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The role of science in understanding (and saving) large carnivores: A response to Allen and colleagues

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ABSTRACT

Allen and colleagues contend that the study designs used to test for indirect effects of large carnivores on lower trophic levels are limited insomuch as they "rely on weak inference when valuing the roles of large carnivores in ecosystems." Based upon their review of gray wolf and dingo studies, they conclude "that evidence for the ecological roles" (i.e., top-down effect) of these species is "equivocal." Further, they assert that large carnivore science is being distorted in both the scientific and popular literature in order to justify restoration of large carnivores. They prescribe the use of manipulative experiments as the best means of understanding the effects of large carnivores on ecological systems, and systematic review of studies that "have used only manipulative experiments to investigate these hypotheses." We take issue with Allen and colleagues' characterization of empirical evidence in the field of ecology, and we question the strength of evidence they present in support of prosecutorial assertions levied against scientists and science communicators. Ultimately, justification for the restoration of large carnivores is provided by two scientific claims that are unperturbed by Allen and Colleagues critique (i.e., that large carnivores routinely have important impacts on ungulate abundance, and overabundant ungulate populations often adversely impact the structure and biodiversity of habitats).

1. Introduction

In the provocatively titled "Can we save large carnivores without losing carnivore science?", Allen and colleagues assert that a growing number of studies documenting the ecological effects of large carnivores "rely on weak inference." Perhaps more alarmingly, they contend this science is being distorted in both scientific and popular accounts, which, from their perspective, overstate the strength and generalizability of carnivores' effects. Allen and colleagues appear particularly concerned with research suggesting large carnivores have important, indirect impacts on ecosystems, as predicted by the meso-predator release (MPRH), and through their influence on large herbivores, as predicted by the trophic cascade (TCH) and behaviorally-mediated trophic cascade (BMTCH) hypotheses. They prescribe the use of "manipulative experiments" as a means of testing these hypotheses, as well as systematic review that excludes non-experimental studies. We are concerned that Allen and colleagues overvalue the role of ecological experiments, and rely on weak evidence in waging serious accusations against their colleagues. We begin by discussing the role of experiments as evidence in ecology.

2. Experiments as evidence

Although we applaud Allen and colleagues' call for additional research and systematic review concerning the top-down effects of large carnivores on terrestrial ecosystems, we are concerned about their call to prejudicially discount other kinds of evidence, such as correlative studies, from review.

The role of experiments as evidence in ecology is the subject of a large, sophisticated literature (e.g., Weber, 2004, Taper and Lele, 2010, Krebs, 1989, 1991, Pearl, 2009, Sugihara et al., 2012). That literature is powerful refutation of the idea that experiments represent an unqualifiedly privileged role as evidence. In particular, the epistemological distinctiveness of experiments is less clear when any of the elements of experimentation (especially, replication, randomization, manipulation, and control, see Montgomery, 2008 for an overview)

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cannot be executed excellently – as is almost always the case for inquiries about the effect of large terrestrial carnivores. Indeed, large scale field experiments in ecology—though meeting Allen and colleagues' requirement of being "manipulative"—often fail to include one or more of the other valuable elements of experimentation – elements that give experiments their epistemological distinctiveness (Weber, 2004). Hereafter, we use the phrase "complete experiment" to refer to a study comprised of replication, randomization, manipulation, and control.

This point is illustrated, in part, by the research reported in Sinclair et al. (2000) and its relative contribution to knowledge on the influence of predation on temporal variation in the abundance of snow shoe hares. Sinclair et al. (2000) is a quasi-experiment that included control. manipulation, and randomization. The experiment did not include replication, nor did it control for the effect of avian predators. Despite the lack of replication, and control of confounding factors, the experiment was heralded, and rightly so, for the difficulty of its execution. Indeed, to our knowledge, no such experiment has been attempted since. In the century-long effort to understand the influence of predation on hares, we believe Sinclair et al. (2000) is the closest thing to a complete experiment on the phenomena of interest (hare abundance, opposed to some mechanism of hare abundance, such as survival). However, though we can robustly infer a great deal about the influence of predation on hare, really quite little of that knowledge comes from the "only" experiment conducted on the topic. The large majority of what we know about the dynamics of hare abundance-and we know a great deal-comes from non-experimental studies, pseudo-experiments or experimental studies on narrow mechanisms within the phenomena of interest (Krebs et al., 2001). This example should inform our expectations for what contributions we should expect from experiments on the indirect influence of apex predators on lower trophic levels.

Another serious and perennial challenge to performing ecological research is ensuring that the response (variable) is adequately assessed. For example, delayed effects—such as maternal effects—can result in a response not being fully realized until after the completion of the study period. Ecological experiments, which are typically shorter in duration than other study designs, may be particularly prone to such challenges.

Many other issues could be raised in judging the importance of experiments relative to other study designs in ecology – doing so is far beyond the scope of this essay. The examples here are intended to be emblematic of the limitations of experiments for addressing questions like trophic cascades involving large predators. The point, for clarity, is that scientific inference on topics as broad as trophic cascades involving large predators is strongest when it relies on a diversity of evidence types. Therefore, we believe it unwise to systematically exclude nonexperimental evidence, especially in cases where all four components of a complete experiment are not well-executed.

We also take issue with Allen and colleagues characterization of the evidence concerning the top-down ecological roles of wolves as "equivocal." There is strong evidence that predation (by large carnivores generally, and wolves especially) has an important negative influence on ungulate density throughout the northern hemisphere (Fig. 3a of Ripple and Beschta (2012) and Fig. 2 of Peterson et al., 2014). Moreover, there is widespread evidence that ungulates adversely impact the structure of the ecosystems that they inhabit, through ungulates' effect on vegetation (Côté et al., 2004). A thorough, systematic review of the literature would indeed be useful, and would likely reveal underappreciated complexities. Nevertheless, it is difficult to imagine that any such review would contradict the simple claims that (a) predation routinely has important impacts on ungulate abundance, and (b) overabundant ungulate populations often adversely impact the structure and biodiversity of habitats. And it is those claims that provide justification for conservation actions aimed at restoring predators to places where they have been extirpated (and would do well enough, given other human-wildlife conflict concerns), and limiting human offtake of predators so as not to impair their ecosystem function (predation).

3. The perceived universality of trophic cascades

Beyond their epistemological concerns, Allen and colleagues worry about popular and scientific discourse surrounding the ecological effects of large carnivores, and what this discourse conveys to the general public. They assert that "evidence for the MRH, TCH and BMTCH is undeniably weaker than is often claimed in journals or public discourse" and worry that this has led to the "perceived universality of topdown control of ecosystems [by large carnivores]."

To be fair, it is relatively easy to find popularized accounts of trophic cascades that do not sufficiently express scientific uncertainty (Mech. 2012)—though we doubt this phenomenon is limited to trophic cascades. But do such accounts represent a growing problem as Allen and colleagues contend? A systematic review of how wolves are depicted in the North American news media that spanned a decade and analyzed more than 6,000 stories found that the idea that wolves "positively impact ecosystems" was expressed in only 2.3% of more than 29,000 paragraphs-precisely the same percentage that expressed the idea that wolves "negatively impact ecosystems" (Houston et al., 2010). The most commonly noted idea was that "wolves negatively impact human activities," (emphasis added) which was expressed in 30.5% of paragraphs (Houston et al., 2010). This systematically-collected empirical evidence undermines the idea that beneficial top-down effects of wolves on ecosystems are wide spread-at least in the news media (see Bruskotter, 2013).

Importantly, our concern is not limited to Allen and colleagues' claims about the perceived universality of trophic cascades. Indeed, the authors levy several serious, prosecutorial assertions against scientists and science communicators. For example, they (i) assert that "there is an increasing tendency to ignore, disregard, or devalue the fundamental principles of the scientific method when communicating the reliability of current evidence," (ii) chastise scientists for a "lack of objectivity and critical thinking underpinning the current 'parental affection'...towards the MPRH, TCH, and BMTCH and the extent to which this affection is used to legitimize selected views on carnivore management," and perhaps most ominously, assert:

(iii) "[t]he actual *science* of large carnivore science is now getting lost, being replaced by catch phrases, slogans, sound bites, YouTube clips, fake news and post-truth politics, or the simplification and popularisation of unsubstantiated or unreliable opinions, theories and hypotheses."

(emphasis in original)

We are deeply concerned that such serious accusations are supported with far weaker evidence than the evidence currently supporting indirect impacts of carnivores—the very evidence that Allen and colleagues are so critical of. In one instance, the authors support the claim that the use of value-laden rhetoric by scientists risks "undermining long-term confidence in large carnivore science" with citation to a popular account, published in the *New York Times*, which provocatively characterized the idea that wolves initiated a trophic cascade in Yellowstone by strongly asserting: "It's not true." (Middleton, 2014). In another instance, Allen and colleagues cite the documentary video, *How Wolves Change Rivers*, which depicts a variety of ecological changes that occurred after wolves' reintroduction to Yellowstone National Park and asserts these resulted from that reintroduction.

Importantly, the need to make accurate, precise and well-supported claims extends beyond communicating the science of trophic cascades. Indeed, if we envision conservation as a truly interdisciplinary effort—one transcending the social and biophysical sciences—then scientists have an obligation to approach claims about social phenomena, including discourse and human perception, with the same skepticism and rigor that we approach claims about ecological processes (Bruskotter, 2013).

4. Management implications

Allen and colleagues warn that managers and policy makers "should exercise caution when making decisions based on the currently available literature describing these processes." For example, they contend that "[s]imply re-establishing or bolstering large carnivores may not fix the many environmental problems that occurred as a result of (and/or in addition to) carnivore extirpation." We agree that managers and policy makers alike should temper expectations regarding what is likely to occur following carnivore restorations. Indeed, the history of natural resources management is replete with examples of interventions gone awry and unintended consequences resulting from well-intentioned management (e.g., fire suppression in U.S. Forests and national parks, introduction of cane toads to control cane beetles in Australia). Nevertheless, Holling and Meffe (1996 p.330), looking broadly across the literature on natural resource management, caution against the "pathology" of approaches that "attempt to replace natural ecological controls, which are largely unknown to us and highly complex and variable, with engineered constructs and manipulation." Such approaches, they contend, ultimately lessen the resilience of ecological systems (see also Gunderson and Holling, 2002). If one were to be simultaneously mindful of (a) what is known in general about ecosystem resilience, (b) what is known in general about the effects of large predators, and (c) the precautionary principle; then one would assume that predators are important to any ecosystem until that proposition were disproved. That perspective provides additional justification for the restoration of large carnivores in terrestrial ecosystems.

Ultimately, we agree with Allen and colleagues on two crucial points relevant to management: (a) human management of systems (e.g., provisioning of water, hunting and lethal control of ungulates, as well as predators) is likely to moderate the effects of large carnivores on lower trophic levels, and (b) such top-down effects are likely to be influenced by other factors outside managers' control. Given such complexity, advancing our understanding of the roles that large carnivores play in terrestrial ecosystems is best achieved by utilizing all of the tools of science—not privileging some over others.

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