



# Conservation Strategies for Species Affected by Apparent Competition

HEIKO U. WITTMER,\* ROBERT SERROUYA,† L. MARK ELBROCH,‡ AND ANDREW J. MARSHALL§

\*School of Biological Sciences, Victoria University of Wellington, P.O. Box 600, Wellington 6140, New Zealand  
email heiko.wittmer@vuw.ac.nz

†Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada

‡Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616, U.S.A.

§Department of Anthropology, University of California, Davis, CA 95616, U.S.A.

**Abstract:** *Apparent competition is an indirect interaction between 2 or more prey species through a shared predator, and it is increasingly recognized as a mechanism of the decline and extinction of many species. Through case studies, we evaluated the effectiveness of 4 management strategies for species affected by apparent competition: predator control, reduction in the abundances of alternate prey, simultaneous control of predators and alternate prey, and no active management of predators or alternate prey. Solely reducing predator abundances rapidly increased abundances of alternate and rare prey, but observed increases are likely short-lived due to fast increases in predator abundance following the cessation of control efforts. Substantial reductions of an abundant alternate prey resulted in increased predation on endangered huemul (*Hippocamelus bisulcus*) deer in Chilean Patagonia, which highlights potential risks associated with solely reducing alternate prey species. Simultaneous removal of predators and alternate prey increased survival of island foxes (*Urocyon littoralis*) in California (U.S.A.) above a threshold required for population recovery. In the absence of active management, populations of rare woodland caribou (*Rangifer tarandus caribou*) continued to decline in British Columbia, Canada. On the basis of the cases we examined, we suggest the simultaneous control of predators and alternate prey is the management strategy most likely to increase abundances and probabilities of persistence of rare prey over the long term. Knowing the mechanisms driving changes in species' abundances before implementing any management intervention is critical. We suggest scientists can best contribute to the conservation of species affected by apparent competition by clearly communicating the biological and demographic forces at play to policy makers responsible for the implementation of proposed management actions.*

**Keywords:** caribou, *Hippocamelus bisulcus*, huemul, island fox, predator control, predator-prey interactions, *Rangifer tarandus*, *Urocyon littoralis*

Estrategias de Conservación para Especies Afectadas por Competencia Aparente

**Resumen:** *La competencia aparente es una interacción indirecta entre 2 o más especies depredadas por un depredador compartido; y cada vez es más reconocida como un mecanismo en la disminución y extinción de muchas especies. Mediante estudios de caso, evaluamos la efectividad de 4 estrategias de manejo para especies afectadas por la competencia aparente: el control de depredador, la reducción en la abundancia de presas alternativas, el control simultáneo de depredadores y presas alternativas, y ningún manejo activo de depredadores o presa alternativa. Con tal sólo reducir la abundancia del depredador, la abundancia de presas alternativas o raras incrementó rápidamente, pero los incrementos observados probablemente sean de corta duración debido al rápido incremento de la abundancia de depredadores una vez que cesa el control. Las reducciones sustanciales de una presa alternativa abundante resultaron en el incremento de la depredación del venado güemul (*Hippocamelus bisulcus*), que está en peligro de extinción, en la Patagonia chilena; lo*

que resalta el riesgo potencial asociado con la sola reducción de especies de presas alternativas. La remoción simultánea de depredadores y presas alternativas incrementó la supervivencia de los zorros isleños (*Urocyon littoralis*) en California (E. U. A.) por encima del umbral requerido para la recuperación de la población. En la ausencia del manejo activo, las poblaciones del caribú de bosque (*Rangifer tarandus caribou*), una especie rara, continuaron su declive en la Columbia Británica, Canadá. Basándonos en los casos examinados, sugerimos que el control simultáneo de depredadores y presas alternativas es la estrategia de manejo con mayores oportunidades para incrementar la abundancia y las probabilidades de la persistencia de presas raras a largo plazo. El conocimiento de los mecanismos que dirigen los cambios en las abundancias de especies antes de implementar cualquier manejo es crítico. Sugerimos que los científicos pueden contribuir de mejor manera a la conservación de las especies afectadas por la competencia aparente al comunicar claramente las fuerzas biológicas y demográficas en juego a los creadores de políticas responsables de la implementación de las acciones de manejo propuestas.

**Palabras Clave:** caribú, ciervo sur andino, control de depredadores, güemul, *Hippocamelus bisulcus*, interacciones depredador - presa, *Rangifer tarandus*, *Urocyon littoralis*, zorro isleño

## Introduction

Apparent competition is defined as an indirect interaction between 2 or more prey species through a shared predator (Holt 1977). Apparent competition has been demonstrated in most vertebrate classes, including amphibians (Pope et al. 2008), reptiles (Norbury 2001), birds (Courchamp et al. 2000), and mammals (Sweitzer et al. 1997), and is implicated in the decline and extinction of many species (reviewed in DeCesare et al. 2010). Similar to exploitative competition, apparent competition is considered a symmetric interaction between 2 prey species because the presence or abundance of each species can be negatively correlated with that of the other. However, when abundances of the 2 prey species differ considerably, their interactions may become asymmetrical. The mechanisms driving this asymmetry vary and may, for example, be related to differences in life history such as fecundity rates or vulnerability to predation between prey species (Roemer et al. 2002). When the interactions are asymmetrical, the more abundant (the primary or alternate) prey is the main determinant of predator abundance, which can lead to the extinction of the rare (or secondary) prey because there is little feedback between the rare prey and predator abundance (Holt & Lawton 1994; Chanton & Bonsall 2000).

Although the mechanisms of apparent competition are well understood (Holt & Lawton 1994), the efficacy of different management strategies to conserve species affected by apparent competition is much less clear. In part this is because numerous mechanisms can alter relative abundances of prey species and thereby influence apparent competition. For example, changes in relative prey abundances have resulted from introductions of non-native species and livestock (Courchamp et al. 2000; Novaro et al. 2000), natural range expansions of native species (Latham et al. 2011), and anthropogenic disturbances, such as logging, to which prey species have different responses (Wittmer et al. 2007; Serrouya

et al. 2011). Because changes in relative prey abundances can result from a number of different mechanisms, it is unlikely that a single management strategy designed to conserve species affected by apparent competition will be effective in all situations.

Regardless of the mechanisms responsible for changes in relative species abundances, some scientists suggest the preservation of species affected by apparent competition may require active management of predators, alternate prey, or both at least temporarily (Lessard et al. 2005; Gibson 2006; Serrouya & Wittmer 2010). Active management of species' abundances, however, is a controversial topic for at least 3 reasons. First, those charged with the conservation of species may be hesitant to manage species' abundances because of increasing public opposition to, for example, active control of native predators (Orians et al. 1997). Second, active management of species' abundances without simultaneously addressing ultimate causes of decline, such as habitat change, may not result in long-term persistence of rare prey (Theberge & Walker 2011). Third, results of several studies show that the removal of predators and alternate prey can have unanticipated negative effects on prey species affected by apparent competition, particularly in systems containing non-native species (reviewed in Bull & Courchamp 2009).

Through case studies, we compared the efficacy of 4 management strategies intended to conserve species affected by apparent competition: predator control, reduction in abundances of alternate prey, simultaneous control of predators and alternate prey, and no active management of either predators or alternate prey. Increasing abundances of alternate prey species to buffer endangered prey affected by apparent competition from predation has also been proposed (Lovari et al. 2009). We did not consider this strategy because current predator-prey theory suggests it will not affect unsustainable rates of predation on the rare prey in the absence of spatial refugia (Holt & Lawton 1994; Messier 1995).

## Predator Control

Predator control has been widely and successfully applied to increase abundances of rare and endangered prey species. For example, a review of the effectiveness of removing predators to increase bird abundances showed that >70% of removal projects resulted in increases in population sizes (Côté & Sutherland 1997). Because of high success rates, predator removal continues to be widely used to protect endangered species where the predator is non-native, particularly on islands (Bull & Courchamp 2009). However, the complete removal of terrestrial predators in mainland systems is nearly impossible to achieve due to immigration (Robinson et al. 2008) or, in the case of native predator species, because both lethal and non-lethal control methods, even to protect an endangered species, have become increasingly controversial (Orians et al. 1997; Roemer & Donlan 2005).

Results of predator-control projects also demonstrate that predator abundances can quickly increase following the cessation of control efforts, and this suggests such interventions, unless applied continuously, do not have sustained long-term benefits for prey species affected by apparent competition. For example, intensive control of wolves (*Canis lupus*) in the Yukon over 4 years resulted in rapid increases in densities of moose (*Alces alces*) and caribou (*Rangifer tarandus*) (moose densities in this system were >20 times higher than those of caribou) (Hayes et al. 2003). During the predator-control period, densities of moose populations increased by approximately 141/1000 km<sup>2</sup> (SD 45) at a mean population growth rate ( $\lambda$ ) of 1.17 (SD 0.03). Simultaneously the low-density caribou population increased by approximately 2.6 individuals/1000 km<sup>2</sup> ( $\lambda = 1.15$ ). Results from a nearby project to control wolves conducted over 7 years, however, showed that wolf densities recovered to preremoval densities of >10/1000 km<sup>2</sup> in approximately 4 years following the cessation of control efforts (Hayes & Harestad 2000).

## Reduction in Abundances of Alternate Prey

Much uncertainty exists regarding the outcomes of solely removing or reducing the abundances of an alternate prey to conserve species affected by apparent competition. For example, predator abundances may respond immediately to the removal of the alternate prey, resulting in a reduction in predation on the rare prey. In contrast, changes in predator abundances may lag behind reductions of alternate prey, and remaining predators may switch to feeding on rare prey, thus exacerbating extinction risks (Messier 1995; Courchamp et al. 2003). Alternatively, prey switching by predators may only result in a temporary loss of rare prey and be outweighed by re-

duction in predator abundance in the long term. Predator responses will almost certainly vary on the basis of their feeding ecology. Generalist and facultative predators are likely buffered against periods of food shortages, whereas specialist and obligate carnivores may be more susceptible to immediate reductions in their prey. Because of uncertainties associated with outcomes of alternate prey reductions, few researchers have considered or tested the effects of the method in the field.

Huemul (*Hippocamelus bisulcus*) is a deer species restricted to Chilean and Argentine Patagonia and considered endangered by the International Union for Conservation of Nature (Jiménez et al. 2008). The current population dynamics of huemul in parts of their range are primarily affected by predation in the form of apparent competition (Corti et al. 2010). The apparent-competition hypothesis was proposed on the basis of high mortality rates of huemul fawns from culpeo foxes (*Lycalopex culpaeus*) and moderate mortality rates of adult huemul from cougars (*Puma concolor*). Across much of Patagonia, both culpeo foxes and cougars feed on abundant alternate prey species that include non-native European hares (*Lepus europaeus*) (Grigera & Rapoport 1983) and domestic sheep (*Ovis aries*) (Novaro et al. 2000).

An opportunity to examine the effectiveness of reducing abundances of alternate prey occurred when Conservación Patagónica, a private conservation organization, removed >30,000 domestic sheep from their property to convert it into the future Patagonia National Park (Conservación Patagónica 2011). Together with 2 protected areas to the south and north, the future Patagonia National Park would support a population of approximately 120 of the estimated 1000 remaining huemul in Chile (Jiménez et al. 2008).

Following the removal of sheep, predation rates on female huemul over 1 year old from cougars increased approximately 5-fold (Wittmer et al. 2012). Concurrent with the removal of sheep, fawn mortalities attributed to culpeo foxes increased 3-fold. The resulting low survival rates of adult female huemul together with already low fawn survival now threaten the viability of huemul in the future Patagonia National Park (Wittmer et al. 2012). These results appear to be consistent with those of previous models that suggest solely reducing abundances of alternate prey is not effective for conserving species affected by apparent competition (Courchamp et al. 2003).

Because the removal of sheep by Conservación Patagónica was ad hoc and did not follow a rigorous experimental design (such as before-after-control-impact [Underwood 1994]), the mechanism underlying the observed reductions in huemul survival remains unknown. Because predator control ceased just before the removal of sheep, it is possible that observed increases in huemul mortality were exacerbated by simultaneous increases in predator abundances independent of the changes in prey

availability (Elbroch & Wittmer 2012a). Also, cougars compensated for the decreased abundance of sheep by preying on guanacos (*Lama guanicoe*). Following sheep removal, guanaco accounted for 88.5% of the biomass killed by cougars in Patagonia National Park (Elbroch & Wittmer 2013). Given that only 2 of 6 cougars whose ranges overlapped with those of huemul were known to kill huemul (Elbroch & Wittmer 2013), it is likely that increased cougar predation rates were stochastic and a consequence of prey preferences of individual cougars rather than prey switching. Such stochastic predation and behavior was reported to have contributed to the decline of small populations of bighorn sheep (*Ovis canadensis*) in Canada (Festa-Bianchet et al. 2006) and California (U.S.A.) (Gibson 2006). Despite uncertainties regarding causal mechanisms, the huemul example suggests that solely reducing abundance of or eradicating an abundant alternate prey species without concurrently controlling predators may not prevent extirpation in some systems. This may apply particularly to systems in which alternate prey species can buffer predators from reductions in abundance of prey or in which predator responses lag behind reductions in prey abundance (Courchamp et al. 2003; Serrouya et al. 2011).

### Predator Control and Reductions in Abundances of Alternate Prey

The island fox (*Urocyon littoralis*), 4 subspecies of which are listed as endangered under the U.S. Endangered Species Act (ESA), is endemic to the Channel Islands off the coast of southern California. Over the past 20,000 years, the species evolved into 6 subspecies, each restricted to a different island (Wayne et al. 1991). Recent declines of the fox population had been attributed to predation from Golden Eagles (*Aquila chrysaetos*), which researchers believed were historically unable to establish permanent populations on the Channel Islands due to insufficient year-around availability of food and possibly competition with Bald Eagles (*Haliaeetus leucocephalus*) (Roemer et al. 2002; Roemer & Donlan 2005). However, Golden Eagles became resident on several islands following the introduction of feral pigs (*Sus scrofa*) and the drastic reduction of Bald Eagles by DDT. Piglets provided eagles with a constant, abundant alternate prey species, which ultimately resulted in increased eagle predation on foxes (Roemer et al. 2002).

Two modeling scenarios were used to develop conservation strategies for island foxes (Roemer et al. 2002; Courchamp et al. 2003). First, Roemer et al. (2002) suggested that in the absence of pigs, the introduction of Golden Eagles to the Channel Islands will fail due to insufficient food availability. However, when pigs are present, Golden Eagles will persist and eventually drive foxes to

extinction (but see Bakker et al. [2009] for an alternative hypothesis). Second, Courchamp et al. (2003) developed models to examine the effects of 3 different management strategies: removal of pigs only, removal of eagles only, and removal of both pigs and eagles. Results from these models suggest that removal of pigs (the alternate prey) will only increase rates of predation on foxes and ultimately result in the foxes' extinction. On the basis of these models, a conservation strategy of removing both pigs and eagles was developed (Courchamp et al. 2003). Because feral pigs are not native to the Channel Islands, pig eradication was met with little opposition. However, because Golden Eagles are federally protected under the Migratory Bird Treaty and Bald and Golden Eagle Protection Acts and because there was considerable public opposition to their eradication, resident Golden Eagles had to be removed from the island via live trapping (Roemer & Donlan 2005; Collins et al. 2009).

The decision to simultaneously remove predators and alternate prey appears to have been effective on the basis of observed outcomes. Although postremoval monitoring is still underway, it appears that survival of island foxes has increased above the threshold required for the subspecies to be designated as recovered by the U.S. Fish and Wildlife Service (Coonan 2009). Initial results of the removal project also indicate the order in which species' abundances are reduced affects the outcome. In particular, one eagle pair that was not initially captured switched prey; they consumed a greater number of foxes following the eradication of pigs (Collins et al. 2009).

### No Active Management of Predators or Primary Prey

The decline of the arboreal lichen-feeding ecotype of woodland caribou (*Rangifer tarandus caribou*) (referred to as mountain caribou) in southeastern British Columbia, Canada, appears largely due to unsustainable predation rates and apparent competition (Wittmer et al. 2005, 2007), a pattern consistent with other declines of woodland caribou across Canada (Festa-Bianchet et al. 2011). Increases in the extent of early successional forests, primarily from logging, and increases in temperature have led to increased abundances of other prey species such as moose and deer (*Odocoileus* spp.) (Latham et al. 2011; Serrouya et al. 2011). Increases in the abundance of these ungulates have resulted in an increased abundance of predators such as wolves and cougars, and greater abundances of predators have led to greater rates of encounter and mortality of caribou (Latham et al. 2011). In addition, the rate of decline in abundance of woodland caribou in British Columbia is negatively correlated with caribou density (Wittmer et al. 2005). Higher rates of woodland caribou decline at

low densities were due to increases in predation rates as group sizes of caribou declined (McLellan et al. 2010). The latter increase in predation rates is the likely mechanism of the observed Allee effect.

The effectiveness of strategies that do not involve active management of either predators or alternate prey can be evaluated by quantifying the population dynamics of mountain caribou within the numerous parks in montane British Columbia (e.g., Wells Gray Provincial Park [5400 km<sup>2</sup>] and Mount Revelstoke and Glacier National Parks [1600 km<sup>2</sup>]) (Serrouya & Wittmer 2010). An additional 10,000 km<sup>2</sup> of old-growth forests have been protected by law on adjacent public lands. Forests within these protected areas have been largely unaffected by the logging that is the cause of apparent competition between caribou and alternate prey in most of the remaining forests in British Columbia (see above). Historically, groups of mountain caribou observed in these protected areas commonly exceeded 500 individuals and, in some years, 1000 individuals (McLellan 2009). Despite protection of forests, population growth rates of mountain caribou continued to decline in Wells Gray Provincial Park ( $\lambda = 0.81$ ) and Mount Revelstoke and Glacier National Parks and surrounding lands ( $\lambda = 0.89$ ) (Hatter 2006). The decline in abundances of mountain caribou in the absence of active management suggests populations in or around protected areas in British Columbia will, like other woodland caribou populations (Hebblewhite et al. 2010), become extirpated despite their access to protected habitat because changes in the abundances of predators and alternate prey occur over much larger spatial extents.

## Synthesis

Because communities of species are defined on the basis of interactions among species and between species and the physical environment (Hairston et al. 1960), any change in species composition can also alter species interactions (Chapin et al. 2000). Thus, before manipulating relative abundances of species, particularly those of abundant prey species, the potential negative effects on rare prey species should be considered (for example via simulation modeling) (Courchamp et al. 2003). Although communities with complex species interactions may be able to compensate for losses of one or several species (Jackson et al. 2001), simple communities with strong interactions among co-evolved species are most likely to respond immediately to changes in species composition (Zavaleta et al. 2001).

Although population models are well suited to predict the consequences of changes in relative species abundances, few studies have been conducted in which effects of management implemented to protect species affected by apparent competition were quantified. Thus, we recommend that researchers conduct experimental,

adaptively managed (Walters 1986) manipulations of relative densities of both predators and alternate prey.

In the meantime, we believe the following inferences can be used to guide management of species affected by apparent competition:

- (1) It is important to understand the mechanisms behind changes in species' abundances before implementing management, especially if species abundances have been altered by human activities, or management may prove unsuccessful.
- (2) Desirable effects of predator and alternate prey control will likely last only as long as control efforts if prey abundances remain high.
- (3) Predator control may have unintended ecological consequences (reviewed in Bull & Courchamp 2009), including the loss of positive contributions of predators to their respective communities (Elbroch & Wittmer 2012*b*).
- (4) Theory and limited empirical data suggest that solely reducing abundant alternate prey species will increase predation rates on rare prey at least in the short term, and it is unclear how the rate of alternate prey removal affects predator switching to rare prey.

## Complexities of Conserving Species Affected by Apparent Competition

Active-management interventions to conserve species affected by apparent competition may be controversial and affected by social values and politics rather than science alone. This is particularly true if evidence suggests active manipulations of charismatic species are warranted. Also, in systems where both predators and alternate prey are native, the decision about which species to cull and which to protect is ethically ambiguous. In situations where such value judgments are required, scientists can best contribute to the discussion by clearly explaining the biology and demography involved. However, active control of animal abundances, although sometimes scientifically advisable (e.g., Roemer et al. 2002; Courchamp et al. 2003; Wittmer et al. 2007), can meet with considerable resistance by both the public (Orians et al. 1997) and managers (Roemer & Donlan 2005; Theberge & Walker 2011).

Attitudes of stakeholders toward active intervention may also be highly context-specific. For example, the public appears more willing to accept active species management when the ultimate causes of the asymmetric competition, such as habitat loss, are addressed through extensive restoration efforts (e.g., British Columbia Ministry of the Environment 2007). Furthermore, cultural values vary greatly. In Alaska, bear and wolf abundance is controlled to increase the availability of moose for hunters (Boertje et al. 2010), whereas in adjacent British

Columbia wolves are not controlled despite the fact that they are endangering caribou (Serrouya et al. 2011). In British Columbia, it is deemed more socially acceptable to reduce moose via sport hunting to indirectly reduce wolf abundance (Serrouya et al. 2011).

Although many conservation biologists endorse restoration of historic regimes of habitat disturbance to minimize the need for active manipulation of species at higher trophic levels (e.g., Grumbine 1994), economic pressures and human values will likely necessitate ongoing species management to conserve rare taxa affected by apparent competition. The extent of management of this type may depend on society's willingness to accept the ultimate causes of apparent competition and in some cases may simply not be realistic or possible to achieve (e.g., restoration of late-successional forests across the entire distribution of mountain caribou in British Columbia).

Ultimately, policy makers are responsible for the implementation of proposed management actions. Unlike scientists, who generally evaluate only the ecological aspects of a proposed conservation strategy, policy makers base their decisions on a variety of factors, including public expectations, current policies, and changing political and societal values (Lackey 2007; Boertje et al. 2010). Thus, there will be times when management decisions are at odds with science-based conservation recommendations, particularly when maintaining a species requires prolonged, expensive, and invasive management.

## Acknowledgments

This manuscript has benefited from discussions with B. McLellan. Comments from D. Armstrong, L. Gibson, E. Roemer, and 2 anonymous reviewers greatly improved previous versions of our manuscript.

## Literature Cited

- Bakker, V. J., et al. 2009. Incorporating ecological drivers and uncertainty into a demographic population viability analysis for the island fox. *Ecological Monographs* **79**:77–108.
- Boertje, R. D., M. A. Keech, and T. F. Paragi. 2010. Science and values influencing predator control for Alaska moose management. *Journal of Wildlife Management* **74**:917–928.
- British Columbia Ministry of the Environment. 2007. Mountain caribou recovery implementation plan. British Columbia Ministry of the Environment, Victoria. Available from <http://www.env.gov.bc.ca/wld/speciesconservation/mc/index.html> (accessed January 2012).
- Bull, L. S., and F. Courchamp. 2009. Management of interacting invasives: ecosystem approaches. Pages 232–247 in M. N. Clout, and P. A. Williams, editors. *Invasive species management: a handbook of principles and techniques*. Oxford University Press, Oxford, United Kingdom.
- Chaneton, E. J., and M. B. Bonsall. 2000. Enemy-mediated apparent competition: empirical patterns and the evidence. *Oikos* **88**:380–394.
- Chapin, F. S., et al. 2000. Consequences of changing biodiversity. *Nature* **405**:234–242.
- Collins, P. W., B. C. Latta, and G. W. Roemer. 2009. Does the order of invasive species removal matter? The case of the eagle and the pig. *Public Library of Science ONE* **4** DOI: 10.1371/journal.pone.0007005.
- Conservación Patagónica. 2011. Building Patagonia National Park. Conservación Patagónica, Sausalito, California. Available from <http://www.conservacionpatagonica.org/> (accessed September 2011).
- Coonan, T. J. 2009. Island fox recovery program San Miguel and Santa Rosa Islands 2008 annual report. Channel Islands National Park, Ventura, California.
- Corti, P., H. U. Wittmer, and M. Festa-Bianchet. 2010. Dynamics of a small population of endangered huemul deer (*Hippocamelus bisulcus*) in Chilean Patagonia. *Journal of Mammalogy* **91**:690–697.
- Côté, I. M., and W. J. Sutherland. 1997. The effectiveness of removing predators to protect bird populations. *Conservation Biology* **11**:395–405.
- Courchamp, F., M. Langlais, and G. Sugihara. 2000. Rabbits killing birds: modelling the hyperpredation process. *Journal of Animal Ecology* **69**:154–164.
- Courchamp, F., R. Woodroffe, and G. Roemer. 2003. Removing protected populations to save endangered species. *Science* **302**:1532.
- DeCesare, N. J., M. Hebblewhite, H. S. Robinson, and M. Musiani. 2010. Endangered apparently: the role of apparent competition in endangered species conservation. *Animal Conservation* **13**:353–362.
- Elbroch, L. M., and H. U. Wittmer. 2012a. Puma spatial ecology in open habitats with aggregate prey. *Mammalian Biology* **77**:377–384.
- Elbroch, L. M., and H. U. Wittmer. 2012b. Table scraps: inter-trophic food provisioning by pumas. *Biology Letters* **8**:776–779.
- Elbroch, L. M., and H. U. Wittmer. 2013. The effects of puma prey selection and specialization on less abundant prey in Patagonia. *Journal of Mammalogy* **94**: in press.
- Festa-Bianchet, M., T. Coulson, J. M. Gaillard, J. T. Hogg, and F. Pelletier. 2006. Stochastic predation events and population persistence in bighorn sheep. *Proceedings of the Royal Society B* **273**:1537–1543.
- Festa-Bianchet, M., J. C. Ray, S. Boutin, S. D. Côté, and A. Gunn. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Canadian Journal of Zoology* **89**:419–434.
- Gibson, L. 2006. The role of lethal control in managing the effects of apparent competition on endangered prey species. *Wildlife Society Bulletin* **34**:1220–1224.
- Grigera, D. E., and E. H. Rapoport. 1983. Status and distribution of the European hare in South America. *Journal of Mammalogy* **64**:163–166.
- Grumbine, R. E. 1994. What is ecosystem management? *Conservation Biology* **8**:27–38.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *The American Naturalist* **94**:421–425.
- Hatter, I. 2006. Mountain caribou 2006 survey results, subpopulation trends, and extinction risks. Pages 4–22 in *Multidisciplinary approaches to recovering mountain caribou in mountain ecosystems*. Columbia Mountains Institute of Applied Ecology, Revelstoke, British Columbia.
- Hayes, R. D., and A. S. Harestad. 2000. Demography of a recovering wolf population in the Yukon. *Canadian Journal of Zoology* **78**:36–48.
- Hayes, R. D., R. Farnell, R. M. P. Ward, J. Carey, M. Dehn, G. W. Kuzyk, A. M. Baer, C. L. Gardner, and M. O'Donoghue. 2003. Experimental reduction of wolves in the Yukon: ungulate responses and management implications. *Wildlife Monographs* **152**:1–35.
- Hebblewhite, M., C. White, and M. Musiani. 2010. Revisiting extinction in national parks: mountain caribou in Banff. *Conservation Biology* **21**:341–344.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* **12**:197–229.

- Holt, R. D., and J. H. Lawton. 1994. The ecological consequences of shared natural enemies. *Annual Review in Ecology and Systematics* **25**:495-520.
- Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**:629-637.
- Jiménez, J., et al. 2008. *Hippocamelus bisulcus*. IUCN red list of threatened species. Version 2010.2. International Union for Conservation of Nature, Gland, Switzerland. Available from <http://www.iucnredlist.org> (accessed August 2012).
- Lackey, R. T. 2007. Science, scientists, and policy advocacy. *Conservation Biology* **21**:12-17.
- Latham, A. D. M., C. Latham, N. A. McCutchen, and S. Boutin. 2011. Invading white-tailed deer change wolf-caribou dynamics in North-eastern Alberta. *Journal of Wildlife Management* **75**:204-212.
- Lessard, R. B., S. J. D. Martell, C. J. Walters, T. E. Essington, and J. F. Kitchell. 2005. Should ecosystem management involve active control of species abundances? *Ecology and Society* **10**:1. <http://www.ecologyandsociety.org/vol10/iss2/art1> (accessed March 2012).
- Lovari, S., R. Boesi, I. Minder, N. Mucci, E. Randi, A. Dematteis, and S. B. Ale. 2009. Restoring a keystone predator may endanger a prey species in a human altered ecosystem: the return of the snow leopard to Sagarmatha National Park. *Animal Conservation* **12**:559-570.
- McLellan, B. N. 2009. A historic perspective of mountain Caribou distribution and abundance. British Columbia Ministry of Forest and Range, Revelstoke.
- McLellan, B. N., R. Serrouya, H. U. Wittmer, and S. Boutin. 2010. Predation-mediated Allee effects in multi-prey systems. *Ecology* **91**:286-292.
- Messier, F. 1995. On the functional and numerical responses of wolves to changing prey density. Pages 187-197 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. *Ecology and conservation of wolves in a changing world*. Occasional publication 35. Canadian Circumpolar Institute, Edmonton.
- Norbury, G. 2001. Conserving dryland lizards by reducing predator-mediated apparent competition and direct competition with introduced rabbits. *Journal of Applied Ecology* **38**:1350-1361.
- Novaro, A. J., M. C. Funes, and R. S. Walker. 2000. Ecological extinction of native prey of a carnivore assemblage in Argentine Patagonia. *Biological Conservation* **92**:25-33.
- Orians, G., et al. 1997. *Wolves, bears, and their prey in Alaska*. National Academy Press, Washington D.C.
- Pope, K. L., J. M. Garwood, H. H. Welsh Jr., and S. P. Lawler. 2008. Evidence of indirect impacts of introduced trout on native amphibians via facilitation of a shared predator. *Biological Conservation* **141**:1321-1331.
- Robinson, H. S., R. B. Wielgus, H. S. Cooley, and S. W. Cooley. 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. *Ecological Applications* **18**:1028-1037.
- Roemer, G. W., C. J. Donlan, and F. Courchamp. 2002. Golden eagle, feral pigs, and insular carnivores: how exotic species turn native predators into prey. *Proceedings of the National Academy of Sciences USA* **99**:791-796.
- Roemer, G. W., and C. J. Donlan. 2005. Biology, policy and law in endangered species conservation: II. A case history in adaptive management of the island fox on Santa Catalina Island, California. *Endangered Species Update* **22**:144-156.
- Serrouya, R., and H. U. Wittmer. 2010. Imminent extinctions of woodland caribou from National Parks. *Conservation Biology* **24**:363-364.
- Serrouya, R., B. N. McLellan, S. Boutin, D. Seip, and S. Nielsen. 2011. Developing a population target for an overabundant ungulate for ecosystem restoration. *Journal of Applied Ecology* **48**:935-942.
- Sweitzer, R. A., S. H. Jenkins, and J. Berger. 1997. Near extinction of porcupines by mountain lions and consequences of ecosystem change in the Great Basin Desert. *Conservation Biology* **11**:1407-1417.
- Theberge, J., and G. Walker. 2011. Managing for caribou and ecological integrity: reply to Serrouya and Wittmer 2010. *Conservation Biology* **25**:858-859.
- Underwood, A. J. 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. *Ecological Applications* **4**:3-15.
- Walters, C. 1986. *Adaptive management of renewable resources*. MacMillan Publishing, New York.
- Wayne, R. K., S. B. George, D. Gilbert, P. W. Collins, S. D. Kovach, D. Girman, and N. Lehman. 1991. A morphologic and genetic study of the island fox, *Urocyon littoralis*. *Evolution* **45**:1849-1868.
- Wittmer, H. U., A. R. E. Sinclair, and B. N. McLellan. 2005. The role of predation in the decline and extirpation of woodland caribou populations. *Oecologia* **144**:257-267.
- Wittmer, H. U., B. N. McLellan, R. Serrouya, R., and C. D. Apps. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. *Journal of Animal Ecology* **76**:568-579.
- Wittmer, H. U., L. M. Elbroch, and A. J. Marshall. 2012. Good intentions gone wrong: Did conservation management threaten endangered huemul deer *Hippocamelus bisulcus* in the future Patagonia National Park? *Oryx*: in press.
- Zavaleta E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology, Evolution and Systematics* **16**:454-459.

