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Using Predator-Prey Theory to Predict Outcomes of Broadscale Experiments to Reduce Apparent Competition

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abstract: Apparent competition is an important process influencing many ecological communities. We used predator-prey theory to predict outcomes of ecosystem experiments aimed at mitigating apparent competition by reducing primary prey. Simulations predicted declines in secondary prey following reductions in primary prey because predators consumed more secondary prey until predator numbers responded to reduced prey densities. Losses were exacerbated by a higher carrying capacity of primary prey and a longer lag time of the predator's numerical response, but a gradual reduction in primary prey was less detrimental to the secondary prey. We compared predictions against two field experiments where endangered woodland caribou (*Rangifer tarandus caribou*) were victims of apparent competition. First, when deer (*Odocoileus* sp.) declined suddenly following a severe winter, cougar (*Puma concolor*) declined with a 1–2-year lag, yet in the interim more caribou were killed by cougars, and caribou populations declined by 40%. Second, when moose (*Alces alces*) were gradually reduced using a management experiment, wolf (*Canis lupus*) populations declined but did not shift consumption to caribou, and the largest caribou subpopulation stabilized. The observed contrasting outcomes of sudden versus gradual declines in primary prey supported theoretical predictions. Combining theory with field studies clarified how to manage communities to mitigate endangerment caused by apparent competition that affects many taxa.

Keywords: apparent competition, predation, *Rangifer tarandus*, *Canis lupus*, *Odocoileus virginianus*, conservation.

Introduction

Understanding the population dynamics of wide-ranging species requires observational or experimental studies that cover broad areas. This generalization is particularly relevant for many carnivores because of the extended areas needed to acquire prey, which are often dispersed or migrate seasonally (Fryxell 1991; Hebblewhite et al. 2008). These broad scales constrain the ability of ecologists to address important questions because replicating or even implementing experimental treatments comes with substantial logistical challenges (Walters and Holling 1990). Furthermore, when policy actions are implemented across large areas, fixing mistakes that stemmed from uncertainty or unexpected processes can be difficult and costly, both economically and ecologically (Carpenter et al. 1999; Doak et al. 2008).

Compared with field experiments, mathematical models have the advantage that they allow for risk-free experimentation with inference to large spatial scales and thus help anticipate consequences of applied actions. Therefore, we modified existing predator-prey models to make predictions involving an indirect food-web interaction termed apparent competition (Holt 1977), an imminent and increasing applied problem that affects many taxa (Holt and Lawton 1994; Courchamp et al. 2003; DeCesare et al. 2010). Our goal was to use these equations to predict population dynamics across a large area and to compare predictions with data from field experiments (Levins 1966).

Apparent competition represents an interaction where the addition of a novel prey negatively affects native prey even though the two species do not compete for resources. Instead, such interactions are mediated through a shared predator. The apparent competition hypothesis predicts that native prey will decline to a lower equilibrium after the invasion of a novel prey. If the native prey are less fecund or more vulnerable to predation relative to the novel prey, this reduction may be substantial and even lead to extinction (Holt 1977). Novel prey can invade because of changes in land use or climate; for example, logging can increase forage for some herbivores, and milder winters can facilitate overwinter survival (Dawe 2011). Finally, humans have introduced many novel prey species on islands where they

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have few natural enemies (Pech et al. 1995; Sinclair et al. 1998; Courchamp et al. 2003). Because novel prey usually comprise a higher proportion of the predator's diet, they are referred to as primary prey, whereas the native prey are termed secondary (Pech et al. 1995).

To mediate the effects of apparent competition, intuition suggests that removing the primary prey would indirectly reduce predator numbers and thus benefit the secondary prey. However, if predator populations do not respond immediately, they may consume more secondary prey during a transient phase. This process may increase rather than mitigate risk to the rarer secondary prey. The degree of risk could be affected by the time lag of the predators' numerical response, the relative abundance of primary to secondary prey, and the magnitude and rate of decline in the primary prey. Each of these factors essentially changes the ratio of predators to prey, which has been shown to affect predation rates (Vucetich et al. 2011; Hebblewhite 2013). Indeed, modeling studies have suggested that this transient risk is possible for rare species affected by apparent competition (Courchamp et al. 2003), and empirical studies suggest that this risk is real (Norbury 2001; Collins et al. 2009; Wittmer et al. 2013). Even though the increased risk would be initiated during the transient phase, effects may be long lasting, particularly when populations are small or driven below a threshold (Allee 1931; Wittmer et al. 2005*b*) as a result of the transient dynamics. These dynamics would clearly be influenced by the specific life histories of prey and predators, but they would also be influenced by the rate at which the primary prey are removed. Pulsed or sudden changes in resource abundance are expected to have cascading ecosystem-level effects (Abrams et al. 1998; Holt 2008; Schmidt and Ostfeld 2008), particularly during the transient phase following the change in resource abundance (Holt 2008). Furthermore, transient dynamics have become particularly relevant in a world where the magnitude and frequency of environmental stochasticity is expected to increase (Easterling et al. 2000). Even if increases in stochastic events fail to materialize, there is growing recognition that stochastic pulses (sudden addition or removal of a resource) can play a key role in shaping community structure (Holt 2008; Schmidt and Ostfeld 2008).

One of the most well documented victims of apparent competition is the woodland caribou (*Rangifer tarandus caribou*), where increases in moose (*Alces alces*) and deer (*Odocoileus* sp.) have led to higher predator abundance, increased predation on caribou, and subsequent widespread declines in caribou populations (Seip 1992; Wittmer et al. 2005*b*; Latham et al. 2011). Increases in moose and deer are thought to have occurred because of forest harvesting that increases forage and a warming climate that reduces winter severity (Dawe 2011; Serrouya et al. 2011). Consequently, there is broad agreement that an unsustainable level of predation is the proximate cause of caribou population declines (Bergerud and Elliot 1986; Seip 1992; Kinley and Apps 2001; Wittmer et al. 2005*b*; Latham et al. 2011; McLellan et al. 2012). However, relative to the research effort placed on identifying causative factors of decline (Seip 1992; Wittmer et al. 2005*b*), there are few theoretical or empirical studies addressing recovery options for endangered caribou populations (Steenweg 2011).

Given that woodland caribou are negatively affected by increases in primary prey, several authors have suggested reducing primary prey as a means of indirectly reducing predation rates on caribou (James et al. 2004; Weclaw and Hudson 2004). This strategy provides an alternative to predator control, which has become less acceptable to the public (Orians et al. 1997). While some predators, such as wolves (*Canis lupus*), are resilient to intensive harvest (Mosnier et al. 2008; Webb et al. 2011), less fecund carnivores, such as cougars and grizzly bears (*Ursus arctos*), could become locally extirpated as a consequence of control efforts, further reducing the appeal of direct predator reductions. Finally, if predator control is implemented in the absence of other measures, it will have to be intensive and long term, because predators such as wolves will quickly recolonize areas where they have been removed if their primary prey are still abundant (Mosnier et al. 2008). Therefore, a reduction in primary prey is gaining appeal as a recovery strategy, despite the risk of predators switching to secondary prey. These processes likely apply to all taxa affected by apparent competition (Norbury et al. 2001; Courchamp et al. 2003; Wittmer et al 2005*b*; DeCesare et al. 2010).

Our broad goals with this article were twofold. The first goal was to make predictions about apparent competition in a large-mammal system by focusing on the removal of primary prey that have become more abundant over time. These predictions have important relevance at an ecosystem scale because manipulations necessarily encompass large areas, and if errors are made they could have important and long-lasting ramifications (Carpenter et al. 1999). The second goal was to confront some of the predictions with data from two case studies. The first case study was a natural experiment where white-tailed deer (*Odocoileus virginianus*) were suddenly reduced following a severe winter, and the population dynamics of cougar and caribou were documented. The second case study was a manipulative experiment with a contemporary control, with treatment units covering >6,500 km^2. In this case study, moose were gradually reduced while the response metrics were the population dynamics of wolves and caribou. Contrasting the rate of removal of primary prey has received neither theoretical attention nor empirical support, but it is expected to affect how secondary prey respond to apparent competition.

Such a comparison of large-mammal predator-prey dynamics is not often possible, but as we show here it is highly informative from both theoretical and applied perspectives (Levins 1966).

Methods

Apparent competition was represented as ordinary differential equations (ODEs) for the population densities of two prey species and their common predator (eqq. [1]–[4]). The ODEs are mathematical representations of Rosenzweig and MacArthur's (1963) graphical predator-prey model but with two important modifications. First, a second prey species was added to reflect the apparent competition scenario (Courchamp et al. 2003). The next modification was to make the predator's mortality density dependent (i.e., the per capita mortality is proportional to the predator density, C). This modification was appropriate because for territorial predators such as wolves and cougars there may be an upper density characterized by a type 2 numerical response set by social factors (Messier 1994; Hebblewhite 2013), independent of prey abundance.

The model takes the following form:

$$\frac{dP_1}{dt} = r_1 P_1\left(1 - \frac{P_1}{K_1}\right) - \frac{a_1 P_1 C}{1 + T_h(a_1 P_1 + a_2 P_2)}, \qquad (1)$$

$$\frac{dP_2}{dt} = r_2 P_2\left(1 - \frac{P_2}{K_2}\right) - \frac{a_2 P_2 C}{1 + T_h(a_1 P_1 + a_2 P_2)}, \qquad (2)$$

$$\frac{dC}{dt} = C\left(\frac{b(a_1 P_1 + a_2 P_2)}{1 + T_h(a_1 P_1 + a_2 P_2)} - mC - h\right), \qquad (3)$$

where P_i are the densities of the two prey species (P_1 is the primary and P_2 is the secondary prey that is the victim of apparent competition), K_i are the corresponding carrying capacities, r_i are the intrinsic growth rates, C is the predator density, a_i are the predator foraging efficiencies on the respective prey species, T_h is the handling time of prey, b is the conversion factor of prey to predator density, m is the natural mortality constant of the predator, and h is an additional mortality imposed on the predator from management. We used a type 2 functional response adjusted to include the handling time for both prey (McLellan et al. 2010).

In the system of ODEs (eqq. [1]–[3]), the densities change in response to the current state of the system. However, predator populations often exhibit time lags of their response to changes in prey populations, in part because of spatial heterogeneity in resources or behavioral changes in foraging patterns (Mech 1977; Krebs et al. 1995; Keeling et al. 2000). Therefore, when simulating predator time lags, we replaced equation (3) with equation (4) so that the rate of change in predator density is a function of the prey densities T_d units of time earlier:

$$\frac{dC(t)}{dt} = C(t)\left(\frac{b[a_1 P_1(t - T_d) + a_2 P_2(t - T_d)]}{1 + T_h[a_1 P_1(t - T_d) + a_2 P_2(t - T_d)]} - mC(t) - h\right). \qquad (4)$$

Social organization within prey or predator populations was not accounted for, yet social organization is important in wolf-caribou systems. Wolves usually hunt as a pack, but in summer that structure breaks down and varies substantially (Metz et al. 2011). Because it would be more complicated to estimate a_i and T_h for wolves, we initially parameterized the model for a simple system involving an asocial predator, cougar, and white-tailed deer as the primary prey, with caribou as the secondary prey. Since handling times of cougars at ungulate kills are influenced by factors other than prey mass (Elbroch et al. 2014), we used the same T_h for deer and caribou despite some difference in weights. However, we varied key parameters, including the predator's foraging efficiency and the carrying capacity of the prey, so the theory's predictions could apply beyond cougar-deer systems, at least qualitatively, including moose, wolves, and potentially other taxa.

Parameter Values

Parameter values for the simulations were estimated using a combination of field data from our system and information from the literature. However, uncertainty among parameter estimates varied greatly; some parameters were estimated using large data sets and mechanistic models (e.g., r_i), whereas others were estimated from few studies (e.g., a_i) or approximated (K_1, m). Therefore, a combination of point estimates and an uncertainty analysis based on sampling parameters from lognormal distributions were used to model the predictions. Point estimates were used to conduct sensitivity analyses and to illustrate specific examples of equilibria and time series, but lognormal sampling was used to determine how robust the conclusions were in the face of uncertainty (details are provided below).

Intrinsic growth rates (r_i) for deer and caribou were obtained from Hennemann (1983) and Heard (1990), respectively. Hennemann specified r for deer as 0.48 but also presented a relationship indicating that larger deer that live at the northern limit of their range have lower intrinsic growth, so we used 0.39. The conversion factor of prey to predators, b, was estimated by dividing the average number of cougar offspring per adult per year by the number of deer eaten per year. Assuming predator satiation, T_h was estimated as the inverse of the number of deer eaten per year per cougar (approximately 30; Bird et al. 2010; Knopff et al. 2010).

Fryxell et al. (2007) estimated a for lions (*Panthera leo*) by taking the product of their velocity, search buffer, and attack success, resulting in a value with the unit square kilometer per time. We adopted a similar approach using cougar data from Bird et al. (2010), which were collected in our study area. The mean distance covered per day was approximately 3.5 km, and we assumed a search buffer of 0.2 km (half of what Fryxell et al. [2007] assumed for lions in the much more open Serengeti). Caribou are more vulnerable to predation than other cervids (Haber 1977), so we used an attack success of 0.1 for deer and 0.25 for caribou. We also used an annual spatial overlap between predators and prey of 0.98 for deer and 0.52 for caribou (Bird et al. 2010). By taking the product of these values, we obtained $a_1 = 25$ km^2/year for deer and $a_2 = 33$ km^2/year for caribou. Yet, to address the high uncertainty of parameters that comprise a_i and to make the model applicable to predators beyond cougars, we varied a_2 from 22 to 42 km^2/year. The carrying capacity of caribou (K_2) was based on the number of caribou per area of old forest when caribou populations were stable to increasing in the early 1990s (McNay et al. 2006). Deer carrying capacity (K_1) was estimated by converting the carrying capacity of moose (1.58/km^2; Serrouya et al. 2011) to 1.0/km^2 for deer. This conversion was based on pellet transects indicating a density of approximately one-tenth the abundance of deer compared with moose, when deer were roughly one-sixth as abundant relative to their peak value in 1997 (Serrouya 2013). We did not have data to directly estimate the mortality parameter, m, but we assumed that all three species can coexist at equilibrium and therefore chose a default value of 30/year, which is in a region of parameter space where coexistence is possible (see "Parameter Uncertainty" below). In summary, the baseline parameters used for the model were $r_1 = 0.39$/year, $r_2 = 0.25$/year, $T_h = 0.035$ years, $K_1 = 1.0$/km^2, $K_2 = 0.4$/km^2, $m = 30$/year, $h = 0$/year, $b = 0.032$, $a_1 = 25$ km^2/year, and $a_2 = 33$ km^2/year.

Scenarios and Simulations

Before modeling different scenarios, we explored how the equilibrium densities of all three species depended on the carrying capacity of the primary prey, with all other parameters held at their default values. Subsequently, the model was used to address five questions relating to the transient population dynamics of the victim of apparent competition, the secondary prey. Specifically, we wanted to know how secondary prey were affected by (1) the magnitude of the reduction in primary prey (0%–90%); (2) the relative carrying capacities (K) of primary to secondary prey ($K_1 =$ 0–2/km^2, with K_2 held constant); (3) time lags of the predator's numerical response (T_d; 0–3 years); (4) management of the predator (h; 0%–85% reduction/year); and (5) a gradual reduction in the primary prey (i.e., through hunting; range: >0–20 years), as opposed to a sudden decline (i.e., a stochastic weather event). For all scenarios, we first ran the model for $t_1 = 1{,}000$ years, a time span that was sufficient to let populations reach a steady state (but see cases of extinction below).

To address questions 1–4, we reduced the primary prey abundance instantaneously by 0%–90%. This reduction was done by using the population densities at $t = 1{,}000$ but replacing the equilibrium density of P_1 with the reduced density of P_1. The range, 0%–90% of prey reductions, included the 82% reduction (95% confidence interval: 71%–90%) estimated by Serrouya et al. (2011) that would reflect ungulate abundance prior to widespread forest harvesting. The estimate was based on a model that relates habitat quality to population abundance (sensu Boyce and McDonald 1999). Serrouya et al. (2011) postulated that this historic density of early seral ungulates (moose and deer) would be more conducive to caribou persistence because caribou were previously much more abundant prior to the expansion of moose and deer into caribou habitat (Seip 1992).

Following this perturbation, all simulations showed a transient oscillation where prey and predators first declined and then increased in abundance beyond their equilibrium values before returning to the equilibrium. We did not consider the portion of the transient phase beyond the decline in all three species because there is little reason to believe that temperate systems are equilibrium based and will always return to prior values following a perturbation (see "Discussion"). Thus, we focused on the transient dynamics of the model and recorded the first local minimum value of the secondary prey $P_2^{\min}$ following the reduction in the primary prey. As the primary response metric for all analyses, we used the percent change of the secondary prey from its equilibrium value, P_2^*:

$$100(P_2^{\min} - P_2^*)/P_2^*. \tag{5}$$

To address the fifth question, how secondary prey are affected by a gradual reduction in the primary prey, we repeated the above process but with one modification. We simulated an elevated death rate by subtracting a function $G(t)$ from the right-hand side of equation (1). Between times t_1 and $t_1 + n$, $G(t)$ was equal to a positive constant G (determined as described below); for all other time points, $G(t)$ was equal to 0. For a given n, we chose the magnitude of G such that the density of P_1 at time $t_1 + n$ was at a certain proportion of the prereduction (equilibrium) density. In other words, G was the hunting rate necessary to achieve the management target for P_1 after exactly n years. This two-point boundary value problem with unknown parameter G was solved using the shooting method (Heath 2002). The model was implemented in R (ver. 3.0.2; R Core Team 2012), and the PBSddesolve package (Schnute et al. 2008) was used to solve the delay differential equations (see supplementary R code, available online).[1]

Parameter Uncertainty

We used two approaches to characterize how uncertainty affected model predictions. First, we conducted a sensitivity analysis for each parameter by varying parameter values by ±5%, ±10%, and ±15% while holding others constant and determining how this variation affected the response metric (eq. [5]). Second, we varied all parameters simultaneously by drawing the value of each parameter independently from a lognormal distribution ($n = 1{,}000$ iterations for each scenario) because other studies have shown that the magnitude and distribution of predictions can vary substantially when uncertainty is incorporated (Elderd et al. 2006). Elderd et al. (2006) used a Bayesian framework to estimate parameter uncertainty, but we had little information with which to consistently estimate uncertainty for these parameters. Therefore, we assigned a standard deviation on the logarithmic scale of log(1.1) for some parameters (r_i, K_2, b, T_h) and log(1.2) for less certain parameters (K_1, m, a_i). We address implications of these assumptions in "Discussion." A standard deviation of log(1.2) means there is 67% certainty that the parameter value falls within 20% of the mean. If the parameter combinations from the parameter uncertainty analysis resulted in the extinction (density of $<0.001/\text{km}^2$) of any species prior to the reduction in the primary prey (at $t < 1{,}000$), additional parameter combinations were sampled until all 1,000 iterations were successfully completed.

Field Evaluations of the Theoretical Predictions

Both case studies occurred in the same area contained within a 6,500-km^2 rain forest ecosystem in the Columbia Mountains of British Columbia, Canada (51°27′N, 118°30′W). Mountain peaks exceed 3,000 m asl, and valley bottoms range from 450 to 600 m. Annual precipitation was 200 cm, with most falling as snow. The vegetation is described in Serrouya et al. (2011). The study area contained 3 of 18 identified caribou subpopulations residing in southern British Columbia and northern Idaho, United States (i.e., Columbia North, Columbia South, and Frisby-Boulder; Wittmer et al. 2005*a*). In May 2014, these subpopulations were listed as endangered by the Committee on the Status of Endangered Wildlife in Canada.

We compared the model's predictions to a case where increasing deer populations declined suddenly following an extreme snow event in 1997. Deer and cougar trend data were based on catch-per-unit-effort (CPUE) harvest indexes. For deer, the index was the percentage of hunters successfully killing a deer, based on hunter survey data. Two independent indexes of cougar abundance were used, one based on compulsory reporting of hunted animals and the other based on nonhunting kills from conservation officers. CPUE indexes are known to have biases (Peacock and Garshelis 2006) and should be validated. However, biases most often occur when humans expand the area being exploited, so a higher CPUE can reflect increased kills but not an increasing animal population (Peacock and Garshelis 2006). In our case, we focused on population decline, so there is less likelihood a bias would occur. The two independent cougar indexes matched with a correlation of $r_{\text{pearson}} = 0.85$, suggesting reliability of the trend. Ungulate CPUE metrics have been validated with empirical population estimates in our region, particularly for moose (Serrouya et al. 2011). Population estimates for the three caribou populations were based on census data updated from Wittmer et al. (2005*a*). However, we combined estimates of the three distinct populations into one because this allowed sample sizes to be large enough to apply mark-resight correction, and rates of change from the 1997–2003 period were similar among the three subpopulations (Wittmer et al. 2005*a*). We superimposed model predictions on the empirical data by setting the model output to the mean value of each species' index for the 3 years preceding the reduction in the primary prey. This calibration was needed because most of the population trends were based on indexes of abundance rather than actual abundance. Finally, we compared the rate of cougar predation on caribou before and after the deer crash using data from radio-collared caribou where mortalities were investigated in the field (Wittmer et al. 2005*b*) and accounted for the number of caribou monitored over time.

We also compared model predictions to a second case study where a gradual decline in moose was initiated as a management experiment in 2003. Moose abundance was estimated using stratified-random block surveys (Serrouya et al. 2011), whereas wolves were enumerated using a complete census (Serrouya 2013). Caribou were estimated as described above except that caribou numbers were analyzed separately for the three subpopulations because after 2003 the patterns of population change were unequal (Serrouya 2013). However, analyzing subpopulations separately meant that it was not possible to present confidence intervals due to reduced sample size, but sightability is >90% when the snowpack exceeds 300 cm (Flaa and

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[1] Code that appears in *The American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.

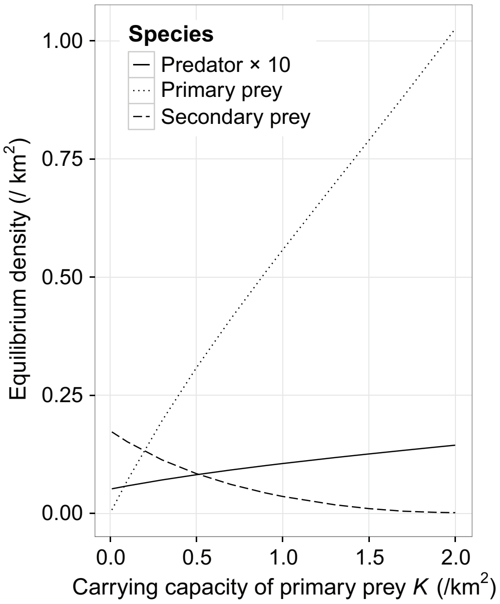

Figure 1: Equilibrium densities for all three species as a function of the carrying capacity of the primary prey. All other parameters were held constant. When the carrying capacity of the primary prey is equal to the fixed value of the secondary prey (0.4/km^2), the primary prey have a higher equilibrium density.

McLellan 1999; Wittmer et al. 2005*a*), so censuses were conducted only under these conditions. For this case study, we did not superimpose predictions because the model was parameterized for the deer-cougar-caribou system. This decision was made given the difficulty of estimating important biological parameters (e.g., *a*) for wolf packs that vary greatly in their cohesion (and hence search rate) depending on season and social dynamics (Metz et al. 2011; discussed above). Therefore, this case study primarily served as a qualitative contrast to the first. Data from both case studies are available in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.6cj48 (Serrouya et al. 2015).

Results

As expected under apparent competition, increasing the carrying capacity of the primary prey resulted in a lower equilibrium density of the secondary prey (fig. 1). When the carrying capacity of the primary prey (K_1) was equal to the estimated carrying capacity of the secondary prey (K_2; 0.4/km^2) and all other parameters were at their default values, the primary prey had a higher equilibrium density than the secondary prey (fig. 1).

An instantaneous reduction in the primary prey resulted in an initial decline in the secondary prey and the predator followed by an oscillation of all three species back to their equilibrium values (fig. 2*A*). The oscillations lasted about one phase (i.e., they were underdamped). In the example shown, an 82% crash in the primary prey combined with a 2-year lag of the predator response resulted in a reduction in the secondary prey species by 18% (fig. 2*A*).

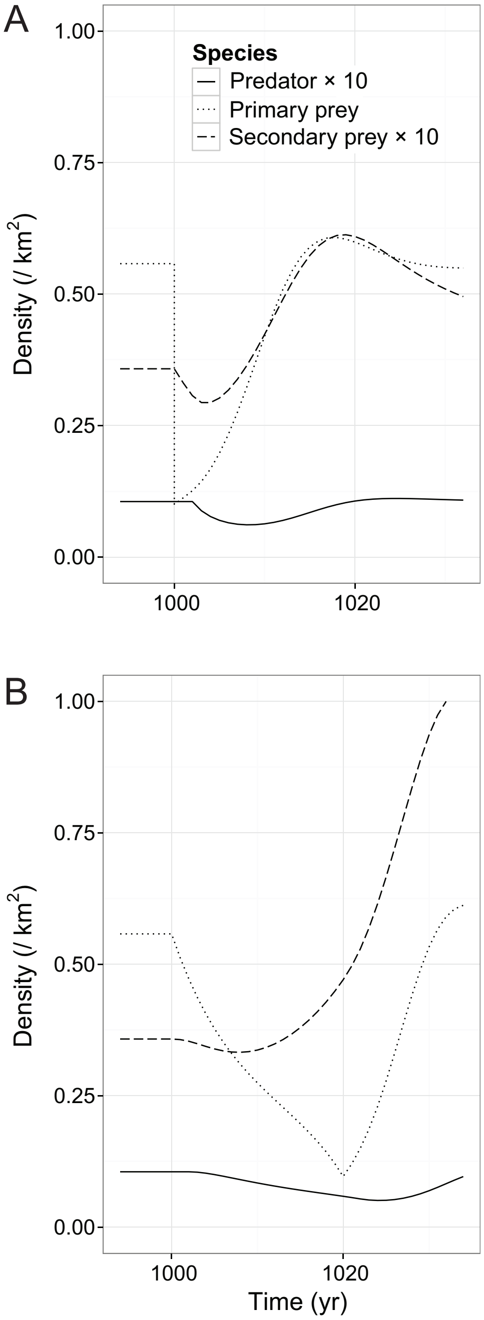

Figure 2: Example time series of the model simulation with 82% reduction in the primary prey and a predator lag of 2 years. The change in the secondary prey's density from its equilibrium value represents a drop of 18.0% when the primary prey is reduced instantaneously (*A*) and 7.0% when the primary prey is reduced over 20 years (*B*).

The magnitude of reduction in the secondary prey increased with an increasing carrying capacity of the primary prey (fig. 3*A*) and an increasing time lag of the predator's numerical response (fig. 3*B*), but it declined with the rate of predator control (fig. 3*C*). In all cases, as the magnitude of the (instantaneous) decline in the primary prey increased, so did the magnitude of decline in the secondary prey (fig. 3). For the range of parameters considered, the most severe reductions occurred when the primary prey's carrying capacity approached 2.0/km^2 or when the time lag of the predator exceeded 2 years, and in these cases the reductions in the secondary prey ranged from 20% to 25% (fig. 3). As the predator's foraging efficiency on the secondary prey increased, so did the magnitude of decline in the secondary prey (fig. 3*D*). Uncertainties corresponding to the mean values (i.e., standard deviations across the lognormal parameter sampling) shown in figure 3 are presented in figure A1 (figs. A1–A5 are available online).

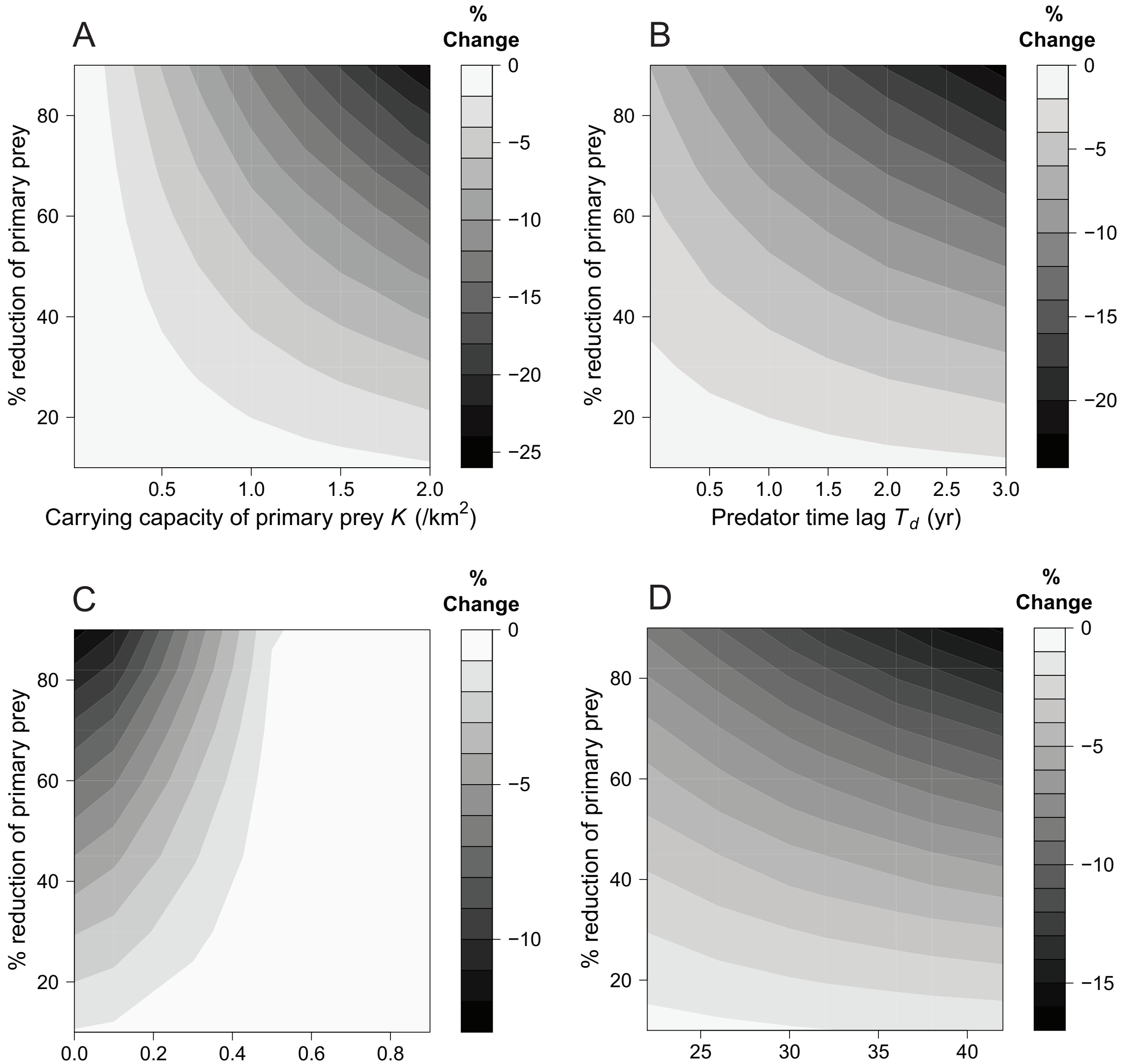

Figure 3: Change in abundance of the secondary prey (as a percentage of its equilibrium value P_2^*: $100 \times (P_2^{\min} - P_2^*)/P_2^*$) as a function of the primary prey's reduction (%) and the carrying capacity of the primary prey (*A*), the time lag of the predator's numerical response (*B*), the rate of predator control (*C*), and the foraging efficiency of the predator (*D*). Results are mean values of 1,000 iterations of stochastic parameter sampling from equations (1)–(3) (corresponding standard deviations are presented in fig. A1, available online), except point values are used for values from the *X*- and *Y*-axes.

Uncertainty and Sensitivity

Results from the sensitivity analysis showed that the response metric (eq. [5]) was most affected by the magnitude of reduction in primary prey (table 1). The parameters described in equations (1)–(4) were most sensitive to changes in the predator's foraging efficiency on the secondary prey (a_2) and the carrying capacity of the primary prey (K_1).

The parameter uncertainty analysis revealed that there was considerable uncertainty in the model output (eq. [5]) as a result of varying all nine parameters simultaneously (fig. 4), but under no parameter combinations did the secondary prey increase directly after the perturbation. Thus, the qualitative patterns of the model were consistent, whether the simulations were based on point estimates (fig. A2) or on the parameter uncertainty analysis (fig. 4). Instantaneously reducing the primary prey produced greater losses to the secondary prey, while spreading out the reduction in primary prey mitigated losses to the secondary prey (figs. 2*B*, 4). Losses to the secondary prey were greater if the time lag of the predators' response increased (fig. 4).

The uncertainty analysis further revealed that many parameter combinations resulted in extinction. For example, 27,000 ODE simulations were required to produce figure 4 (3 time lags × 9 time scenarios × 1,000 iterations), but an extra 11,084 were required to achieve 27,000 successful simulations. For the 11,084 simulations that did not run successfully, it was because the secondary prey became extinct before an equilibrium was reached (i.e., before the reduction in the primary prey at $t = 1{,}000$). None of the other species ever became extinct. In addition to the extinctions, 588 simulations failed because of numerical problems, with most (99%) occurring when the gradual decline in P_1 exceeded 10 years because the hunting rate was too high.

Field Evaluations of the Theoretical Predictions

Following the deep-snow event in 1997, the deer CPUE (primary prey) during the next fall's hunting season was reduced by 78% (fig. 5), indexing a substantial decline. Cougar populations began to decline 1–2 years thereafter. In

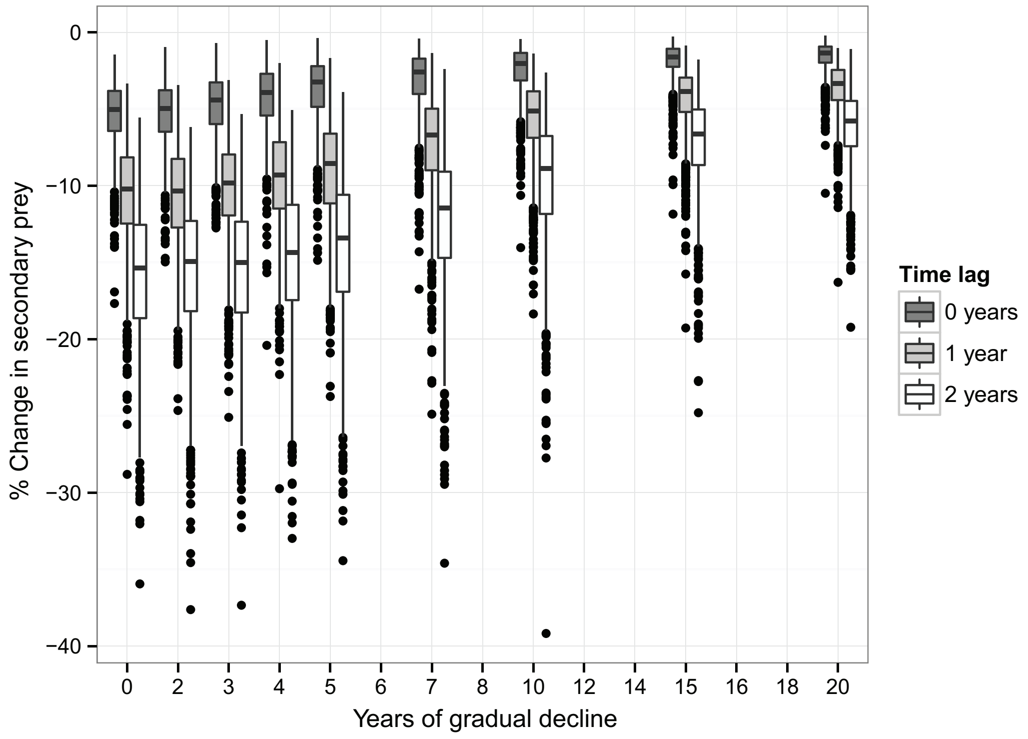

Figure 4: Change in abundance of the secondary prey (as a percentage of its equilibrium value P_2^*: $100 \times (P_2^{\min} - P_2^*)/P_2^*$) as a function of how spread out the decline is for the primary prey (primary prey are reduced by 82% in all cases). Results are stratified by an immediate numerical response of the predator ($T_d = 0$), along with a lag of 1 and 2 years ($T_d = 1$ and $T_d = 2$). The variation shown by the box-and-whisker plots are the result of 1,000 iterations of stochastic sampling of parameters in equations (1)–(4), except the time lag and years of gradual decline are point values.

Table 1: Sensitivity analysis for parameters shown in equations (1)–(4)

Change in parameter	pr[a]	T_h	a_1	a_2	K_1	K_2	b	T_d	r_1	r_2	m
−15%	−20.4	−10.8	−6.8	−18.7	−15.8	−.1	−5.9	−7.8	−11.7	4.0	7.3
−10%	−13.9	−6.8	−4.1	−12.6	−10.5	−.1	−3.4	−5.1	−7.2	4.0	5.4
−5%	−7.1	−3.2	−1.9	−6.4	−5.3	−.1	−1.4	−2.5	−3.4	2.0	2.7
5%	7.8	4.2	1.7	.0	5.6	.1	2.0	3.7	.0	−2.0	−2.8
10%	16.0	7.8	3.0	6.5	11.2	.1	3.7	7.2	3.0	−3.8	−5.7
15%	24.6	10.8	3.8	12.9	16.7	.2	5.0	10.5	5.6	−5.6	−8.5

Note: Values represent the percent change in the response metric (eq. [5]) as the parameter is changed by ±5%, ±10%, and ±15%.

[a] The parameter pr is the proportional reduction in the primary prey (in one time step), set at 0.82 and shown here for contrast because it is an extrinsic parameter, not one of the biological parameters in equations (1)–(4).

1998, there was a peak in cougars killed by conservation officers (i.e., nonhunting kills; fig. 5), likely reflecting hungry cougars searching more broadly and having more human conflicts near settled areas. From 1997 to 2002, the caribou populations (secondary prey) in the study area declined by approximately 40%, a more pronounced decline than the approximately 17% predicted by our model over a similar timescale (fig. 5, based on point values of the parameters; model predictions based on the parameter uncertainty analysis, which covers most of the *Y*-axis, are shown in fig. A3). Prior to the deep-snow event, the caribou population was approximately stable with an annual finite rate of change (λ) of 0.99, but λ after the deep-snow event was 0.90 (λ of 1 means no change). From the time radio collaring began in 1992 to 1997, 129.1 caribou-years of telemetry data were collected. During this period, one collared caribou was killed by a cougar—in 1996, when the cougar population was near its peak. In the 2 years following the deer crash, based on 65.3 collar-years of data, three collared caribou were killed by cougars. Increased predation by cougars on caribou following the collapse of deer was consistent with the higher rate of decline for caribou predicted by the model.

In our second case study, the more gradual reduction in moose resulted in a decline in wolf abundance (fig. 6), but the resulting caribou population trends depended on their initial population size. The two smaller caribou populations numbered <50 and 20 at the beginning of the moose reduction and continued to decline. In contrast, the larger caribou population appeared to stabilize and may have increased. In the control region where moose were not reduced, both large and small caribou populations continued to decline (figs. A4, A5; see Serrouya 2013 for details).

Discussion

Our goal was to use predator-prey theory to address five questions focused on reducing apparent competition for secondary prey, with a specific emphasis on removing primary prey. The scenarios represented some of the key factors linked to the apparent competition mechanism affecting many species (DeCesare et al. 2010), including woodland caribou in North America (Schaefer 2003; Wittmer et al. 2005*b*; Courtois et al. 2007; Latham et al. 2011). By varying the carrying capacity of the primary prey, we represented either climate change or forest harvesting, both of which influence the abundance and distribution of moose and deer (Rempel et al. 1997; Dawe 2011). Increasing the predator's mortality rate reflected the option of conducting predator control. Finally, a sudden reduction in primary prey could represent a stochastic weather event or a particularly effective management action like a biocontrol agent (Fagan et al. 2002), whereas gradually reducing the primary prey was more likely to reflect management such as liberalized harvest (Steenweg 2011; Serrouya et al. 2012).

Reducing primary prey to counteract apparent competition is increasingly suggested as a strategy to recover a secondary prey species that is at risk of extinction (Roemer et al. 2002; James et al. 2004; Weclaw and Hudson 2004; Steenweg 2011; Wittmer et al. 2013). Yet our analysis highlights important risks that may not have been anticipated when this recovery option was suggested. Our results predict higher losses to the secondary prey when there are more primary prey and a more rapid reduction in those primary prey. Predictions suggest that a substantial reduction in primary prey (>80%) would produce a mean reduction in secondary prey by 10%–25%, depending on the primary prey's carrying capacity, the predator's time lag, and its efficiency at consuming a given prey. Given the uncertainty in parameter values, more severe reductions of close to 40% are possible (fig. 4). In biological terms, the more deer in the system, the more predators can be sustained and switch to caribou if deer are reduced. The apparent switching of mortality agents on caribou—that is, increased cougar predation observed during and following the deer collapse—supports this mechanism. However, the model suggests that the magnitude of the caribou loss can be reduced if predators are removed following periods of sudden collapses in primary prey (fig. 3*C*). This approach has also been proposed by Norbury (2001) for conserving

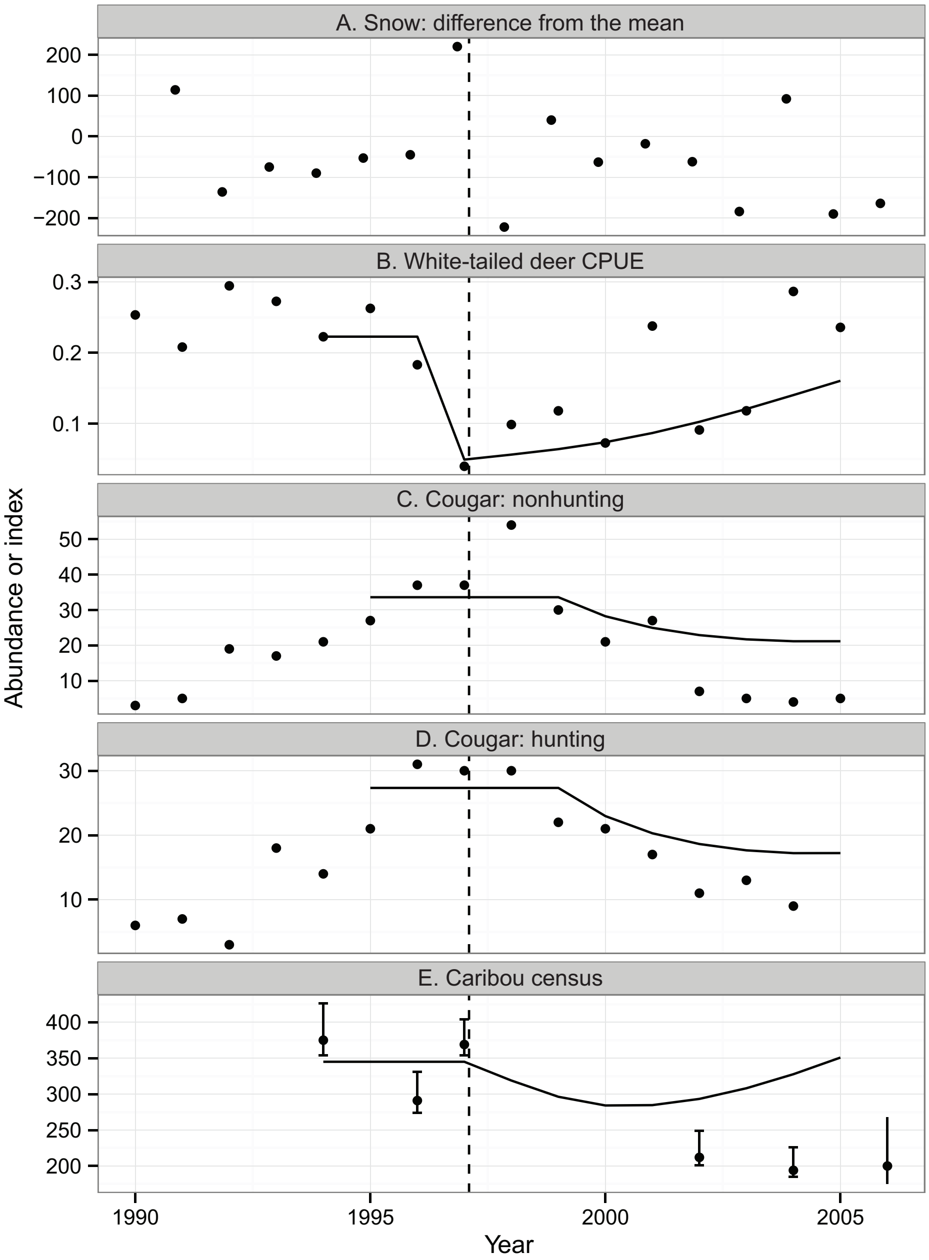

Figure 5: Case study 1: instantaneous reduction in primary prey. *A*, Snow fall (cm) represents the difference from the mean value (mean = 396 cm, $n = 100$ years) in Revelstoke, British Columbia. *B*, Deer represent catch-per-unit-effort (CPUE) harvest data for management units within and adjacent to the study area (*B*). *C*, *D*, Two independent indexes of cougar abundance (hunter and conservation officer kills; $r = 0.85$). *E*, Caribou abundance from winter censuses for subpopulations in the Columbia Mountains, British Columbia, Canada (Wittmer et al. 2005*b*). The year 1997 was an extreme snowfall year (vertical line) that initiated some major changes in the ecosystem. Model predictions are shown as solid lines, and the uncertainty of these predictions are shown in figure A3 (available online). Note the different scales on the *Y*-axes.

native skinks (*Oligosoma* sp.) in New Zealand following sudden declines in rabbit (*Oryctolagus cuniculus*) abundance and by Collins et al. (2009) to conserve island foxes (*Urocyon littoralis*) in California. Short-term predator control may be even more effective when we consider that time lags of the predator's response to a lower prey density greatly increased the modeled rate of predation on the secondary prey (fig. 3*B*). Predator time lags of 1–2 years or longer have

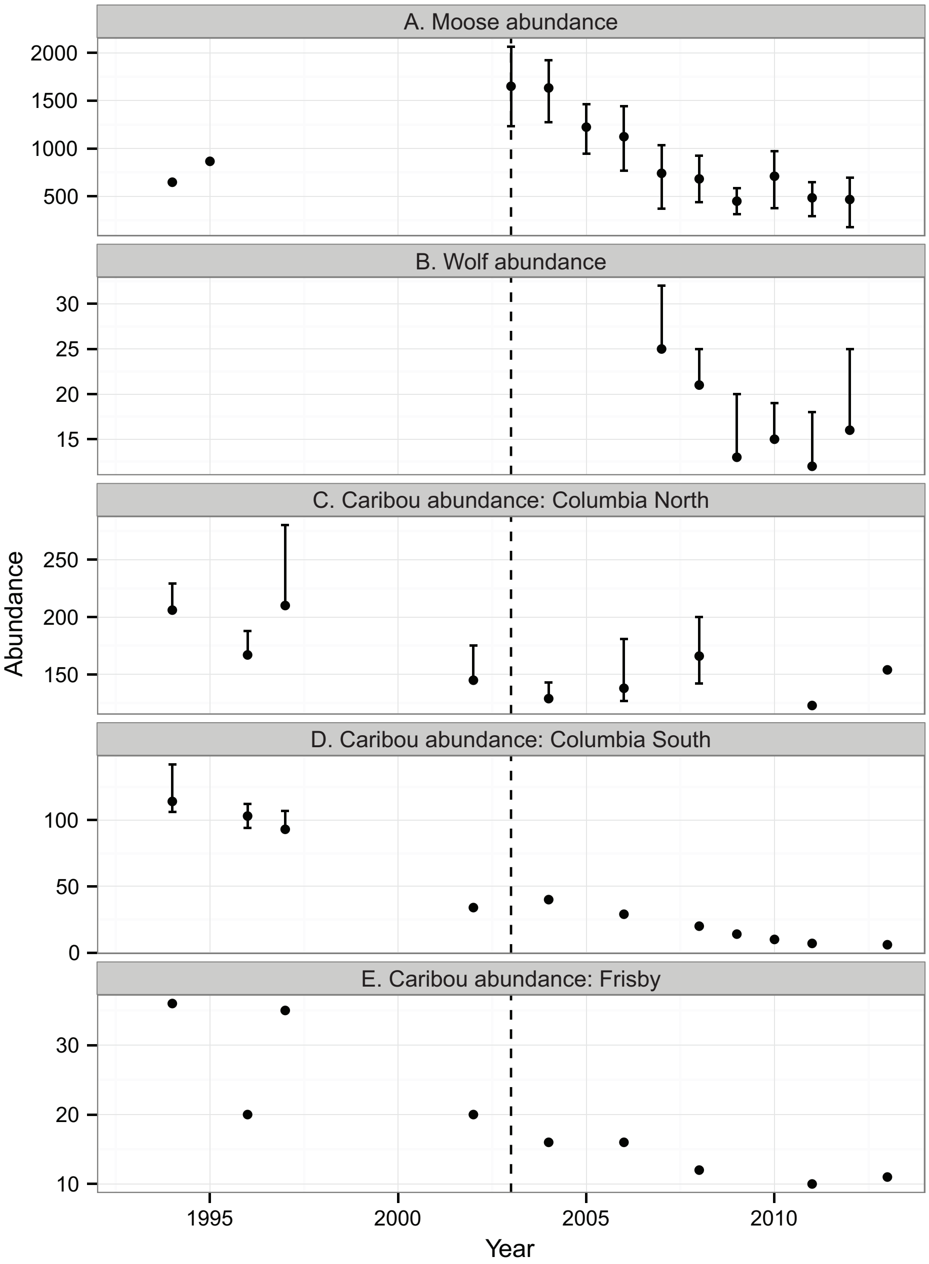

Figure 6: Case study 2: gradual reduction in primary prey. A moose reduction experiment began in 2003 (vertical line), with the abundance of moose (*A*), wolves (minimum and maximum estimates are shown by point and error bars, respectively; *B*), and three caribou subpopulations (*C*–*E*) monitored as responses. The study took place in the Columbia Mountains, British Columbia, Canada. Note the different scales on the *Y*-axes.

been observed in many terrestrial systems (Mech 1977; Krebs et al. 1995).

Two other modeling studies involving predator-mediated apparent competition (Courchamp et al. 2003; Zhang et al. 2006) suggested caution in reducing primary prey in the absence of predator reductions, and our simulations matched their predictions. Courchamp et al. (2003) used ODEs to model the reduction in introduced feral pigs (*Sus scrofa*) and found that predation by golden eagles (*Aquila chrysaetos*) on native island foxes increased unless eagles were reduced concurrently. By using analytical stability and equilibrium analyses, Zhang et al. (2006) examined the parameter space where two prey and one predator could coexist. They demonstrated that for secondary prey to persist in a situation where novel prey are invading, secondary prey must have a high intrinsic growth rate or suitable antipredator strategies. The relatively high rate of caribou extinction in our simulations and the empirical evidence of widespread caribou declines (Vors and Boyce 2009) support Zhang et al.'s theoretical work. In contrast to this equilibrium analysis, we focus on transient effects. In particular, the additional questions we addressed dealt with the time lag of the predator's numerical response and whether spreading out the primary prey's decline over a number of years would benefit or harm the victim of apparent competition. Gradually reducing the primary prey was beneficial and mitigated losses from 18% to 7% if spread over 20 years. Generalizing these results would require consideration of the generation times of the organisms under study. Nonetheless, of the 18 endangered caribou subpopulations remaining in 2004, only one exceeded 500 in number, most were less than 100, and two have recently become extinct. With such small numbers, any further loss increases extinction risk (Shaffer 1981; Wittmer et al. 2010). Therefore, a concurrent predator reduction (fig. 3*C*) would be of greater value than relying solely on primary prey reduction, even if the prey reduction is spread out over a number of years. This is an important result for agencies that are considering a broadscale manipulation of the predator-prey system to try and recover endangered caribou or other species at risk from apparent competition (DeCesare et al. 2010; Wittmer et al. 2013).

In addition to exploring theoretical predictions, a major aim of our study was to compare some of the predictions with empirical data in a broadscale setting (Levins 1966), a task that is difficult to accomplish in field ecology whether the experiment is observational (deer-cougar) or experimental (moose-wolf). A key factor we attempted with the field component of this study was to contrast the effect of a gradual versus a pulsed removal of primary prey. We found that the predictions of the model were qualitatively supported by the field studies, with higher losses to caribou observed following the pulsed removal of deer, whereas the gradual removal of moose resulted in stability for at least the larger caribou subpopulation. An important conclusion from the deer-cougar case study was that the model underestimates the magnitude of reduction for the secondary prey. For an 80%–85% reduction in primary prey, the model predicted a 13%–18% reduction in caribou depending on whether we assumed a 1- or 2-year lag of the predator's numerical response. In comparison, the caribou population in the study area declined by >40% following the collapse of deer populations over a similar time period (approximately 10 years). Caribou are affected by more than just deer-cougar dynamics because they are also consumed by bears and wolves (Wittmer et al. 2005*a*). These mortality sources are likely additive because woodland caribou are far below their forage-based carrying capacity, so that density-dependent changes in vital rates are unlikely to occur (Fowler 1981; Wittmer et al. 2005*b*). Moose populations doubled from 1994 to 2003 (Serrouya et al. 2011), likely resulting in increased wolf abundance during the time period that coincided with the deer collapse and subsequent cougar decline. These important community dynamics were not captured with our simple model. Allee effects have also been documented with these same caribou populations (Wittmer et al. 2005*b*) and in other systems where apparent competition occurs (Pech et al. 1995), but this mechanism was not included in the ODEs. Finally, demographic and environmental stochasticity were not accounted for but have negatively affected woodland caribou (Hebblewhite et al. 2010). A combination of these factors probably explains why the model underestimated the magnitude of decline in real caribou populations.

In the second field study, moose were intentionally reduced to an ecologically determined target that was based on estimating the abundance of moose prior to broadscale habitat modification by humans (Serrouya et al. 2011). This experiment was designed to test the hypothesis that wolves could be controlled by reducing their primary prey. This experiment benefited from having a reference area where moose populations were not reduced, confirming that the experimental management action had the intended effect of reducing moose in the treatment area (Serrouya 2013). The approach of reducing primary prey presents a more ultimate solution to the apparent competition problem because it addresses trophic levels that are closer to the root cause (habitat change leading to more noncaribou ungulates) rather than focusing solely on predator control, which only addresses the proximate cause. In this case, the model predicted a more modest reduction in caribou, especially if the decline was spread out over 10 years. By spreading out the decline in moose, the largest caribou population stabilized rather than declined, as in the previous case study. In support of this numerical pattern, wolf diets as recorded by scat analyses and kill-site investigations did not reflect a shift from moose to caribou for the duration of the experiment (Serrouya 2013). The two very small caribou populations (<50) were apparently subjected to Allee effects (Wittmer et al. 2005*b*; McLellan et al. 2010), so at such small numbers it is not surprising that they continued to decline (Hebblewhite et al. 2010).

The parameter uncertainty analysis revealed two important patterns. First, before any equilibria were established, roughly one-third of the simulations resulted in the extinction of the secondary prey despite relatively modest variation about each parameter. This result underscores the narrow parameter space where caribou and other secondary prey that have low fecundity can survive (Vors and Boyce 2009; Sinclair et al. 1998). Second, the general patterns from the uncertainty analysis and the simulations based on point estimates of parameters were similar. This concordance suggests that had we used a broader range of uncertainty estimates, the mean values—and hence general predictions of the theory—would still hold.

Our approach may be challenged because we focused only on the declining portion of the transient phase, not the subsequent oscillation including population increase with the eventual return to equilibrium. However, any return to equilibrium is predicated on the concept of "balanced" equilibrium systems, which ecologists have questioned repeatedly since Charles Elton first pointed out in the 1930s that this view is simplistic (Elton 1930; Andrewartha and Birch 1954; Connell and Sousa 1983; Chesson and Case 1986; Connell et al. 1997). If systems are dominated by changing environments with frequent destabilizing events, then focusing on the initial transient phase becomes increasingly appropriate. Ultimately, reducing primary prey is expected to increase the abundance of secondary prey, as figure 1 illustrates. However, this conclusion essentially ignores any transient dynamics and is likely an oversimplification. If population sizes are reduced during the transient phase, demographic stochasticity and Allee effects become more important (Wittmer et al. 2005*b*; Hebblewhite et al. 2010) and will contribute to threatening species affected by apparent competition.

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The woodland caribou (*Rangifer tarandus caribou*) is now suffering from apparent competition. Photograph by Heiko U. Wittmer.