

## Opinion

## Trophic Cascades by Large Carnivores: A Case for Strong Inference and Mechanism

Adam T. Ford<sup>1,\*</sup> and Jacob R. Goheen<sup>2</sup>

**Studies on trophic cascades involving large carnivores typically are limited by a lack of replication and control, giving rise to a spirited debate over the ecological role of these iconic species. We argue that much of this debate can be resolved by decomposing the trophic cascade hypothesis into three constituent interactions, quantifying each interaction individually, and accommodating alternative hypotheses. We advocate for a novel approach that couples the rigor characterizing foundational work on trophic cascades (i.e., from studies carried out in mesocosm and whole lake systems) with the conservation relevance of large carnivore-dominated food webs. Because of their iconic status, it is crucial that inferences about the ecological role of large carnivores rise to meet the same rigorous standards to which other studies in community ecology are held.**

**Carnivores, Cascades, and Controversy**

Large carnivores are hypothesized to shape ecosystems both by consuming and scaring herbivores, thus indirectly affecting plants and abiotic processes through trophic cascades [1–3]. It has recently been suggested that trophic cascades are ‘...a universal property of ecosystem functioning, a law of nature as essential and fundamental to ecology as natural selection is to evolution’ ([4], p. 354). Moreover, and because of their potential to trigger trophic cascades, some argue that the conservation of large carnivores is a moral obligation of humanity [5]. Notwithstanding the scientific or conservation promise that trophic cascades, the majority of evidence for this ‘law’ comes from studies on the dynamics of small and short-lived species observed in mesocosm or whole lake experiments [3,6–11]. Typically, these studies are characterized by strong inference, quantification of underlying mechanisms, and multiple hypothesis testing.

By contrast, evidence for the role of large carnivores as drivers of trophic cascades is ensconced in controversy, partly because of a reluctance to entertain multiple alternative hypotheses [12], partly because of a reliance on correlative methods [13], and partly because of a lack of clarity over the appropriate responses to measure [14,15]. Perhaps the most high-profile example of this controversy occurred in the Greater Yellowstone Ecosystem, where changes to the landscape that had been widely attributed to the reintroduction of wolves coincided with other sources of environmental change. As a result of these potential confounds, ecologists have questioned the mechanisms and the strength of the indirect effect of wolves in Yellowstone [15–23]. Similarly, variation in land use, rainfall, and soil conditions coincided with the extirpation of dingoes in Australia [24,25], confounding the reported impact of this apex predator on ecosystem function [26]. In the Eastern Pacific, environmental toxins and predation by sharks [27] obfuscated the putative cascading effects of orcas on nearshore ecosystems [28]. Given that the distribution of large carnivores is changing rapidly across the earth [5,29,30], it is crucial to better predict how, where, and when these iconic species generate trophic cascades.

**Trends box**

Large carnivores are believed to play a key role in determining ecosystem properties via trophic cascades. While the recovery of large carnivore populations is generally heralded as a conservation success story, the common assertion that such recoveries alter plant communities and other ecosystem properties is currently not supported by the standards of evidence expected in other scientific disciplines.

There have been very few replicated and controlled experiments documenting evidence for trophic cascades involving large carnivores, leaving a knowledge gap with crucial implications for ecology and wildlife conservation.

The absence of a mechanistic understanding of food web dynamics and weak inference in many studies combine to obfuscate the mechanisms underlying if and how large carnivores affect ecosystems.

<sup>1</sup>Department of Integrative Biology, University of Guelph, Guelph, ON, Canada

<sup>2</sup>Department of Zoology and Physiology, University of Wyoming, Laramie, WY, USA

\*Correspondence: adamford@uoguelph.ca (A.T. Ford).

Here, we illustrate the salient limitations and opportunities in the approaches used by ecologists to test the trophic cascade hypothesis in food webs comprising large carnivores, herbivorous prey, and autotrophic plants. We then present a novel framework for testing cascades that is based on strong inference, quantifies the constituent interactions giving rise to indirect effects, and tests alternative hypotheses for each interaction. We highlight the particular challenge of assigning causation to a focal carnivore (i.e., relating to the focus of a particular study, such as a species reintroduction) in a speciose food web.

### The Gold Standard: A Mechanistic Approach under Controlled and Replicated Conditions

A mechanistic and strongly inferential approach to studying trophic cascades has been used by ecologists for several decades, typically in systems with plankton, arachnids, insects, fish, and other small fauna as the top carnivore [3,6–10]. Taxonomy aside, the approach used in many of these studies might be viewed as the ‘gold standard’ by which the trophic cascade hypothesis is tested for both small and large carnivores. Through at least three key developments, the use of the gold standard approach generated a body of work that is convincing evidence for trophic cascades.

The first development was that of methodological advances to quantify the constituent interactions giving rise to trophic cascades. In its archetypal form [1], a trophic cascade results from the dampening of herbivory caused by carnivores’ numerical suppression of herbivorous prey (but see [Box 1](#)), leading to plants’ enhanced growth, biomass, cover, reproduction, or survival (hereafter referred to as ‘plant abundance’). Thus, a trophic cascade requires demonstration of at least three interactions: (i) reduction of herbivore abundance by carnivores; (ii) reduction of plant abundance by herbivores; (iii) indirect facilitation of plants by carnivores via suppression of herbivory. The most powerful test of these three interactions occurs through species-removal

#### Box 1. The Special Case of Behaviorally Mediated Trophic Cascades

Trophic cascades occur through two nonexclusive pathways – density mediation and behavioral mediation. Density mediated trophic cascades (DMTCs) require a numerical reduction of herbivores caused by predation. Behaviorally mediated trophic cascades (BMTCs) involve nonlethal, antipredator responses of herbivores to the risk of predation [54]. BMTCs are believed to have stronger effects on plant abundance than DMTCs, particularly when antipredator behavior manifests as risk-averse habitat selection [7]. Understanding how predator hunting mode and the nature of herbivore resource limitation shape herbivore–plant interactions will determine if the indirect effect of carnivores on plants manifests as DMTCs, BMTCs, or not at all [35].

Unlike an archetypal DMTC [1], BMTCs arising from risk-averse habitat selection can lead to either positive or negative effects on plants. For instance, plants in areas that are risky for herbivores are browsed less often than plants occurring in safe habitats [35,39]. Consequently, a BMTC can generate positive indirect effects of carnivores on plants in risky areas and negative indirect effects of carnivores on plants in safe areas. Compared with food chains confined to the spatial boundaries of a mesocosm [9], these habitat shifts by the herbivore can be particularly important in large carnivore-dominated systems. In these open systems, large herbivores and their predators move over vast areas and spatial heterogeneity in landscape structure can greatly alter the direction and distribution of trophic cascades [39].

The framework for quantifying trophic cascades involving large carnivores ([Figures 1 and 2](#)) is identical for DMTCs and BMTCs in that evidence for the predicted direction and strength of interactions between trophic levels needs to be quantified individually. The occurrence of BMTCs requires that prey are risk-averse and that this aversion translates into a perceptible change in plant abundance [15,17]. Of these two requirements, researchers have struggled more with ways to quantify perceptions of risk in large mammals. In particular, researchers attempting to quantify how risk shapes habitat selection might first identify if ‘risk’ entails areas where predators are most abundant (increased probability of encounters between carnivores and herbivores), where prey are least abundant (loss of dilution and the ‘many eyes’ effect or because prey avoid risky areas), where probability of detecting a carnivore is lowest (increased probability of attack), or where probability of being captured following an encounter is highest [63]. In the few systems where the distribution of risk from large carnivores has been measured, these different types of ‘risk’ do not always coincide in space and time [16,64,65]. Thus, in testing for a BMTC, researchers must first identify which types of risk are avoided by the prey, and then whether this avoidance has a meaningful effect on plant abundance.

Download English Version:

<https://daneshyari.com/en/article/142325>

Download Persian Version:

<https://daneshyari.com/article/142325>

[Daneshyari.com](https://daneshyari.com)