

How do multi-predator, multi-prey systems affect predator-prey population dynamics?

Introduction: Large carnivores are re-colonizing North America^{1,2} and parts of Europe³, following decades of systematic eradication⁴. The expansion of large carnivore populations is creating novel and complex predator-prey interactions⁵. One well-known example is trophic cascades and associated declines in herbivore abundance⁶. Predator-prey interactions are among the most fundamental ecological processes and have been the focus of ecology since its origin⁶. They are integral processes that shape biological communities, affect coupled human-wildlife systems, and drive conservation and management ecology⁷. Despite this, our understanding of the effect of predators on prey populations, especially in complex food-webs, is in its infancy^{5,7}.

Predator-prey theoretical and empirical research is dominated by single predator-single prey systems like the Isle Royale wolf-moose system⁸. While useful, it is unclear if these simplified models are capable of predicting dynamics where multiple predators are interacting with multiple prey species^{6,7}. For example, the recent recovery of wolves, expansion of grizzly bear populations, and expanding range of mountain lions across the Western United States are increasing the number and complexity of interactions between predator and prey species^{1,2,4}. Mounting evidence that the growing number of interactions can cause previously unknown ecological effects suggests that there is much left to be understood in multi-predator, multi-prey food webs^{6,9,10}. For example, these complex dynamics can spur changes in direct ecological interactions, such as prey switching by predators in response to prey abundance⁹.

A key conceptual way in which single predator-prey interactions differ from more realistic, complex, multiple predator-prey food webs is the inclusion of competition in addition to direct predator-prey dynamics. For example, predator-prey dynamics can lead to indirect ecological interactions, such as apparent competition, where one prey species supports predator populations, thereby reducing alternative prey populations¹⁰. With various competitive interactions within a trophic level occurring, the complexity of competition must also be considered¹¹. Ecology has long studied the tension between how the forces of predation and competition structure communities and population dynamics¹¹. Unfortunately, the inherent complexity of such systems has often rendered purely statistical/empirical approaches limited in their utility.

Compared to laboratory studies and field experiments, mathematical models, such as multiple predator-prey models (MPPMs) allow ecologists to study these dynamics¹². Complex food webs cannot be easily resolved with statistical/empirical approaches because of the large number of parameters to estimate and the scant data to do so with, as well as the challenges presented by some parameters and mechanisms that are impossible to estimate (e.g., carrying capacity). MPPMs are also very powerful in evaluating the consequences of management decisions¹². Commonly, natural resource agencies manage populations using independent management strategies for each species; therefore they do not reflect the complexity of predator-prey population dynamics. By failing to incorporate food web interactions into species management strategies and ignoring the role of multi-species predation and competition, agencies may be sub-optimally preserving and managing wildlife populations.

I hypothesize that MPPMs which consider alternative interactions will explain empirical systems better than single-predator, single-prey models (SPPMs). I will address these major questions: **a)** Are MPPMs better at predicting population dynamics in real-world systems than SPPMs? **b)** If so, are the main advantages of MPPMs in terms of predictive performance driven by predation or inclusion of competitive interactions? **c)** What are the conditions (e.g.,

environmental, stochastic) in which predation vs. competition drive food webs? With these ecological questions answered, I will finally address: **d)** How does management of one species affect populations of other predators and prey within a food web?

Research Approach: I will use wildlife agency-collected datasets from the Idaho Department of Fish and Game for predator and prey populations. Then, through funding from my NSF GRFP proposal, I will generalize my results to other high-profile multi-species predator-prey datasets from Banff National Park, Yellowstone National Park, and Serengeti National Park, with the help of my Ph.D. supervisors who have connections to these 3 systems. First, I will gather information about predator or prey population dynamics from previous studies to inform the structure of my models¹². Then, I will estimate functional and numerical responses for each predator-prey pair from across systems. I can then incorporate each predator and prey species into a set of coupled equations, one for each species in the food web. If there are i predator species and j prey species, the corresponding predator-prey equations can be written as such:

$$[1] \frac{dV_j}{dt} = f(V_j) - \sum_i f(V_j, P_i) - \sum_j f(V_j) \quad [2] \frac{dP_i}{dt} = \sum_j f(V_j, P_i) - f(P_i) - \sum_i f(P_i)$$

where [1] describes the population growth rate for prey (1st term), reduced by the effects of predation (2nd term) and competitive interactions with other prey j (3rd term) and [2] represents the population growth rate for predators (1st term), decremented by predator mortality (2nd term) and, when present, competition from other predators (3rd term). For example, V_1 could represent white-tailed deer, V_2 elk, whereas P_1 could represent wolves, P_2 mountain lions, and so on. The shape and dynamics of these functions, $f(\cdot)$, will be determined from field data.

Intellectual Merit: I will address questions fundamental to predator-prey theory, and also more broadly, the ecological theory about the role of competition vs. predation in driving population dynamics. For example, I will investigate if functional and numerical responses, thought to be integral to predator-prey theory^{7,9,13}, are sufficient or even necessary to understand predator-prey population dynamics. By applying these models to a broad variety of ecosystems, I will identify general properties that drive not only predator-prey systems, but other consumer-resource relationships¹⁴. Moreover, I will help natural resource agencies avoid mistakes stemming from un-integrated management, which can be economically and ecologically costly¹².

Broader Impacts: Through an increased understanding of how management controls predator-prey population dynamics, wildlife agencies will be able to determine how human harvest strategies of one species will affect others in a food web. Additionally, I will work to establish an accurate public image of large carnivores throughout local communities, and bridge the gap between ecologists-wildlife agencies-citizens. I will do so by giving talks at local high schools, writing articles for newspapers and online blogs, and partnering with local radio/TV programs, much of which I have done in the Falkland Islands (see Personal Statement). In sum, I envision that my work will develop ecological principles general enough to transcend ecosystems, but also specific enough to assist management of the natural resources of local communities.

Literature Cited: 1) Mech, L. (1995). *Cons. Bio.* 9(2):270-278. 2) LaRue, M. et al. (2012). *J. Wildl. Mgmt.* 76(6):1364-1369. 3) Chapron, G. (2014). *Science.* 346: 1517-1519. 4) Ripple, W. et al. (2011). *Science.* 343:151-162. 5) Berger, J. et al. (2001). *Science.* 291:1036-1039. 6) Shurin, J. et al. (2002). *Ecol. Lett.* 5(6): 785-791. 7) Abrams, P. & Ginzburg, L. (2000). *TREE.* 5(278): 535-541. 8) Messier, F. (1994). *Ecol.* 75(2):478-488. 9) Hebblewhite, M. (2013). *Pop. Ecol.* 55(4):511-522. 10) Holt, R. (1977). *Theor.Pop.Bio.* 12(2): 197-229. 11) Chesson & Kuang. (2008). *Nature.* 456: 235-238. 12) Serrouya, R. et al. (2015). *Am. Natl.* 185(5): 665-679. 13) Berryman, A. (1992). *Ecol.* 73(5):1530-1535. 14) Vucetich, J. et al. (2011). *J. Anim. Ecol.* 80(6):1236-1245.