://www.toledoblade.com/StevePollick/2010/03/19/Wolf-shooting-piques-curiosity.html
Jul-10	Rich County, Utah	Unknown	Unknown	Shot and killed	Linnell, M. 2013. Personal communication with Mike Linnell, State Director, Utah, USDA-Wildlife Services. May 10, 2013.
2010	Cache County, Utah	Unknown	Northern Rocky Mountain DPS	Shot and killed in Idaho	Love, C. 2010. Wolf Range Expands into Utah. Field and Stream. Accessed at: http://www.fieldandstream.com/blogs/hunting/2010/07/wolf-range-expands-utah
2010	12 miles northeast of Carrolton, Carroll County, Missouri	Unknown	Western Great Lakes DPS	Shot and killed (MC)	Jerek, J. 2013. DNA shows hunter-shot canine from October to be wandering wolf. Missouri Department of Conservation. Accessed at: http://mdc.mo.gov/newsroom/dna-shows-hunter-shot-canine-october-be-wandering-wolf; Beringer, J. Personal communication with Jeff Beringer, Resource Scientist, Missouri Department of Conservation. May 9, 2013.
2011	Western Washington	Unknown	Northern Rocky Mountain DPS	Two packs established outside of NRM DPS	U.S. Fish and Wildlife Service. 2012. Northern Rocky Mountain Wolf Recovery Program 2011 Interagency Annual Report. M.D. Jimenez and S.A. Becker, eds. USFWS, Ecological Services, 585 Shepard Way, Helena, Montana, 59601.
2011	Southeast Jo Daviess County, Illinois	Unknown	Unknown	Shot and killed (male)	University of Illinois. 2013. Wildlife Directory: Gray Wolf (Canis lupus). Accessed at: http://web.extension.illinois.edu/wildlife/directory_show.cfm?species=wolf; Kath, J.A. 2013. Personal Communication with Joseph A. Kath, Endangered Species Manager, Illinois Department of Natural Resources. May 15, 2013.
2011	Southeast Jo Daviess County, Illinois	Unknown	Unknown	Shot and killed (female)	University of Illinois. 2013. Wildlife Directory: Gray Wolf (Canis lupus). Accessed at: http://web.extension.illinois.edu/wildlife/directory_show.cfm?species=wolf; Kath, J.A. 2013. Personal Communication with Joseph A. Kath, Endangered Species Manager, Illinois Department of Natural Resources. May 15, 2013.
Jan-11	Hillsboro, North Dakota	Unknown	Unknown	Shot and killed (MC)	Associated Press. 2011. Federally protected gray wolf shot in North Dakota. Twin Cities Pioneer Press. Accessed at: http://www.twincities.com/news/ci_17555251
Oct-11	Clinton County, Missouri	Unknown	Western Great Lakes DPS	Shot and killed (MC)	Beringer, J. Personal communication with Jeff Beringer, Resource Scientist, Missouri Department of Conservation. May 9, 2013; Leonard, J. 2012. Gower man unknowingly bags wolf. News-Press Now. Accessed at: http://www.newspressnow.com/sports/outdoors/article_917229af-fbd3-5ba4-9386-05f9e928cec9.html

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Date	Location	Origin	Distance (miles)	Disposition	Reference
12/28/11	Northern California	Northeastern Oregon (Imnaha pack)	350	Travelled back to Oregon in March 2013	Oregon Department of Fish and Wildlife. 2013. Wolves in Oregon: Wolf Program Updates. Accessed at: http://www.dfw.state.or.us/wolves/; California Department of Fish and Wildlife. Wildlife and Habitat Management: OR-7 - A Lone Wolf's Story. Accessed at: http://www.dfg.ca.gov/wildlife/nongame/wolf/OR7story.html
Feb-12	Custer County, South Dakota	Western Great Lakes DPS	Unknown	Killed	Woster, K. 2012. Wolf killed near Custer likely from Great Lakes population. Rapid City Journal. Accessed at: http://rapidcityjournal.com/news/wolf-killed-near-custer-likely-from-great-lakes-population/article_92dc1eb8-6be8-11e1-8ce3-00187e3ce6c.html; Custer County Chronicle Online. 2012. Wolf killed near Custer. Accessed at: http://www.custercountynews.com/cms/news/story-427443.html
May-12	Pine Ridge, South Dakota	Southeast Yellowstone NP	400	Found dead, likely hit by motor vehicle	Woster, K. 2012. Wolf found near Pine Ridge migrated from Yellowstone. Rapid City Journal. Accessed at: http://rapidcityjournal.com/news/wolf-found-near-pine-ridge-migrated-from-yellowstone/article_f6d01210-9f07-11e1-a76d-001a4bcf887a.html
Oct-12	Franklin Island Conservation Area, Howard County, Missouri	Western Great Lakes DPS	Unknown	Shot and killed (MC)	Jerek, J. 2013. DNA shows hunter-shot canine from October to be wandering wolf. Missouri Department of Conservation. Accessed at: http://mdc.mo.gov/newsroom/dna-shows-hunter-shot-canine-october-be-wandering-wolf; Beringer, J. Personal communication with Jeff Beringer, Resource Scientist, Missouri Department of Conservation. May 9, 2013.
Dec-12	Trego County, Kansas	Western Great Lakes DPS	Unknown	Shot and killed (MC)	Kansas Department of Wildlife, Parks and Tourism. 2013. Weekly News: Wolf Found In Kansas. Accessed at: http://kdwpt.state.ks.us/KDWPT-Info/News/Weekly-News/1-31-13/WOLF-FOUND-IN-KANSAS; Peek, M. 2013. Personal Communication with Matt Peek, Wildlife Research Biologist, Kansas Department of Wildlife, Parks & Tourism. May 10, 2013.
Dec-12	Coleta, Whiteside County, Illinois	Unknown	Unknown	Trapped and released	University of Illinois. 2013. Wildlife Directory: Gray Wolf (Canis lupus). Accessed at: http://web.extension.illinois.edu/wildlife/directory_show.cfm?species=wolf; Kath, J.A. 2013. Personal Communication with Joseph A. Kath, Endangered Species Manager, Illinois Department of Natural Resources. May 15, 2013.
Mar-13	Apple Canyon Lake, Jo Daviess County, Illinois	Wisconsin	250	Found dead	University of Illinois. 2013. Wildlife Directory: Gray Wolf (Canis lupus). Accessed at: http://web.extension.illinois.edu/wildlife/directory_show.cfm?species=wolf; Kath, J.A. 2013. Personal Communication with Joseph A. Kath, Endangered Species Manager, Illinois Department of Natural Resources. May 15, 2013.
Dec-13	La Salle County, IL	Unknown	Unknown	Killed by vehicle	University of Illinois. 2013. Wildlife Directory: Gray Wolf (Canis lupus). Accessed at: http://web.extension.illinois.edu/wildlife/directory_show.cfm?species=wolf; Kath, J.A. 2013. Personal Communication with Joseph A. Kath, Endangered Species Manager, Illinois Department of Natural Resources. May 15, 2013.
Mar-14	Munfordville, Kentucky (Hart County)	Western Great Lakes DPS	750	Shot and killed	Associated Press. 2013. Officials confirm gray wolf killed in Ky. Accessed at: http://www.wkyt.com/home/headlines/officials-confirm-gray-wolf-killed-in-ky-219749481.html

Date	Location	DPS	Count	Disposition	Source
Feb-14	Fairbank, Iowa (Buchanan County)	Western Great Lakes DPS	250	Shot and killed (MC)	Love, Orlan. 2014. First wolf in Iowa in 89 years killed in Buchanan County. Accessed at: http://www.kcrg.com/subject/news/first-wolf-in-iowa-in-89-years-killed-in-buchanan-county-20140506
May-14	Jones County, Iowa	Awaiting info from Iowa DNR	Unknown	Shot and killed (MC)	Love, Orlan. 2014. http://thegazette.com/subject/environment/nature/endangered-species/another-wolf-slain-in-iowa-20140717

MC – Wolf was mistaken for coyote when shot.
[1] shot by bear hunter who was prosecuted by USFWS

THE ROLE OF PREDATION IN DISEASE CONTROL: A COMPARISON OF SELECTIVE AND NONSELECTIVE REMOVAL ON PRION DISEASE DYNAMICS IN DEER

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THE ROLE OF PREDATION IN DISEASE CONTROL: A COMPARISON OF SELECTIVE AND NONSELECTIVE REMOVAL ON PRION DISEASE DYNAMICS IN DEER

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ABSTRACT: Effective measures for controlling chronic wasting disease (CWD), a contagious prion disease of cervids, remain elusive. We review theoretic relationships between predation and host-parasite dynamics and describe a mathematical model to evaluate the potential influence of random removal through harvest or culling and selective predation by wolves (*Canis lupus*) upon CWD dynamics in deer (*Odocoileus* spp.) populations. Imposing nonselective mortality representing a 15% annual harvest or cull 51 yr after CWD introduction lowered both deer population size and steady state CWD. Selective (4×) mortality at the same 15% predation rate caused a more modest reduction in deer population size accompanied by a relatively rapid decline in CWD prevalence and elimination of the disease from a closed population. The impacts of selective predation on epidemic dynamics were sensitive to assumptions on parameter estimates; however, within expected ranges, the results of selective predation were consistent and robust. We suggest that as CWD distribution and wolf range overlap in the future, wolf predation may suppress disease emergence or limit prevalence.
Key words: *Canis lupus*, chronic wasting disease, deer, host-parasite, *Odocoileus* spp., predator-prey, selective predation, wolf.

INTRODUCTION

Disease emergence and reemergence threaten the abundance and viability of wildlife species worldwide (Daszak et al., 2000). Although a variety of factors appear to be contributing to the recent surges in diseases impacting natural populations, ecosystems altered by human activities seem particularly vulnerable to such effects (Harvell et al., 1999; Daszak et al., 2000, 2001; Kutz et al., 2005; Johnson et al., 2007; Pedersen et al., 2007). Ecologic imbalances can diminish the resilience of host species to natural fluctuations in pathogens and the host's capacity to resist or recover from pathogen introductions. Such impacts on resiliency can be observed with alterations to host-parasite relationships resulting in changes in host survival and contact rates among susceptible and infected individuals (Harvell et al., 1999; Daszak et al., 2001; Kutz et al., 2005; Johnson et al., 2007; Pedersen et al., 2007).

Changes in predation rates or predator-prey dynamics are among the factors that may affect patterns of disease emergence, reemergence, and persistence (Choo et al., 2003; Packer et al., 2003; Holt and Roy, 2007). The potential effects of predation on epidemic dynamics vary depending on both the nature of predation occurring upon hosts and attributes of the host-parasite relationship. Nonselective predation could dampen epidemic dynamics by reducing host densities and contact rates or by lowering the total number of infected individuals in a host population (Heesterbeek and Roberts, 1995; Barlow, 1996; Packer et al., 2003). Similarly, selective predation on infected individuals could eliminate pathogens or prevent their establishment under some circumstances (Heesterbeek and Roberts, 1995; Gross and Miller, 2001; Packer et al., 2003).

Alternatively, both nonselective and selective predation might facilitate pathogen emergence and persistence in cases where resistant individuals become less abundant (Choisy and Rohani, 2006; Holt and Roy, 2007) and in cases where infected individuals are avoided by predators (Packer et al., 2003). It follows that ecosystems altered by removal of natural predators by humans may respond differently to endemic or novel pathogens than intact systems.

In light of the potential influence of predation on host-parasite dynamics, the role of predators should be considered in devising strategies for control of emerging or reemerging pathogens in natural populations. We review the theoretic relationships between predation and host-parasite dynamics, using the term parasite broadly to describe any infectious agent capable of infecting a host, utilizing host resources, and spreading to new hosts (Altizer et al., 2003). We then describe a simple mathematical model developed to evaluate how dynamics of prion disease in deer (*Odocoileus* spp.) populations may respond to nonrandom removal resulting from selective predation by wolves (*Canis lupus*) and compare this outcome with effects of random removal through harvest or culling.

Predation and host-parasite dynamics

Nonselective predation: The interplay among host regulation, immune response, and the pattern of predator selectivity determines whether predation reduces or increases the prevalence of disease in a population (Holt and Roy, 2007). Under many scenarios, increasing mortality rates in diseased populations can retard disease transmission and reduce disease prevalence (Barlow, 1996; Lafferty and Holt, 2003; Packer et al., 2003; Ostfeld and Holt, 2004). Increasing mortality slows transmission via two mechanisms. First, it reduces the average lifetime of infected individuals. Reduced lifespan, in turn, can truncate the time interval when animals are infectious, thereby reducing the number of infections produced per infected

individual. Second, the effect of reduced intervals of infectivity is amplified by reductions in population density that occur as mortality increases; such reductions cause declines in the number of contacts between infected and susceptible individuals. Both of these mechanisms slow rates of transmission of disease. If these mechanisms cause the number of new infections produced per infected individual to fall below one, then the disease will be eliminated from the population.

Selective predation: Any elevation in mortality rate has the potential to cause the foregoing effects. Reductions in transmission rates and disease prevalence can be particularly large if mortality rates are disproportionately higher in the infected portion of the population than in the susceptible portion (Heesterbeek and Roberts, 1995). This explains why diseases that cause rapid death fail to persist. However, other, nondisease, agents of selective mortality can exert the same beneficial effect. For example, if predators prey selectively on diseased individuals, it is reasonable to expect that they might reduce disease prevalence much more rapidly than would occur if mortality were nonselective.

Evidence that predators have a greater selectivity for diseased prey has been widely observed. Voříšek et al. (1998) found parasitized voles in buzzards' diets in a greater proportion than they occurred in the population. Birds with high blood parasite loads (Moller and Nielsen, 2007) and birds with weakened immune systems (Moller and Erritzoe, 2000) were preyed upon at higher rates than uncompromised birds. Murray et al. (1997) reported increased predation on snowshoe hares (*Lepus americanus*) with heavy burdens of the sublethal nematode *Obeliscoides cuniculi* during periods of limited food supplies.

It is logical to assume that predators' high success with diseased prey may be due to poorer body condition of the prey and consequently prey's slower avoidance behavior, decreased awareness, or re-

duced stamina. Studies have suggested that predators may also use visual pattern, scent, or behavioral cues to select compromised prey. Hudson et al. (1992) suggested that heavily parasitized female red grouse (*Lagopus lagopus scoticus*) emitted more scent, and were, as a result, more easily detected by mammalian predators. Larks (*Calandrella rufescens*) that were infected with poxvirus had shorter, lower-pitched distress calls than uninfected birds, indicating a behavioral change that could affect predation rates (Laiolo et al., 2007). Lafferty and Morris (1996) reported that parasitized killifish (*Fundulus parvipinnis*) exhibited more conspicuous behavior than uninfected killifish, and were also preyed upon more heavily by birds. Red-legged frog (*Rana aurora*) tadpoles also exhibited modified behavior when infected with yeast (*Candida humicola*), resulting in changes in thermoregulatory behavior, compromised predator avoidance behavior, and increases in being preyed upon (Lefcort and Blaustein, 1995). Examples of increased vulnerability to selective predation in large mammals are less numerous; however, diseased moose (*Alces alces*; Joly and Messier, 2004a) and bison (*Bison bison*; Joly and Messier, 2004b) appeared to be more susceptible to predation by wolves than apparently healthy animals. White-tailed deer (*Odocoileus virginianus*) killed by wolves may appear normal to human inspection, but subtle alterations may be present as demonstrated by the correlation of fawn and subadult survival to maternal and grand-maternal nutrition (Mech et al., 1991). Further, Krumm et al. (2009) recently reported that mountain lions (*Puma concolor*) prey selectively on prion-infected mule deer (*Odocoileus hemionus*) in Colorado, USA.

Wolves, selective predation, and prion disease dynamics

Chronic wasting disease (CWD; Williams and Young, 1980) is a contagious prion disease of at least four North American cervid species (Spraker et al., 1997; Baeten et al., 2007). The origins and evolutionary history of CWD are unclear, but uncontrolled epidemics have the potential to depress deer populations (Williams and Young, 1992; Miller et al., 2000, 2006; Gross and Miller, 2001; Williams et al., 2002) and to impact ecosystems dominated by these species (Hobbs, 1996). Epidemics of CWD are sustained naturally by horizontal transmission (Miller and Williams, 2003; Miller et al., 2006), with both infected animals and contaminated environments serving as sources of infection (Miller and Williams, 2003; Miller et al., 2004, 2006; Mathiason et al., 2006, 2009; Tamgüney et al., 2009). Under some conditions, the CWD agent persists in the environment for years in residues from excrement and infected carcasses (Miller et al., 2004). Mechanisms for both direct (animal-animal) and indirect (animal-environment-animal) prion transmission have been demonstrated empirically (Miller et al., 2004; Mathiason et al., 2006, 2009; Tamgüney et al., 2009), but models incorporating indirect transmission best represent epidemic dynamics in captive deer (Miller et al., 2006).

Effective measures for controlling CWD remain elusive. In the absence of vaccines or therapies, strategies undertaken to combat CWD have focused on depressing the abundance of host species either locally or regionally in an attempt to disrupt prion transmission (Williams et al., 2002; Grear et al., 2006; Conner et al., 2007). Thus far, control strategies relying on hunting or culling by humans to lower deer numbers and subsequently CWD prevalence have not yielded demonstrable effects (Conner et al., 2007). However, these results are not surprising given the limited duration of such management actions and because theory suggests that randomly removing individuals from an infected population should have less effect on epidemic dynamics than selectively removing infected individuals (Heesterbeek and Roberts, 1995; Gross and Miller,

2001). The protracted course of CWD in deer (Williams and Young, 1980, 1992; Fox et al., 2006) and occurrence of agent shedding well before the hallmark signs of emaciation and behavioral changes are discernable to human observers (Mathiason et al., 2009; Tamgüney et al., 2009) suggest that selectively removing only obviously ill deer from a population would not be an effective control strategy (Gross and Miller, 2001). If infected deer were detectable earlier in the disease course, however, selective removal might be more effective than random removal in controlling epidemics (Gross and Miller, 2001; Wolfe et al., 2004).

Increased vulnerability of CWD-infected mule deer to vehicle collisions (Krumm et al., 2005) suggests that lowered vigilance also might make them more vulnerable to large predators. It follows that if natural predators were able to develop a search image for subtle behavioral changes of CWD infection in deer, then fostering predation upon CWD-infected deer populations might offer a viable adjunct or alternative to other control measures. Although mountain lions do appear to preferentially prey on mule deer infected with CWD (Krumm et al., 2009), epidemics persist in mule deer herds in the presence of mountain lion predation (Miller et al., 2008; Krumm et al., 2009). Based on the subtlety of the behavioral changes early in the course of CWD infection, we would expect coursing predators like wolves to show even greater potential selective capability than ambush predators like mountain lions; however, wolves were extirpated and packs are presently absent from the areas in North America where CWD is endemic in deer, so field data are not available for comparison. Consequently, to assess this possibility we developed and explored the behavior of models representing the effects of selective predation by wolves and compared these with nonselective predation, such as through harvest or culling, on CWD dynamics in deer.

MATERIALS AND METHODS

Model structure

We explored the potential impacts of predation on dynamics of deer populations using a simple model of interactions among infected animals, susceptible animals, and infectious residue in the environment in a closed population. We derived the model used here (Appendix A) from the indirect transmission model of Miller et al. (2006), which was the best approximating model of two CWD epidemics in a captive population of mule deer. Because of the similarities in CWD epidemiology between mule deer and white-tailed deer (Miller and Wild, 2004), here we generalize inferences to "deer." We modified the best approximating model found by Miller et al. (2006) to portray disease dynamics in free-ranging populations as follows:

1) We assumed that transmission rates were approximately 25 times lower in natural populations than in captive ones. This assumption was based on the elevated densities of deer in captive populations (Miller et al., 2006). Adjusting transmission rates for differences in density was plausible; however, the magnitude of the adjustment for transmission was uncertain. Therefore we targeted this adjustment as one of the variables to be explored in simulation studies through the use of a scaling coefficient.
2) Per-capita birth rates were assumed to decline linearly with increasing population density.
3) We added a term representing predation. This term could be adjusted to reflect selective predation, where predators favored infected animals over susceptible ones, or nonselective predation, as would occur with hunting or culling, where removals were assumed to be random. In the case of selective predation on diseased animals, we also included a term to represent the extent to which predation mortality was compensatory with CWD mortality.

We sought to use the simplest model possible to achieve the greatest generality of results (Levins, 1966) and to reduce the number of parameters that had to be estimated. We avoided the use of an age-structured model, which would have required estimating unknown transmission rates for several age classes. Dynamics of the prey population was not coupled to the dynamics of predators and predation intensity did not change with prey abundance. In the interest of parsimony, we

used a constant relative rate for predation. Preliminary modeling included a type II functional response and did not yield results that were qualitatively different than those presented here. More importantly, by holding predation constant, we could be sure that observed dynamics resulted from the interplay between CWD and deer, rather than between deer and wolves (analogous to choosing to hold one factor constant in a designed experiment). Although our model is simple, we believe it represents the essential interactions in the deer-CWD system. As knowledge of parameters improves, more detailed models will be justified.

Model experiments

We exercised the model to examine how selective and nonselective predation may influence CWD prevalence. We made three model runs using our most plausible estimates of model parameters to examine differences among trajectories of diseased populations in the presence and absence of predation. We first conducted a reference simulation introducing a single infected animal into a population of 1,000 deer at time=0 and allowed the model to equilibrate over 100 yr. In two experimental simulations, we introduced predation in year 51. In one of these simulations, predation was assumed to occur randomly; in the other, predators were assumed to favor infected individuals. In the case of selective predation, the modeled 15% predation rate was equivalent to about seven wolves removing 16 deer/wolf/yr (Mech and Peterson, 2003).

Although most parameters in the model were derived from Miller et al. (2006) or from reasonable assumptions on deer biology (See Table 1 in Appendix A for all parameter values), there was substantial uncertainty in our best guesses of the value of several parameters controlling the effects of the disease and of predation. Notable among these were the extent of predator selectivity for CWD-infected animals, the extent of compensation between CWD and predator mortality, and the adjustment for the rate of transmission in free-ranging populations. We explored consequences of these uncertainties by conducting model experiments varying these parameters singly and in pairs to examine the sensitivity of model predictions to uncertainty in their estimates.

RESULTS

In the absence of CWD and predation, the modeled deer population stabilized at an ecologic carrying capacity of about 1,000 animals. Adding a single infected deer in year 1 produced oscillatory dynamics typical of epidemics. With disease and no predation, the equilibrium density was 736 deer and disease prevalence was 29%. Thus, the disease reduced animal abundance in our model by almost a third (Fig. 1A, B). Our model resembles classic susceptible-infected (SI) models with an additional mortality source from predation and an environmental reservoir of infection. Models of this general type are known to have conditions that allow steady states (Miller et al., 2006), and the model used here shows that equilibrium.

Simulated selective and nonselective predation affected epidemic dynamics to different degrees. Imposing nonselective mortality representing a 15% annual harvest or cull in year 51 lowered both deer population size and steady state CWD prevalence; however, under the assumptions of this simulation, the disease was able to persist in the population (Fig. 1C, D). Selective (4×) mortality at the same 15% predation rate beginning in year 51 caused a more modest reduction in deer population size accompanied by a relatively rapid decline in CWD prevalence and elimination of the disease from this closed population (Fig. 1E, F). The impacts of selective predation on epidemic dynamics were sensitive to assumptions on vulnerability of infected animals and compensation between predation and mortality due to CWD, as well as overall predation and CWD transmission rates (Fig. 2). Doubling the vulnerability of infected animals to selective predation accelerated the rate of decline in prevalence (Fig. 2A). Increasing the proportion of compensatory deaths among infected deer dampened the predicted decline in prevalence (Fig. 2B); when compensation exceeded ca. 60%, selective predation had less of a predicted effect on epidemic dynamics than nonselective predation. The overall predation rate also affected the rate and magnitude of decline in steady state prevalence (Fig. 2C). Epidemic dynamics also were sensitive to assumptions on values for the scaling of transmission rate (Fig. 2D), with asymptotic prevalence varying by a
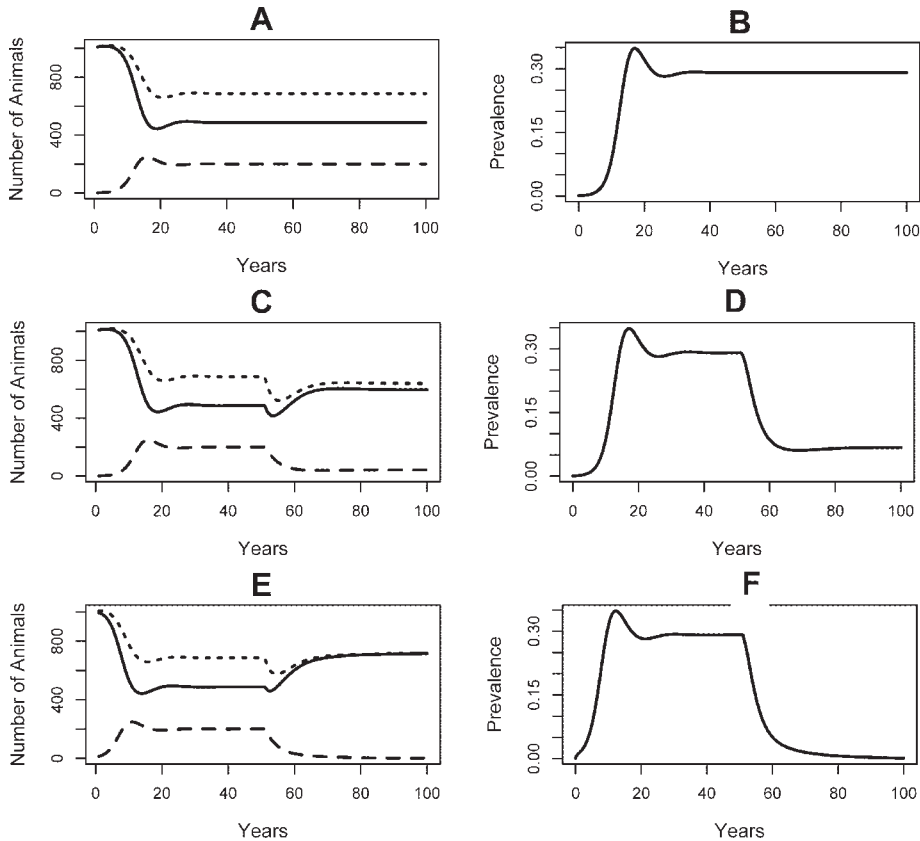
FIGURE 1. Simulations of deer abundance and disease prevalence in populations infected with CWD assuming no predation (A, B), nonselective predation (C, D), and selective predation (E, F). Lines in population-number graphs are number of susceptible deer (solid), number of infected deer (dashed), and total population (dotted). In the absence of CWD and predation, the population would reach equilibrium at 1,000 animals. We assumed that predators consumed four times more infected animals than would be expected by random selection among susceptible and infected deer and that compensation of predation for disease is 0.3. The predation rate was set at 0.15 beginning in year 51 and the scaling factor for transmission rate was 25 in all simulations.

factor of more than 10 when changing the scaling coefficient from 20 to 40.

Our models predicted that interactions between the relative selectivity of predation and the degree to which mortality in infected deer is compensatory also will influence epidemic dynamics in emergent CWD foci (Fig. 3). Predicted CWD prevalence 20 yr after introducing a single infected deer into simulated populations subjected to 15% annual predation under different combinations of selectivity and compensation varied from ~0 to 8%. In general, simulations suggested that even modest levels of selectivity might be

expected to greatly diminish the persistence of CWD in a susceptible deer population provided that such pressure was largely additive; however, models predicted that sufficiently strong selection could still dampen the dynamics of emergent CWD epidemics even in cases where mortality among infected deer was largely compensatory.

DISCUSSION

Results from these simulations suggest that predation could markedly decrease prevalence of CWD under certain condi-
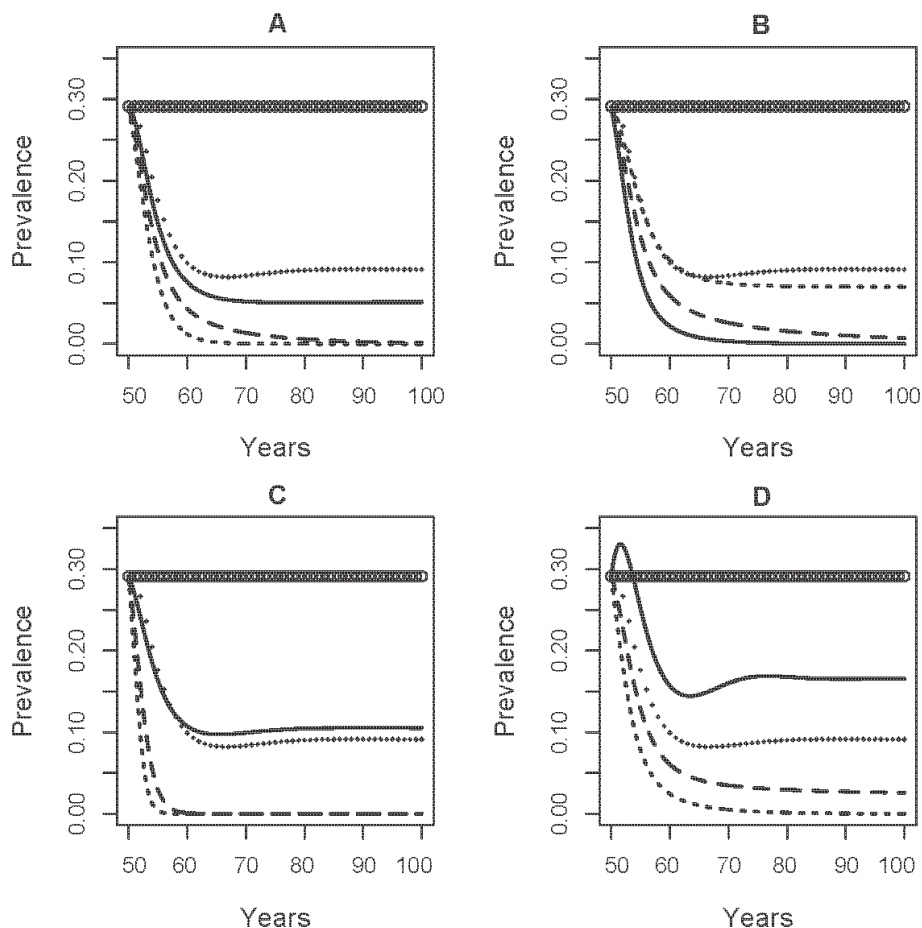
FIGURE 2.   Results of model experiments to examine sensitivity of variation in uncertain model parameters. Open circles show results from simulations with no predation, diamonds show nonselective predation at a rate of 0.15. A. Effect of variation in prey vulnerability to selective predation ($v=2$, solid line; 4, dashed line; 8, dotted line). Increasing values of v indicate greater selection for infected over susceptible animals. In all cases, compensation was held constant at 0.3 and predation rate at 0.15. B. Effect of variation in the level of compensation between predation and CWD mortality ($c=0.1$, solid line; 0.3, dashed line; 0.6, dotted line). Increasing values of c indicate greater compensation between predation and CWD. In all cases, selectivity was held constant at four and the predation rate at 0.15. C. Effect of variation in predation rate (δ; solid line, 0.10; dashed line, 0.30; dotted line, 0.50). In all cases, vulnerability to selective predation was held constant at 4 and compensation at 0.3. D. Effect of variation in the scaling coefficient for the transmission rate (solid line, 20; dashed line, 30; dotted line, 40). The scaling coefficient reduces the transmission rate to account for differences between captive and free-ranging deer. A scaling coefficient of 20 indicates that transmission is 20 time more rapid in captivity than in the wild. For other parameter values, see Table 1 in Appendix A.

tions. Nonselective predation, as might occur with hunting or culling by humans, may decrease disease prevalence over time but the disease was not eliminated under modeled conditions (Fig. 1C, D). Alternatively, selective predation by wolves at the same rate would result in a more precipitous drop in CWD prevalence that would culminate in disease elimination in a closed system (Fig. 1E, F). Selective predation does not allow a larger population of susceptible animals to persist relative to the nonselective case because wolves are assumed to consume
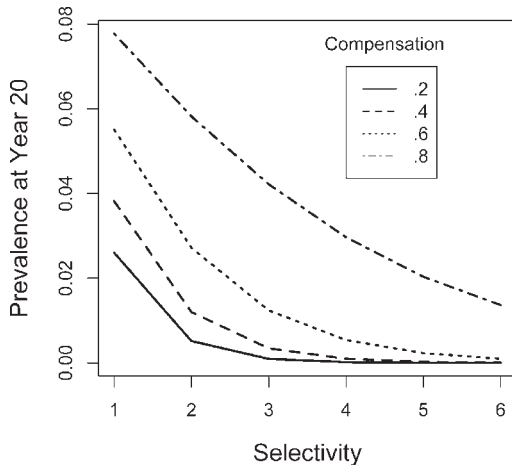
FIGURE 3. Predicted CWD prevalence 20 yr after introducing a single infected deer into simulated populations subjected to 15% annual predation. Results of this model experiment revealed interactions between selectivity and compensation: for example, low compensation and high selective predation result in inability of disease to emerge. The benefits of selectivity for reducing prevalence are opposed by increasing compensation.

more susceptible animals as infected ones become rare. Although the time required to achieve results depends in a fundamental way on assumptions about prey vulnerability to selective predation and the nature of compensation among different sources of mortality, as well as parameters regulating disease transmission, it appears that prevalence could be halved within a decade and eliminated within the century through sustained predation by a pack of wolves that removed 15% of deer per year in a closed population.

Although uncertainty in parameter estimates limits our confidence in predicting the precise timeframe required for control or elimination of disease, these time estimates provide a basis for comparison of approaches. What is most clear is a consistent and robust trend toward decreasing CWD prevalence in populations subject to predation, particularly selective predation, over a range of parameter estimates (Fig. 2). A similar decreasing trend would be predicted in a population subject to predation where CWD was

repeatedly introduced at low levels (i.e., an open population); however, the slope of decline would be variable and elimination might never be achieved because high rates of disease reintroduction may offset selective predation of CWD-positive individuals. Although they are not the most likely scenarios, other combinations of parameters, in particular high excretion rates leading to increased levels of transmission, also may result in an inability to eliminate the disease within a reasonable period of time.

Simulation results suggested that selective predation could also dampen or eliminate the emergence of CWD in new locations (Fig. 3), adding support to speculation that the absence of large predators presents an amplification risk factor for establishment of CWD (Samuel et al., 2003). Our prediction may prove testable in the future as geographic distribution of CWD expands to areas such as the Greater Yellowstone Ecosystem and northern Wisconsin, USA, and Prince Albert National Park, Canada, where wolves are present but adjacent areas lack wolves. The simulated influences of large predators on the outcomes of CWD epizootics also may lend insight into circumstances surrounding the original emergence of CWD in Colorado, where wolves have been absent since 1943 and where mountain lion populations were suppressed by bounty hunting at the time of likely CWD emergence in the mid-1900s (Barrows and Holmes, 1990; Miller et al., 2000). The origins of CWD are unknown but may have been a result of spillover of scrapie from domestic sheep or may represent a spontaneous, naturally occurring spongiform encephalopathy of cervids (Williams and Young, 1992; Spraker et al., 1997). Regardless, our simulations suggest that had selective predation by wolves been present during that period, CWD may never have been established or detected. In combination with influences of human-assisted movement of infected cervids (Williams et al., 2002) and land use

alterations (Farnsworth et al., 2005), the absence of large predators, particularly wolves, over much of their native range in the United States (Laliberte and Ripple, 2004) has likely played a significant role in the current unnatural distribution and prevalence of this disease.

The decrease in CWD prevalence observed in simulations with selective predation is most likely a result of removing infectious individuals earlier in the disease course. Chronic wasting disease exhibits a prolonged disease course of about 18–36 mo (Williams and Miller, 2002). Transmission models (Miller et al., 2006) reveal little support for a disease latency period and instead support early onset of prion shedding, potentially from peripheral lymphoid tissue. Accumulation of abnormal prion protein (PrP^{cwd}) in deer has been observed in alimentary tract–associated lymphoid tissues as early as 42 days following experimental oral inoculation (Sigurdson et al., 1999) and in tonsils as much as 20 mo prior to death from naturally occurring CWD (Wild et al., 2002). Moreover, orally inoculated deer shed infectious prions in saliva and feces 6–11 mo or more before the onset of clinical signs (Mathiason et al., 2009; Tamgüney et al., 2009). Therefore, early removal of infected individuals should markedly truncate CWD shedding and resultant opportunities for disease transmission.

The prolonged clinical course and type of clinical abnormalities associated with CWD make it the prototypic disease for selection by predators. Chronic wasting disease produces subtle changes in behavior and body condition that progress over weeks or months to overt signs of end-stage disease typified by loss of attentiveness or response to external stimuli, emaciation, and weakness (Williams and Young, 1980, 1992; Wild et al., 2002). Loss of attentiveness and cognitive function due to the neurodegenerative process likely account for the marked increase in risk for vehicle collision of CWD infected

mule deer compared to hunter-harvested deer (Krumm et al., 2005). It follows that infected deer also would be less attentive to predators, and in later stages, that emaciation and weakness would decrease both their fight and flight response capabilities (Krumm et al., 2005, 2009; Miller et al., 2008); a nearly fourfold greater relative risk of infected mule deer succumbing to mountain lion predation (Miller et al., 2008) supports this notion. Furthermore, predators—particularly coursing predators such as wolves—focus on animals vulnerable due to odd behavior or compromised body condition (Temple, 1987; Mech et al., 1991). Field observations also suggest that predators can select CWD-infected deer: mule deer killed by mountain lions were much more likely (odds ratios ≥3.2) to be infected with CWD than same-sex deer killed in the vicinity by hunters (Krumm et al., 2009). Based on the prolonged course of CWD, the ability of wolves to detect vulnerable prey, and field observations of mountain lion predation patterns in a system where CWD occurs naturally, we believe that selective predation modeled at a rate four times higher than that of healthy deer is a reasonable, if not conservative, estimate.

Overall, our modeling results also are likely a conservative portrayal of the beneficial impacts that selective predation could have on damping prion epidemic dynamics in deer. The model we developed did not include carcasses of infected deer as a source of infectivity because necessary parameter estimates were not available (Miller et al., 2006). However, carcasses of CWD-infected deer would be an added source of environmental infectivity in natural systems (Miller et al., 2004), and thus their consumption by wolves or other carnivores either via selective predation or scavenging would be expected to reduce the contribution of carcass material to the overall pool of environmental infectivity through local dispersal and dilution (Krumm et al., 2009). Passage through the alimentary

tract of wolves likely markedly degrades infectivity of tissues. In sheep, in vitro incubation of a dilute scrapie brain inoculum with alimentary tract fluids resulted in almost complete degradation of PrP (Jeffrey et al., 2006). Moreover, changes in deer behavior due to the presence of predators, i.e., predation risk effects or what has been termed the ecology of fear (Brown et al., 1999; Ripple and Beschta, 2004), include changes in use of space through habitat preferences or foraging patterns within a given habitat, or both (Lima and Dill, 1990). If deer move more within established home ranges due to fear of predation, then contact rates with environmental deposits of infectivity also might diminish. Given the sensitivity of epidemic dynamics to such contact rates, even relatively small reductions would further dampen epidemic dynamics beyond effects arising from selective predation on infected deer alone.

Although here we modeled wolf predation on deer, similar outcomes would be expected for wolf predation on other species susceptible to CWD. Hobbs (2006) used CWD and elk (*Cervus elaphus nelsoni*) population data from Rocky Mountain National Park (Colorado, USA) to model the impact on CWD that may be achieved through maintaining a pack of wolves in the park. Results from these simulations supported the idea that predation could drive decreases in CWD prevalence over a range of parameter estimates. Impacts by predators other than wolves may also reduce CWD prevalence to varying degrees, as seen in our results from nonselective removal by humans. We consider the wolf, a large coursing predator, to be most effective in selective removal of deer vulnerable from CWD infection; however, opportunistic mountain lions (Krumm et al., 2009), and potentially coyote (*Canis latrans*) packs, would likely benefit from lack of vigilance by CWD-affected deer as well.

The potential impact on wolves and other native North American predators

from consumption of CWD-positive ruminants is unknown; however, no evidence of naturally occurring CWD has been reported outside four species in the family Cervidae. Limited surveillance of predators and scavengers in CWD-affected areas (Jennelle et al., 2009; Miller and Wild, unpubl. data) has not revealed evidence of abnormal prion accumulation. Naturally occurring transmissible spongiform encephalopathies (TSE) other than CWD have been documented in domestic mink (transmissible mink encephalopathy), domestic sheep and goats (scrapie), and domestic cattle (bovine spongiform encephalopathy [BSE]), as well as in humans (variant Creutzfeldt-Jacob disease) and domestic and captive wild felids (feline spongiform encephalopathy) that consumed BSE-contaminated feed (Hörnlimann et al., 2007). Interestingly however, no TSE has been observed in a canid despite dietary challenge of BSE to dogs (Kirkwood and Cunningham, 1994). A species barrier is generally believed to be responsible for the specificity of prion diseases to their respective hosts, although some spillover, as with BSE, has been documented for at least one prion strain. Raymond et al. (2000) demonstrated a barrier at the molecular level that they suggest limits the susceptibility of noncervid species to CWD. The dog and wolf are very similar in PrP sequence and quite different from cattle, domestic cats, and elk (Schätzl, 2007).

We suggest that predation, particularly wolf predation, may be a useful tool for management of CWD. Currently, the range of wolves (Boitani, 2003) does not overlap with the distribution of CWD (Chronic Wasting Disease Alliance, 2009) so our predictions on the effects of wolves on CWD prevalence remain untested. However, as wolf range expands through Wyoming and Wisconsin, USA, and Alberta and Saskatchewan, Canada, and into Colorado and Utah, USA, the possibility for such evaluation may occur. Alternatively, CWD may be detected in a new

geographic location where wolves are present. Based on our simulations, disease may be difficult to detect in these areas unless unique methods of surveillance, such as monitoring of wolf-killed cervids for presence of PrP^{res}, are implemented. Beschta and Ripple (2009) suggest that restoration of large predators, such as wolves, provides a recovery strategy for native flora, functional predator-prey-scavenger food webs, and ecosystems degraded by overabundant wild ungulates. Wolf restoration also provides an opportunity to observe and evaluate the effects that selective predation may have on prevalence of an invariably fatal chronic disease in deer and elk. In areas where predator restoration is not possible, deployment of wolves as stewardship tools for the primary purpose of disease control could provide a novel approach to management.

Although somewhat novel, the concept of using wildlife species as stewardship tools to provide ecosystem services is not new. Restoration of bison to reestablish healthy landscapes of prairie vegetation in the United States (United States Department of the Interior, 2008) and large carnivore, (e.g., lion [*Panthera leo*]), translocations to restore ecologic integrity in fenced parks in Africa (Hayward et al., 2007) are occurring. Licht et al. (2010) propose use of small populations of wolves for ecosystem restoration in North America. Public tolerance of wildlife, particularly predators, may dictate intensive management in species used in such restoration efforts. Regardless of whether wolves are managed under natural regulation or primarily for fulfilling their ecologic role, they provide a promising approach for control of CWD that warrants further evaluation.

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APPENDIX A—MODEL STRUCTURE

Using data from two epidemics of chronic wasting disease (CWD) in a captive population of mule deer (*Odocoileus hemionus*), Miller et al. (2006) found that models of indirect transmission of CWD from excreta had almost seven times more support in data than more traditional models of direct, animal-to-animal transmission. The best approximating model in their studies used three linked differential equations representing the number of infected and susceptible animals and the mass of infectious material in the environment:

$$\frac{dS}{dt} = a(I+S) - S(\gamma E + m),$$

$$\frac{dI}{dt} = \gamma SE - I(m + \mu), \qquad (1)$$

$$\frac{dE}{dt} = \varepsilon I - \tau E,$$

where

S=number of susceptible (uninfected) animals, I=number of infected animals, E=the mass of infectious material in the environment, α=the per capita birth rate, m=the per

capita death rate from causes other than CWD, γ=the indirect transmission coefficient, μ=the additive, per capita death rate from CWD, ε=the per capita rate of excretion of infectious material by infected animals, and τ=the mass specific rate of loss of infectious material from the environment.

This model is based on two assumptions, that the instantaneous per capita rate of infection was directly proportionate to the mass of infectious material in the environment (i.e., $dI/dtS = \gamma E$) and that the rate of uptake of infectious material by deer has negligible effects on the pool size.

We modified this model to include density-dependent effects on recruitment into the population and to include selective and nonselective predation:

$$
\begin{aligned}
\frac{dS}{dt} &= a(S+I)\left(1 - \frac{S+I}{K_a}\right) - S(\gamma E + m) \\
&\quad - (1-p)\delta(S+I), \\
\frac{dI}{dt} &= \gamma SE - I(m+\mu) - p(1-c)\delta(S+I), \\
\frac{dE}{dt} &= \varepsilon I - \tau E,
\end{aligned}
\tag{2}
$$

where K_a is the population level where birth rate=0 and δ is the additive, instantaneous per capita rate of predation when predators select prey randomly. Predation rates were adjusted to account for selectivity by the term p, which represents the proportion of the total kill that was infected. We calculated p as

$$
p = \frac{vI}{vI+S}
\tag{3}
$$

where v is the vulnerability of infected animals relative to susceptible ones. Relative vulnerability is a multiplier giving the number of infected animals in the total kill per suscepti-ble animal, assuming equal abundance of infected and susceptible. Thus, a value of $v=2$ means that if susceptible and infected animals were equally abundant, wolves would

selectively kill twice as many infected animals as susceptible ones. A value of $v=1$ indicates no vulnerability of infected animals and increasing values of v above 1 indicate increasing vulnerability to selective predation.

If predators select prey totally at random, then the probability of dying from CWD is independent of the probability of dying from predation, as δ is defined. In this case the probability that an infected animal will survive, φ, over an interval of time=Δt is

$$
\phi = e^{-(m+\mu+\delta)\Delta t}.
\tag{4}
$$

However, when predators are selective, then it follows by definition that the probability of dying from predation is not independent of the probability of dying from the disease:

$$
\phi = e^{-[m+\mu+\delta(1-c)]\Delta t}
\tag{5}
$$

The term c allows us to represent the extent to which predation mortality compensates for CWD mortality. Because $1/m+\mu+\delta$ is the average lifetime of an infected animal assum-ing that disease mortality and predation mortality are completely additive, it follows that $1/[m+\mu+\delta(1-c)] - 1/(m+\mu+\delta)$ is the in-crease in the average lifetime of an infected animal that results because predation mortality may not fully add to disease mortality. The value of c ranges from 0 to 1. When $c=0$, then predation mortality is completely additive with CWD mortality, as in equation (4). When $c=1$, predation mortality is completely com-pensatory and does not add to deaths from disease (i.e., deer would have died from CWD within the year had they not been preyed upon).

To solve the system of equations in (2), we used numeric integration implemented in the lsoda package of the R computing environ-ment (R Development Core Team, 2008). Values for parameters used in simulations are derived from Miller et al. (2006) and plausible assumptions about deer population dynamics in the absence of CWD (Table 1).

TABLE 1.   Values for model parameters used in example simulations.

Parameter	Definition	Value[a]	Reference or source
a	Birth rate[b] at population=0	0.6	Medin and Anderson, 1979
m	Non-CWD[c] death rate[d]	0.1	White and Bartmann, 1998
K_a	Population at which birth rate=0	1,230	Assigned
γ	Transmission rate[e]	0.787	Miller et al., 2006
μ	CWD death rate	0.567	Miller et al., 2006
ε	Rate of excretion of infectious material	0.111	Miller et al., 2006
τ	Rate of loss of infectious material from the environment	2.55	Miller et al., 2006

[a] Units for all rates are per year.

[b] The birth rate in continuous time, which corresponds to a discrete time birth rate of 1.8 fawns per female.

[c] CWD=chronic wasting disease.

[d] The continuous-time death rate corresponds to an annual adult survival probability of 0.90.

[e] The transmission rate was scaled to account for differences in density between the wild and the captive setting where it was measured by Miller et al. (2006). The default scaling factor was allowed for densities in paddocks that were 25 times higher than in the wild, thus 0.787/25.

Gray Wolves as Climate Change Buffers in Yellowstone

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Understanding the mechanisms by which climate and predation patterns by top predators co-vary to affect community structure accrues added importance as humans exert growing influence over both climate and regional predator assemblages. In Yellowstone National Park, winter conditions and reintroduced gray wolves (Canis lupus) together determine the availability of winter carrion on which numerous scavenger species depend for survival and reproduction. As climate changes in Yellowstone, therefore, scavenger species may experience a dramatic reshuffling of food resources. As such, we analyzed 55 y of weather data from Yellowstone in order to determine trends in winter conditions. We found that winters are getting shorter, as measured by the number of days with snow on the ground, due to decreased snowfall and increased number of days with temperatures above freezing. To investigate synergistic effects of human and climatic alterations of species interactions, we used an empirically derived model to show that in the absence of wolves, early snow thaw leads to a substantial reduction in late-winter carrion, causing potential food bottlenecks for scavengers. In addition, by narrowing the window of time over which carrion is available and thereby creating a resource pulse, climate change likely favors scavengers that can quickly track food sources over great distances. Wolves, however, largely mitigate late-winter reduction in carrion due to earlier snow thaws. By buffering the effects of climate change on carrion availability, wolves allow scavengers to adapt to a changing environment over a longer time scale more commensurate with natural processes. This study illustrates the importance of restoring and maintaining intact food chains in the face of large-scale environmental perturbations such as climate change.

Introduction

Average earth temperatures have increased by 0.6 °C over the last 100 years [1] and are predicted to increase by 1.4–5.8 °C over the next century [2]. Commensurate with rising global temperatures are regional changes in weather patterns affecting the quantity and timing of precipitation and moisture levels. A challenge facing ecologists is to understand how these changes in the abiotic environment will impact populations and communities of organisms. Already, studies have documented the effect of a changing climate on the phenology, range, reproductive success, and synchrony of certain plants and animals (see [1] for a comprehensive review). In addition, climate-caused community-level changes have been documented when range shifts lead to the transfer of an entire assemblage of species [3].

Given such responses by individual species, we can expect consequent shifts in trophic structure and competitive hierarchies at the community scale [4]. Studies addressing this problem have focused primarily on how species-specific responses in phenology and geographic range alter competitive balances and the timing of food availability for neonates [5,6,7,8]. In Britain, for instance, winter warming has precipitated disparate responses in the breeding phenology of different amphibian species, exposing frog larvae (*Rana temporaria*), which have shown no phenological response, to higher levels of predation from newts (*Triturus* spp.) that are entering ponds earlier than before [5].

As predicted by community stability theory, the impact of climate change on communities may vary in relation to levels of species diversity [9,10,11,12]. Depauperate communities or those lacking keystone species [13,14] may be more vulnerable

to the perturbing effects of climate change than more speciose communities. As such, understanding the mechanisms or pathways that confer community resistance to climate change will be important to conservationists and managers in mitigating the effects of a changing climate on shifting community patterns and local extinctions.

The reintroduction of gray wolves (*Canis lupus*) to Yellowstone National Park (NP) in 1995 [15] provides a research opportunity for comparing the response of an ecosystem to climate change in scenarios with and without direct human alteration of species composition. Wolf restoration is already realizing a change on the Yellowstone ecosystem by altering the quantity and timing of carrion availability to scavengers [16]. Ravens (*Corvus corax*), bald eagles (*Haliaeetus leucocephalus*), golden eagles (*Aquila chrysaetos*), magpies (*Pica pica*), coyotes (*Canis latrans*), grizzly bears (*Ursus arctos*), and black bears (*Ursus americanus*) are each frequent visitors at wolf kills [17] and are highly reliant on winter carrion for survival and reproductive success [16,18,19,20,21,22].

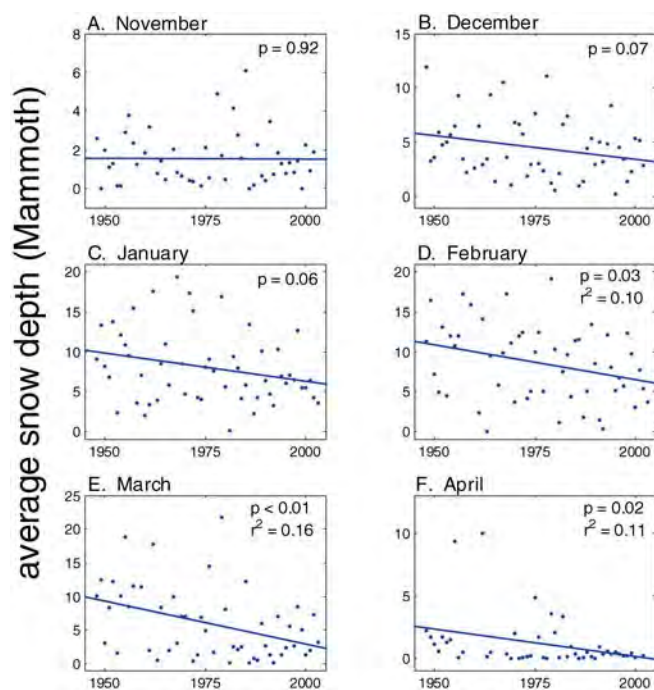Prior to wolf reintroduction, winter mortality of elk (*Cervus*

Abbreviations: NP, National Park; SDTH, snow depth; SNFL, snowfall; TMAX, maximum temperature; TMIN, minimum temperature

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Figure 1. Winter Snow Depths 1948–2003 at Mammoth Hot Springs

Average monthly SDTH for November (A), December (B), January (C), February (D), March (E), and April (F) 1948–2003 at the Mammoth Hot Springs weather site.

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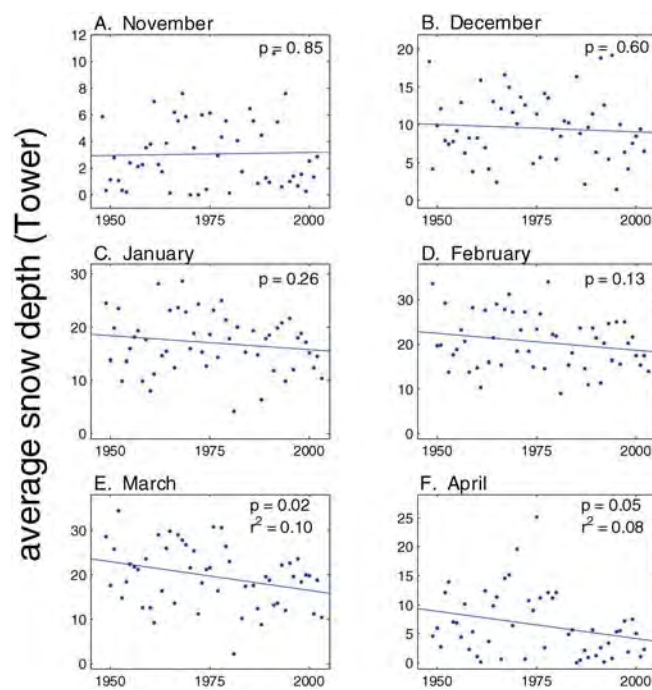
Figure 2. Winter Snow Depths 1948–2003 at Tower Falls

Average monthly SDTH for November (A), December (B), January (C), February (D), March (E), and April (F) 1948–2003 at the Tower Falls weather site.

DOI: 10.1371/journal.pbio.0030092.g002

elaphus), the most abundant ungulate in Yellowstone, was largely dependent on snow depth (SDTH) [23]. Deep snows lead to increased metabolic activity [24] and decreased access to food resources, thereby causing elk to weaken and die [25]. In the absence of wolves, carrion was plentiful both during severe winters and at the end of moderate winters, but more scarce in early winter or during mild winters [23]. Reintroduced wolves are now the primary cause of elk mortality throughout the year [26]. Scavengers that once relied on winter-killed elk for food now depend on kleptoparasitizing wolf-killed elk [16]. Hence carrion availability has become primarily a function of wolf pack size, with SDTH an important but secondary factor.

As global temperatures rise, evidence suggests that northern latitude and high elevation areas will experience shorter winters and earlier snow melts [27]. Given the overwhelming influence of gray wolves on scavenger food webs, community-level responses to climatic changes in the absence of wolves may differ substantially from those in the presence of Yellowstone's newly restored top carnivore. As such, we analyzed over 50 y of weather data from Yellowstone's northern range for trends in winter conditions, and constructed empirically and dynamically grounded scenarios to investigate how changes in SDTH and seasonality differentially affect scavengers in the presence and absence of wolves.

Results

Weather Data Analysis

Over the past 55 y, average monthly SDTH at the Mammoth Hot Springs weather site show a steady decline

in all winter months except November [the effect is significant at $p \leq 0.05$ for February through April and nearly significant for December and January (Figure 1)]. Furthermore, the slope of the line relating SDTH to year becomes more negative with each month, indicating a more pronounced effect of climate change in late winter. The result for April, however, is confounded by a number of zeros, which created a violation of the normality assumption for the linear regression. Average monthly SDTH at the Tower Falls weather site (Figure 2) did not indicate a strong pattern in the early winter, but showed a significant decline in the late-winter months of March and April (Figure 2E and 2F).

Winters in Yellowstone are getting shorter. While we did not detect a difference in the date of the arrival of the first snow, we did detect a declining trend in the date of last snow on the ground (Figure 3A and 3B).

At both the Tower and Mammoth weather sites, the number of days that maximum temperature (TMAX) exceeded freezing for the period of January through March increased significantly (Figure 3C and 3D). Furthermore, midwinter snowfall is decreasing, and late-winter minimum temperature (TMIN) and TMAX show signs of increasing in certain months (Table 1).

Wolf Effects

Statistical model. The presence of wolves in Yellowstone significantly mitigates the reduction in late-winter carrion expected under climate change (Figure 4). In the scenario without wolves, late-winter carrion availability is reduced by 27% in March and by 66% in April. In contrast, the scenario with wolves reveals a reduction in carrion availability of only 4% in March and 11% in April. There was not a significant
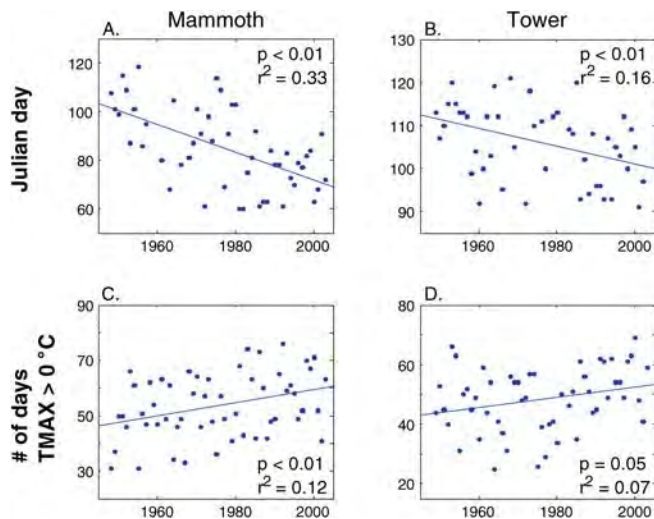
Figure 3. Changes in the Last Day of Snow Cover over the Last 55 Years at Mammoth Hot Springs and Tower Falls

Last day of snow cover is reported as the number of days from January 1 of that year until the first day of bare ground. Changes in last day of snow cover over the last 55 y are shown for Mammoth Hot Springs (A) and Tower falls (B). The number of days from January through March that temperatures exceeded freezing at Mammoth (C) and Tower (D) are increasing with time.
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difference in the reduction of early- to midwinter carrion (December through February) between the two scenarios.

Dynamic model. Percent change, z, in late-winter carrion from 1950 to 2000 was not sensitive to changes in any of the parameters in either scenario with or without wolves. Specifically, r^2 values did not exceed 0.02 for any of the parameters regressed upon z. Mean monthly percent change in carrion availability from 1950 to 2000 under scenarios with and without wolves reveals a relative reduction in late-winter carrion from 1950 to 2000 and an increase in early-winter carrion (Figure 5). Note that this change in carrion availability is much less pronounced in the presence than in the absence of wolves.

Table 1. Regression Analyses Predicting Mean Monthly SNFL, and Average Late-Winter TMIN and TMAX

Site	Dependent Variable	Month	Intercept	Slope	r^2	p-value
Tower Falls	SNFL	February	84	−0.04	0.08	0.055
	TMIN	March	−148	0.08	0.08	0.04
	TMAX	March	−77	0.06	0.07	0.06
Mammoth Hot Springs	SNFL	December	106	−0.05	0.13	<0.01
		January	121	−0.06	0.11	0.02
		February	71	−0.03	0.07	0.056
	TMIN	March	−237	0.13	0.18	<0.01
	TMAX	March	−118	0.08	0.11	0.02

Included are results from regression analyses using year as the independent variable to predict dependent variables SNFL, TMIN, and TMAX for given winter months. We present results for $p < 0.10$.
DOI: 10.1371/journal.pbio.0030092.t001
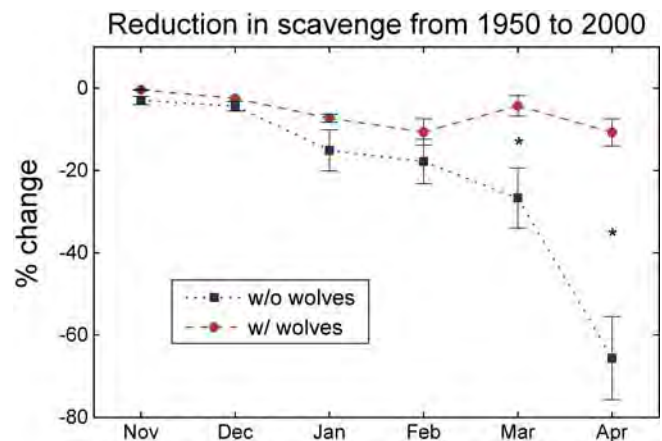
Figure 4. Reduction in Winter Carrion Available to Scavengers due to Climate Change 1950–2000: Statistical Model

Shown are percent reductions (± standard error) in winter carrion available to scavengers due to climate change from 1950 to 2000 with and without wolves in our statistical model. * Significant difference between the two scenarios.
DOI: 10.1371/journal.pbio.0030092.g004

Discussion

The winter period on the northern range of Yellowstone NP is shortening. Both late-winter SDTHs and the overall duration of snow cover have decreased significantly since 1948 (see Figures 1–3). There are several potential causes of reduced snow pack. Average TMIN and TMAX values are increasing in late winter, while midwinter snowfall appears to be declining (Table 1). Compounding the effects of declining snowfalls on SDTH is an increase in the number of winter days with temperatures above freezing (see Figure 3C and 3D).

Decreases in late-winter snow pack and in the date of last snow cover imply that elk will recover sooner from the detrimental stresses of winter: Smaller snow packs allow elk easier access to food and decrease energy expenditures required for movement. In addition, herbaceous plant growth usually begins within a few days to weeks of last snow cover [28], so elk may increase the quality and quantity of food intake earlier in the year, thus shortening the physiologically stressful winter period. These factors are likely to influence the timing and abundance of carrion as late-winter elk mortality declines. As we demonstrate here, climate change serves to sharply reduce the amount of late-winter carrion available to Yellowstone's scavengers (see Figure 4). According to our statistical and dynamic models, however, this reduction is much less pronounced in the presence of wolves. In our statistical model, for instance, we found an 11% reduction with wolves versus a 66% reduction without wolves in April (see Figure 4). Our dynamic model, which incorporates wolf and elk population growth, also reveals a decline in late-winter carrion, especially in the absence of wolves (Figure 5). In contrast to the statistical model, our dynamic model predicts an increase in early winter carrion, but less so with wolves. As the winter period shortens, elk that normally would die in March and April will increasingly die in the early winter months, November through February. This will lead to an increasingly pulsed or seasonal carrion resource. It is important to note that our model has more detailed elk than

Change in scavenge from 1950 to 2000

Figure 5. Change in Carrion Available to Scavengers due to Climate Change 1950–2000: Dynamic Model

Shown is the mean monthly change (± standard error) in carrion available to scavengers due to climate change from 1950 to 2000 with and without wolves in our dynamic model.

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wolf dynamics. As suitable data become available, future work can attempt to tease out such factors as the effects of SDTH and territoriality on wolf kill-rate. In both our dynamic and statistical models we find that wolves buffer the effects of climate change on carrion abundance and timing.

This effect will be crucial to scavenger species in the Yellowstone area that are highly dependent on winter and spring carrion for overwinter survival and reproduction. Under scenarios without wolves, these species could face food bottlenecks in the absence of late-winter carrion. The magnitude of this effect will depend on how quickly these species adapt to a changing environment and how their other food resources respond to a shortening of the winter period.

Asynchrony of organismal responses to climate change has been prevalent in other areas, leading to changes in the competitive balance between species and to food shortages at important times of year [1]. Yellowstone should prove no exception. Species that respond to weather cues, such as many herbaceous plants, will simply start growing earlier in the year in response to earlier snow melt. Species that respond primarily to day length cues, such as some hibernating species, may change less. Coyotes, for instance, are highly dependent on late-winter and early-spring carrion to carry them over until late spring, when elk calves and ground squirrels become abundant. If late-winter carrion were to disappear without a corresponding change in the timing of elk calving or ground squirrel emergence, a serious food bottleneck could develop.

As carrion becomes more concentrated over a shorter window of the year, the relative access to carrion among different scavenger species may change. Highly aggregated or pulsed resources saturate local communities of scavengers, allowing species with better recruitment abilities (animals capable of covering large distances and communicating about the location of resources such as ravens and bald eagles) to dominate consumption at carcasses [17]. Resources that are more dispersed, conversely, do not saturate local scavenger communities, so that a competitive dominance hierarchy (with grizzly bears and coyotes at the top) determines which

species consume the bulk of available scavenge. Our analysis suggests that winter carrion in the absence of wolves will become increasingly pulsed during winter. Consequently, areas without wolves may experience an increase in scavengers with high recruitment abilities. Actual numerical responses by scavenger species to wolf-provided carrion can now be tested in field studies by comparing areas with wolves to those without wolves in order to determine if changes in scavenger population sizes following wolf reintroduction are consistent with the predicted magnitude of the temporal subsidy due to wolves.

As the climate warms, those species will persist that are able to adapt to differences in the environment. Late-winter carrion in Yellowstone will decline with or without wolves, but by buffering this reduction, wolves extend the timescale over which scavenger species can adapt to the changing environment. It is important to note that under present-day climatic conditions, we expect wolves to decrease the long-term average elk population in Yellowstone [29]. This will lead to a corresponding decrease in average yearly carrion levels, which is expected to be small, however, because declines in carrion due to a drop in elk numbers will be partly offset by a higher turnover in the elk population due to wolf predation on old animals [29]. Scenarios both with and without wolves therefore provide a meaningful and roughly equivalent (see Figure 4 in [29]) amount of carrion to scavengers. What we demonstrate here is that scavengers in areas without wolves will experience carrion as an increasingly pulsed resource under climate change, whereas in areas with wolves carrion will remain spread out over the winter months.

The primary objective of this study is to understand the influence of winter climate and predation on trophic dynamics. Our analysis is retrospective, examining what would have happened to scavenge availability in scenarios with and without wolves over the last fifty years of climate change. One may ask, however, what these results imply in light of predictions for continuing global warming into the future. Elk population numbers in Yellowstone are currently constrained by the availability of winter range, where snow levels are low enough to allow for elk movement and cratering through the snow to access food resources. If snow levels in Yellowstone continue to decline in the future, winter range expansion and thus higher elk densities are likely to occur. We expect, therefore, that the wolf-elk-scavenger complex will accrue added importance in the years to come. Future studies examining climate change impacts on spring and summer rainfall, which sets forage levels for elk, will be crucial to further deciphering the effects of global change on trophic relationships in Yellowstone.

We are just beginning to understand the interaction between top predators, such as wolves, and global climate patterns. On Isle Royale, trophic effects have recently been shown to be mediated by behavioral responses to climate. There, gray wolf pack size is partly controlled by climatic conditions that, in turn, affect wolf kill-rates on moose (*Alces alces*) and consequent herbivory levels on balsam fir (*Abies balsamea*) [30]. In Yellowstone, our scenarios demonstrate that wolves act to retard the effects of a changing climate on scavenger species. Together these results begin to elucidate the expected changes that may occur to boreal ecosystems as a result of climate change effects on top predators.

Materials and Methods

The northern range of Yellowstone NP is the wintering area of the park's largest elk herd and home to 4–6 gray wolf packs. Elevations range from 1,500 to 3,400 m, with 87% of the area between 1,500 and 2,400 m [25]. The climate is characterized by short, cool summers and long, cold winters, with most annual precipitation falling as snow. Mean annual temperature is 1.8 °C, and mean annual precipitation is 31.7 cm [25]. Large, open valleys of grass meadows and shrub steppe dominate the landscape, with coniferous forests occurring at higher elevations and on north-facing slopes.

Weather data analysis. Since 1948, meteorological data has been collected daily from two permanent weather stations on the northern range of Yellowstone NP. One is located in Mammoth Hot Springs at park headquarters near the northern entrance to the park. The other is located at the Tower Falls ranger station about 29 km east of Mammoth. Data for the period 01 August 1948 to 01 June 2003 were made available to us by the Western Regional Climate Center in Reno, Nevada, United States.

Using linear regression, we investigated multiannual trends in monthly average SDTH over the 55 y provided in the data set. SDTH is treated as the response variable and regressed upon year. We also examined trends in the timing of the date of first bare ground. This was defined as the first day of the year for which SDTH was zero. In order to understand changing patterns in SDTH, we analyzed average monthly snowfall (SNFL), average TMIN and TMAX, and the number of days per winter that TMAX exceeded freezing.

Wolf effects: Statistical model. In order to compare the effects of carrion availability to scavengers under climate change in scenarios with and without wolves, we used previously published regression equations [23] relating SDTH, S, to monthly carrion availability, C_p, prior to wolf reintroduction given by

$$C_p = -14.48 + 21.04S \qquad (1)$$

and relating SDTH and wolf pack size to carrion availability, C_a, after wolf reintroduction [16] obtained using

$$C_a = K \cdot P \cdot 30 \cdot (1 - Q) \qquad (2)$$

where K is the wolf kill-rate per wolf, P is the wolf pack size, 30 is the number of days in a month, and Q is the percent of the edible biomass of a carcass consumed by a wolf pack given by Wilmers et al. [16]. We used Monte Carlo methods, as elaborated below, to reconstruct how much carrion would have been available to scavengers during each of the winter months (November through April) in the years 1950 and 2000 under scenarios with and without wolves. Specifically, for each scenario [1950 without wolves, 2000 without wolves, 1950 with wolves, and 2000 with wolves], we drew 100 random SDTH values for each of the months, where SDTH was assumed to be normally distributed with mean and standard error for the years 1950 and 2000 given by the regression analyses of the Tower Falls weather data (see Figure 2). This incorporated uncertainty into our estimate of SDTH for the years 1950 and 2000, allowing us to draw random SDTH values from those years for our Monte Carlo simulation. In the scenarios without wolves, we inserted our randomly chosen monthly SDTH values for each year and each run into equation 1 to yield the amount of carrion available per month without wolves. We used the same procedure for selecting SDTH in our scenario with wolves. In order to select wolf pack size, we assumed that wolf pack sizes were normally distributed, with a mean (± standard deviation) pack size of 10.6 (± 5)

representing the current distribution of Yellowstone wolves [31]. We then inserted our randomly chosen monthly SDTH values and wolf pack sizes into equation 2 to yield the amount of carrion available per month with wolves. For each run of each scenario, we recorded the reduction in monthly winter biomass available to scavengers in 2000 as a proportion of what was available in 1950.

Our statistical modeling approach, although rooted empirically, is limited by the fact that it does not take into account the possible effects of wolf and elk population dynamics on carrion availability. In order to explore these effects, therefore, we used a previously published model [29] that was originally built to explore the effects of wolf and elk population dynamics on monthly carrion flow to scavengers.

Wolf effects: Dynamic model. The details of the model are exactly the same as in Wilmers and Getz [29], except for the following changes. In the original model, SDTH was incorporated into the elk population dynamics but was treated as a random variable. In the present study, we modified the model so that the actual progression of winter weather from 1950 to 2000 was used. We ran the model for 51 y, from 1950 to 2001. We selected SDTH, V, for the year and month in question from the Tower Falls regression equations in exactly the same manner that we describe above in the statistical model. Since the distribution of elk among age classes from 1950 is not known, we performed, as a baseline, a 50-y run of the model under average 1950 weather conditions. This is long enough for the effects of initial conditions to dissipate. We then used the numbers and age structure of the final month of the baseline run as the initial conditions of the run using observed weather data from 1950 to 2000.

Sensitivity analyses were conducted using Monte Carlo methods to assess the relative effects of different parameter values on model output [29,32]. Since the primary goal of using the dynamic model is to assess whether late-winter carrion will be affected by elk and wolf population dynamics in the context of a changing climate, we defined an output variable, z, as the percent change in late-winter carrion from 1950 to 2000. We assigned March and April to late winter for comparison to Figure 4, since these are the two months showing a significant effect between scenarios with and without wolves. For each scenario, we conducted 1,000 runs of the model, choosing a different set of parameter values at random from the ranges provided in Table 1 of Wilmers and Getz [29]. Each model parameter was then regressed against z to determine its effect.

Acknowledgments

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