

Endangered, apparently: the role of apparent competition in endangered species conservation

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Abstract

Conservation biologists have reported growing evidence of food-web interactions as causes of species endangerment. Apparent competition is an indirect interaction among prey species mediated by a shared predator, and has been increasingly linked to declines of prey species across taxa. We review theoretical and empirical studies of apparent competition, with specific attention to the mechanisms of asymmetry among apparently competing prey species. Asymmetry is theoretically driven by niche overlap, species fitness traits, spatial heterogeneity and generalist predator behavior. In real-world systems, human-induced changes to ecosystems such as habitat alteration and introduced species may be ultimate sources of species endangerment. However, apparent competition is shown to be a proximate mechanism when resultant changes introduce or subsidize abundant primary prey for predator populations. Demonstration of apparent competition is difficult due to the indirect relationships between prey and predator species and the potential for concurrent exploitative competition or other community effects. However, general conclusions are drawn concerning the characteristics of prey and predator species likely to exhibit asymmetric apparent competition, and the options for recovering endangered species. While short-term management may be required to avoid imminent extinction in systems demonstrating apparent competition, we propose adaptive conservation efforts directed at long-term recovery.

Introduction

Habitat degradation and introduced species are ultimate threats to many species (Wilcove *et al.*, 1998; Venter *et al.*, 2006), though the proximate mechanisms of population decline can be indirect and complex. Conservation biologists have reported growing evidence of food-web interactions as causes of species endangerment (Sinclair & Byrom, 2006). Extinction is more typical of inter-trophic interactions such as predation than intra-trophic competition (Davis, 2003), and predator populations can mediate ecosystem change through altering abundance or behavior of prey (Schmitz *et al.*, 2008), as well as those of other predators (Russell *et al.*, 2009). Additionally, interactions among intra-trophic species can lead to extinction when indirectly mediated by shared predation. In such cases, the extinction of one prey species may be driven by a predator population that is enhanced by an abundant, alternate prey species. The end result resembles that of direct competition, where a decline in one species coincides with an increase in the other. Holt (1977) appropriately coined the term 'apparent competition' to describe this indirect ecological interaction between (at least) two prey species and a shared predator. Similar to

exploitative competition, apparent competition can be defined as a reciprocal negative interaction (–, –), theoretically promoting coexistence among prey (Chase *et al.*, 2002; Tilman, 2007). However, asymmetrical (–, 0) interactions may be more common in nature (Chapin & Bonsall, 2000), and could cause declines in one prey species (Fig. 1). It is precisely this asymmetry that puts some species at risk while others flourish under predation by a shared predator.

Predators play important roles in the maintenance of ecosystems (Ray, 2005), and the restoration of apex predators is an important conservation goal in many systems (Berger & Smith, 2005). However, predator effects may be intensified in human-altered landscapes, where introduced species and habitat alteration alter prey assemblages (Kariva *et al.*, 2007; Shapira, Sultan & Shanas, 2008). The documented role of apparent competition in the endangerment of prey species thus warrants concern for all multiple-prey systems. Researchers have elucidated many details of apparent competition, though a synergism of theoretical and empirical findings is needed to unite the 'sea of special cases' which Holt, Grover & Tilman (1994) had hoped to avoid. Studies of hyperpredation (Moleón, Almaraz & Sánchez-Zapata, 2008), Allee effects (Angulo *et al.*, 2007),

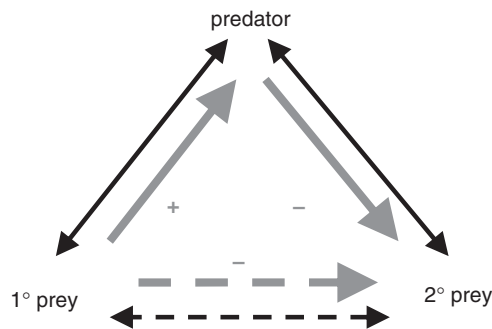


Figure 1 Food web schematic depicting direct (solid) and indirect (dashed) interactions characteristic of apparent competition dynamics between primary (1°) and secondary (2°) prey under a shared predator; adapted from Holt *et al.* (1994).

facilitation (Pope *et al.*, 2008), indirect amensalism (Garrott *et al.*, 2009), incidental predation (Schmidt, 2004), subsidized predation (Gompper & Vanak, 2008) and target predation (Harmon & Andow, 2004) all emphasize the role of indirect community interactions consistent with apparent competition. A synthesis of results may better allow conclusions to be generalized and conservation action to be implemented across systems. In this review on the role of apparent competition in endangered species conservation, we have three primary objectives: (1) to review the mechanics of apparent competition dynamics among predator and prey, including revisiting Holt's (1977) original theoretical model; (2) to review recent studies showing apparent competition and the sources of human-induced asymmetry that lead to endangerment; (3) to consider strategies for detecting and managing apparent competition in the dynamics of endangered species.

Theoretical parameters of apparent competition

Predator–prey dynamics are often quantified according to the numeric response (number of predators) and the functional response (number of kills per predator per unit time) of predators to prey density (Solomon, 1949; Holling, 1959). A third, movement-based numeric response, or aggregative response, might also occur at shorter time scales if predator space use is driven by prey distribution (Holt & Kotler, 1987). The product of predator functional and numerical responses is the predation rate, expressed as the percentage of the prey population lost to mortality. At low prey density, a depensatory (negatively density dependent) predation rate would lead to prey extinction whereas a regulatory (positively density dependent) predation rate would promote persistence (Garrott *et al.*, 2009). Depensatory predation is particularly possible in multiple-prey systems, where predators can persist even if one prey species is driven to extinction. This produces a numeric response to secondary prey with a positive y -intercept, a key symptom of apparent competition (Messier, 1995). In such multiple-prey systems, the shape of the predator functional response becomes

particularly important in generating depensatory or regulatory predation (Hebblewhite *et al.*, 2007). Spatial heterogeneity and predator behavior offer theoretical mechanisms for regulatory predation, discussed in detail below. Additionally, McLellan *et al.* (2009) used simulations of a multi-prey functional response to show a theoretical relaxation of predation on secondary prey at low density, driven by the increased handling time devoted to primary prey. In general, understanding the parameters driving numerical and functional responses and ultimately predation rate is central to conservation of endangered prey (Sinclair *et al.*, 1998; Sinclair & Byrom, 2006).

Below we review the characteristics of multiple-prey systems that shape predator–prey dynamics, with specific attention to the drivers of asymmetric effects on prey. We consider a single-predator, two-prey system (predator, primary prey and secondary prey) for simplicity, but we acknowledge that each role can be occupied by multiple species (Owen-Smith & Mills, 2008). The first model of apparent competition dynamics (Holt, 1977) incorporated parameters for asymmetry among prey according to the vital rates of prey species, predator preference and caloric benefit per prey species. Below we discuss these and additional causes of asymmetry among prey species, summarizing both theoretical and empirical findings into a small set of important parameters for apparent competition in all systems.

Niche overlap

Exploitative (shared resource) and apparent (shared predator) competition can occur concurrently among sympatric prey species (Holt *et al.*, 1994; Chase *et al.*, 2002). Chesson & Kuang (2008) recently summarized these interactions in terms of niche overlap, ρ , subdivided into overlap of resource consumption niches ρ^R , and source of predation niches, ρ^P . We liken ρ^R to overlap in resource preference often modeled in habitat suitability studies (Hirzel & LeLay, 2008), and ρ^P to a comparison of Holt's (1977) per-capita attack rates, a , among prey species (Noonburg & Byers, 2005). Apparent competition implies a shared predator, or $\rho^P > 0$, including completely proportionate predation among prey species ($\rho^P = 1$) and disproportionate selection for one species ($\rho^P < 1$). Noonburg & Byers (2005) used a food-web model to explain coexistence of prey species when both exploitative and apparent competition occurred simultaneously. Their modeling of a single-resource system, however, assumed that prey species must compete for the same resource in order to exist, whereas Holt's (1977) model assumed the opposite. What both models revealed is that relative attack rates, as one measure of niche overlap, can affect persistence (Fig. 2).

Competitive fitness of prey species

Holt's (1977) model of dynamics among apparently competing prey also parameterized the ability of a prey species to withstand predation, as driven by life-history traits of both

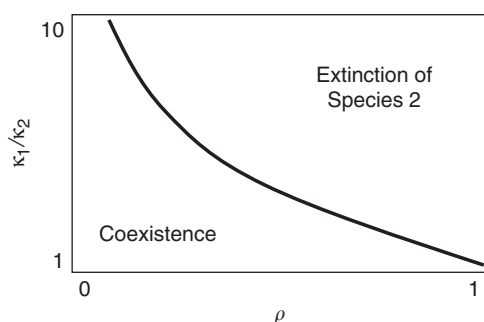


Figure 2 Theoretical implications for extinction of the relative species fitness ratio and niche overlap between a primary (1°) and secondary (2°) prey species; adapted from Chesson & Kuang (2008).

the prey and their food source. In addition to demographic traits, prey behavior such as grouping may also affect relative susceptibility to apparent competition, as predator encounter rates decline proportionately slower for grouping prey (McLellan *et al.*, 2009). In exploitative competition models, the species fitness ratio (κ_1/κ_2) has been used to compare average fitness among consumer species, according to the maintenance requirements of prey species per unit resource, and their maximum rate of resource harvest (MacArthur, 1970; Chesson, 2000; Chesson & Kuang, 2008). This ratio compares the theoretical competitive ability of prey species such as comparing potential population growth allowed by inherent life history. In systems with shared predation, the species fitness ratio is expanded to include both resource driven growth rates and sensitivity to predation among apparently competing prey (Chesson & Kuang, 2008). Coexistence can then be theoretically represented as a function of both the species fitness ratio and niche overlap among prey species, where the degree of niche overlap constrains allowable fitness differences (Fig. 2). For example, when niche overlap among two species is high, the difference between low and high species fitness ratios might represent the difference between persistence and extinction for a species (Fig. 2).

Endangered species are often secondary prey to predators subsisting on an abundant primary prey with higher average fitness (Sinclair *et al.*, 1998), and prey species would be expected to contribute disparately to the predator numerical response. Contrary to single prey systems ($\rho^P = 0$) with regulatory predation, asymmetric apparent competition among multiple prey ($\rho^P > 0$) produces a positive y -intercept in the numeric response to secondary prey, depensatory predation, and thus a mechanism of extinction via apparent competition. The lack of numeric response to secondary prey is a hypothesized link to declines of threatened species in several multiple-prey systems (Angulo *et al.*, 2007; Hebblewhite *et al.*, 2007).

Spatial heterogeneity

Spatial heterogeneity can be a stabilizing factor in the dynamics of both exploitative and apparent competition

(Holt, 1984; Snyder, Borer & Chesson, 2005; Tilman, 2007). In a previous section, we discussed niche overlap, or the sympatry of species' resource requirements in environmental space. Here we consider the spatial arrangement of environmental niche resources, which determines the degree of actualized spatial overlap or separation among species in natural ecosystems (Hirzel & LeLay, 2008). Spatial separation of apparently competing prey species can decouple shared predation dynamics by isolating predator–prey relationships distinctly among heterogeneous habitats. However, this is dependent upon the scale of predator movement among each prey's resource patches (Holt, 1984); spatial sympatry should thus be measured according to the movements of the predator (Holt, 1984). This theoretical finding offers two mechanisms of apparent competition even in situations of complete habitat partitioning and no direct overlap of food resources among prey. First, predators can exhibit movements at the individual level (within-generation) that encompass habitat of both prey and elicit apparent competition (Holt, 1984). Second, a spill-over effect of predator emigration from source (occupied by primary prey) to sink (occupied by secondary prey) habitats can also indirectly link prey species in apparent competition within a predator metapopulation (Harmon & Andow, 2004; Rand & Louda, 2006).

Spatial heterogeneity can also create refuges, or space unexploited by predators. We categorize these refuges as either not visited by predators (ecological refuges; e.g. Schmidt, 2004) or not available to predators (structural refuges; e.g. Forrester & Steele, 2004). Refuges can induce positive density dependence in the predation rate for low-density secondary prey (Forrester & Steele, 2004) by protecting an increasing proportion of the prey population from predation as density decreases. Given asymmetric apparent competition (numeric response to secondary prey with a positive y -intercept), the shape of the functional response to secondary prey distinguishes whether depensatory predation towards extinction or regulatory predation at low density (Messier, 1995; Garrott *et al.*, 2009). Sinclair *et al.* (1998) found that endangered prey species could be conserved only if they found spatial refuge from predation at low numbers. Thus spatial refuges provide one of few empirically supported mechanisms of preventing depensatory predation and extinction of secondary prey (Sinclair *et al.*, 1998).

Generalist predation behavior

Apparent competition dynamics are typically associated with generalist predators, capable of foraging on multiple prey species. A population-level pattern of generalist predation can be the result of generalist individual predators, or locally specialized predators that appear collectively general (Harmon & Andow, 2004). Harmon & Andow (2004) suggested that shared predation systems require each individual predator to be a generalist, as locally specialized predators would spatially decouple the dynamics of each prey species. We suggest that spill-over or metapopulation

effects, as discussed above, may offer an exception. Abundant primary prey may result in an abundant predator source population, thus maintaining high predator density dispersers in sink habitats via dispersal. In this way, primary prey in source habitat may negatively impact secondary prey in sink habitat despite local specialization of predators on each.

Predator preferences and foraging strategies can also be dynamic with respect to prey density (Holt, 1977), climate (Owen-Smith & Mills, 2008) or other covariates, though many predator–prey models assume them to be fixed (Garrott *et al.*, 2007). Changes in prey selection have recently been empirically linked to stabilizing (Siddon & Witman, 2004) and destabilizing (Owen-Smith & Mills, 2008) population effects. Whether called frequency-dependent selection (Merilaita, 2006), optimal foraging (Holt, 1984), apostatic selection (Merilaita & Ruxton, 2009) or prey switching (Garrott *et al.*, 2007), plasticity in predator preference implies shared predation and thus apparent competition. More importantly, such plasticity may reduce predation rates for secondary prey at low density. This offers an additional hypothesized mechanism of the Type III functional response, and as such might promote coexistence of apparently competing prey species if predation pressure

relaxes with declined density. Effects of prey switching would vary according to the behavioral plasticity of the predator and the relative vulnerability or profitability of prey species (Garrott *et al.*, 2007).

Empirical studies of asymmetric apparent competition and species decline

Our overview highlights the critical relationships existing between apparent competition, predation rates and dynamics of prey species. Asymmetry in apparent competition has theoretical implications for endangered species decline, though we have shown potential mechanisms for relaxed predation at low prey density. Here we use examples in the literature to identify the empirical conditions associated with asymmetry in apparent competition. Typical of all examples is human-induced change to resource, prey or predator communities (Table 1). Changes at the resource level include alteration of habitats which affect the density and range of prey species (Harrington *et al.*, 1999; Wittmer *et al.*, 2007; Cooley *et al.*, 2008). Humans also affect predator and prey communities with introduced species

Table 1 Hypothesized cases of species decline induced by asymmetric apparent competition among prey, including parameters such as their role of declining species as primary (1°) or secondary (2°) prey to the predator, resource niche overlap (ρ^R), relative species fitness ratio (κ_1 = fitness of alternate prey, κ_2 = fitness of declining prey; all values assumed > 1), and the suspected ultimate cause of asymmetry among sympatric prey

Declining species	Alternate prey	Shared predator	Role of declining prey	ρ^R	κ_1/κ_2	Ultimate cause	References
Island fox	Feral pig	Golden eagle	2°	None	High	Species introduction	Roemer <i>et al.</i> (2001), Angulo <i>et al.</i> (2007)
Cascade frogs	Trout	Garter snake	2°	None	High	Species introduction	Pope <i>et al.</i> (2008)
Macquarie Island parakeet	Rabbit	Feral cat, weka	2°	None	High	Species introduction	Taylor (1979)
Conilurine rodents	Rabbit	Feral cat, fox	2°	High	High	Species introduction	Smith & Quin (1996)
Skinks	Rabbit	Feral cat, ferret	2°	None	High	Species introduction	Norbury (2001)
Guanaco	Sheep, hare, red deer	Cougar	2°	High	High	Species introduction	Baldi <i>et al.</i> (2004), Novaro & Walker (2005)
Przewalski horse	Livestock, red deer	Wolf	2°	Moderate	High	Species introduction	Van Duyn <i>et al.</i> (2009)
Woodland caribou	Deer, elk, moose	Cougar	2°	Low	High	Human disturbance	Kinley & Apps (2001)
Woodland caribou	Moose	Wolf	2°	Low	High	Human disturbance	Wittmer <i>et al.</i> (2007)
Mule deer	White-tailed deer	Cougar	2°	Moderate	Low	Human disturbance	Robinson <i>et al.</i> (2002), Cooley <i>et al.</i> (2008)
Vancouver island marmot	Black-tailed deer	Cougar, wolf	2°	Low	Moderate	Human disturbance	Bryant & Page (2005)
Sierra Nevada bighorn sheep	Mule deer	Cougar	2°	Low	Low	Human disturbance	Gibson (2006)
Roan antelope	Wildebeest, zebra	Lion	2°	High	High	Human subsidy	Harrington <i>et al.</i> (1999)
Desert tortoise	Human (garbage)	Common raven	2°	None	High	Human subsidy	Kristan & Boarman (2003), Kristan <i>et al.</i> (2004)
Seabirds	Human (fish discards)	Gull	2°	None	High	Human subsidy	Oro & Martínez-Abraín (2007), Sanz-Aguilar <i>et al.</i> (2009)
Elk	Bison	Wolf	1°	Moderate	Low	Predator reintroduction	Garrott <i>et al.</i> (2009)

(Clavero & García-Berthou, 2005). In combination, habitat alteration and introduced species are major sources of species endangerment (Wilcove *et al.*, 1998), and we show that the mechanism of such declines is often asymmetric apparent competition.

Common to most systems linking apparent competition and species endangerment is a predator population supported by an abundant primary prey species. A now classic example is that of apparent competition among endangered island foxes *Urocyon littoralis* and feral pigs *Sus scrofa* (Roemer *et al.*, 2001; Angulo *et al.*, 2007) in the California Channel Islands. Introduced to the islands by humans, feral pigs have high species fitness, and became abundant on the islands where island foxes, an endemic predator, also occurred. Pigs and foxes did not compete directly ($\rho^R = 0$), but abundant pig populations allowed the colonization of an apex predator, golden eagles *Aquila chrysaetos*, native to mainland California ($\rho^P > 0$). Eagle populations subsidized by pigs were implicated in immediate crashes of fox populations on three islands, including two local extirpations (Courchamp, Woodroffe & Roemer, 2003). Roemer *et al.* (2001) referred to this phenomenon as 'hyperpredation,' a term with specific reference to the effects of introduced prey on native prey via shared predation (Smith & Quin, 1996). However, our review reveals that the role of primary prey can be filled by both introduced and native species. For example, similar dynamics are suspected with declines of threatened woodland caribou *Rangifer tarandus caribou* across Canada, but without introduced prey. Wolf *Canis lupus* populations may be subsidized by moose *Alces alces*, whose increasing density and range are associated with forestry conversion of mature forests to preferred early seral stages (Wittmer *et al.*, 2007; McLellan *et al.*, 2009).

Cougar *Puma concolor* predation on both woodland caribou and mule deer *Odocoileus hemionus* may be similarly elevated by abundant, native white-tailed deer *Odocoileus virginianus* populations enhanced by forestry and agriculture (Kinley & Apps, 2001; Robinson, Wielgus & Gwilliam, 2002). Dynamics between mule deer and white-tailed deer are further complicated with exploitative competition ($\rho^R > 1$) for shared resources (Robinson *et al.*, 2002; Cooley *et al.*, 2008). In the Patagonian steppe, native guanaco *Lama guanicoe* declines are associated with both exploitative competition with introduced sheep *Ovis aries*, European hare *Lepus europaeus* and red deer *Cervus elaphus* (Baldi *et al.*, 2004) and apparent competition mediated by elevated puma populations (Novaro & Walker, 2005). Sheep removals increased some guanaco populations, but other competitors remain as sources of both exploitative and apparent competition. Though predator limitation is a leading hypothesis for some threatened guanaco populations, concurrent exploitative competition can complicate conclusions (Novaro & Walker, 2005).

Common ravens *Corvus corax* are an exemplary generalist predator (White, 2006) whose growth in the Mojave Desert was linked to human-induced food subsidy from garbage (Kristan, Boarman & Crayon, 2004). Predation by ravens was a significant source of mortality for juvenile

desert tortoises *Gopherus agassizii*, a threatened species. Predation risk for tortoises increased with proximity to raven aggregation sites, many of which were linked to anthropogenic subsidies (Kristan & Boarman, 2003). Thus, ravens mediated an indirect negative effect of humans on desert tortoises. In terms of niche overlap, $\rho^R = 0$ but $\rho^P > 0$, and a theoretical species fitness ratio would be infinitely skewed toward human garbage; this combination suggests probable tortoise extinction (Fig. 2). Kristan & Boarman (2003) also found spill-over raven predation into areas unassociated with garbage, supporting our theoretical conclusion that apparent competition may be driven by generalist predation by both individuals and populations. The human subsidy of another generalist predator, the yellow-legged gull *Larus michahellis*, is associated with similar negative effects on threatened seabird species in marine environments (Oro & Martínez-Abraín, 2007; Sanz-Aguilar *et al.*, 2009).

Apparent competition has also been recently implicated in declines of the following species: Sierra Nevada bighorn sheep *Ovis canadensis californiana* (Gibson, 2006); Vancouver Island marmots *Marmota vanancouverensis* (Bryant & Page, 2005); Roan antelope *Hippotragus equinus* (Harrington *et al.*, 1999); multiple conilurine rodent species (Smith & Quin, 1996); Cascades frogs *Rana cascadae* (Pope *et al.*, 2008); the now extinct Macquarie Island parakeet *Cyanoramphus novaezelandiae erythrotis* (Taylor, 1979). A rich literature of experimental studies has also developed documenting predator- and parasitoid-mediated apparent competition in invertebrate and plant communities (van Veen, Morris & Godfray, 2006). Coexistence among prey species has been regulated by shared resources (Jones, Godfray & van Veen, 2009), predators (Tschanz, Bersier & Bacher, 2007), and parasites (Morris, Lewis & Godfray, 2004) and the degree of spatial separation among prey species (Bonsall *et al.*, 2005; Cronin, 2007), and predation on a single prey species has both increased (Morris *et al.*, 2004) and decreased (Tschanz *et al.*, 2007) with the addition of a second prey species.

Review of the many species and systems studied revealed practical patterns linking theoretical mechanisms to both the occurrence and strength of apparent competition in natural systems (Table 1). First, shared predation among prey species inherently implies some level of realized apparent competition just as shared resources imply exploitative competition for food. Many examples of asymmetric apparent competition occur in the absence of exploitative competition. Thus, increased consideration of predation as a crucial component of the niche of species and niche overlap among species is warranted. Given predation niche overlap among prey, theory predicts that primary prey species should experience regulatory predation, but secondary prey should be more susceptible to compensatory predation (Sinclair *et al.*, 1998). In our review of asymmetry in apparent competition this prediction is well supported, with rare or endangered species often succumbing to a predator population that is otherwise sustained by an abundant primary prey (Table 1). This pattern is less the result of being

secondary prey, than that of coexisting with a primary prey species that has disproportionately higher growth rates or species fitness. Typically the result of introduced species or human subsidy to native species, the presence of a primary prey with higher species fitness appears consistently linked to declines in endangered prey species (Table 1). Also common to cases of asymmetry are generalist predators, such as canids, felids or corvids, which forage beyond the spatial scale of habitat partitioning between primary and endangered prey (Table 1). This likely reduces the potential for ecological refuges from predation and promotes opportunistic predation on endangered prey (Schmidt, 2004).

With both observational and experimental studies, researchers have developed these links between theoretical mechanisms and the dynamics of apparent competition. However, there remains much need for further research. The spatio-temporal relationship between prey density and predator preference or prey switching, in shared predation systems is a key question facing conservation practitioners today. For example, when reduction of primary prey density is one management strategy, hypothetical outcomes might include both a short-term rise (changes in predator preference) and a long-term decline (changes in predator density) in predation rates on endangered prey. Additionally, the sustaining effect of spatial refuges has been documented (Sinclair *et al.*, 1998), but more research is warranted on the spatial relationship between predator foraging, prey density and fine-scale habitat partitioning among prey species (Orrock, Witter & Reichman, 2008).

Conservation challenges and solutions

Conservation biologists face two difficult challenges concerning apparent competition and the decline of prey species. First, researchers must reliably demonstrate where and how apparent competition occurs, including the identification of mechanisms responsible for asymmetry among prey species. Second, managers must quickly prescribe management to reverse declines, considering both ultimate (e.g. habitat alteration and introduced species) and proximate (predation) causes.

Efforts to detect apparent competition will benefit from the increased acknowledgment of its role in community dynamics in all systems of shared predation. In this review, we identify several mechanisms commonly associated with asymmetry in these dynamics, and thus with probable species decline (Table 1). Two recent studies of wolf predation in multi-prey systems provide examples for highlighting these mechanisms. Van Duyne *et al.* (2009) studied wolf predation in a system containing both domestic and native ungulates, including the endangered Przewalski horse *Equus ferus przewalskii*. They did not discuss apparent competition as a factor in Przewalski horse recovery but describe a system with several characteristics found to be indicative of apparent competition in our review, including: (1) shared predation under a wide-roaming generalist predator; (2)

subsidized domestic and abundant native competing prey with higher relative species fitness; (3) a predator diet suggesting the use of domestic prey as primary prey and abundant native ungulates as preferred prey; (4) an ultimately human-driven subsidy to the predator's prey base. Thus, asymmetric apparent competition should be considered as a mechanism of decline, with augmentation of domestic and other native ungulates as an ultimate source of compensatory predation upon the endangered Przewalski horse. In another system, Garrott *et al.* (2009) recently predicted that compensatory wolf predation observed on elk *C. elaphus* was due to apparent competition with bison *Bison bison*. In this case the declining species, elk, are the predator's primary prey, and the ultimate cause of compensatory predation may be an inflated initial density before wolf reintroduction (White, Olmsted & Kay, 1998). These relationships are inconsistent with those typically associated with endangerment in our review (Table 1). Continued monitoring is encouraged and may reveal new patterns as elk density lowers to a level more characteristic of the historic system.

Many possibilities are available to researchers and managers aimed to assess asymmetry in apparent competition systems. While experimental methods are rarely possible when dealing with endangered or wide-ranging species, quasi-experimental approaches using naturally occurring treatment and control landscapes offer one means of separating the effects of resource and predation niche overlap among prey (Rand & Louda, 2004; Angulo *et al.*, 2007). Predator exclosure or removal experiments may also offer a means of detecting the role of shared predation in structuring prey communities (Spiller & Schoener, 1998), though we discuss the use of predator removal as a conservation strategy below. Sinclair *et al.* (1998) suggested that managers monitor per-capita rates of change for prey species, to directly assess if mortality is compensatory. This could strengthen justification for conservation action but should be combined with research aimed to understand mechanistic causes. Orrock *et al.* (2008) found that predators can dictate the spatial scale over which competition occurs, further justifying the importance of predator-driven spatial scale for research and conservation. Competition kernels involve mapping the spatial intensity of competition among species (Morris, Lewis & Godfray, 2005), and extending this concept to include apparent competition may aid in identifying the appropriate scale for conservation actions. Each of the mechanisms discussed above should be considered when designing research or monitoring programs in systems of apparent competition. Previous observational approaches have included measurement of resource and predation niche overlap (Caut *et al.*, 2006; Cooley *et al.*, 2008; Pope *et al.*, 2008), prey fitness or predation rates (Roemer *et al.*, 2001; Robinson *et al.*, 2002; Wittmer *et al.*, 2007), and predator functional and numeric responses (Norbury, 2001), as well as correlative analyses of resource, prey and predator density data over space or time (Taylor, 1979; Harrington *et al.*, 1999; Roemer *et al.*, 2001; Robinson *et al.*, 2002; Pope *et al.*, 2008). In all studies, we encourage explicit

acknowledgment of untested assumptions in discussion of apparent competition and its contribution to species decline.

Conservation solutions to asymmetric apparent competition will vary according to the mechanisms driving asymmetry among prey, including consideration of both ultimate and proximate causes of decline. In apparent competition systems, the search for proximate cause will likely point to predator and/or primary prey density. As such, control of predator or primary prey density is a popular strategy for conservation problems involving predation or competition stressors (Lessard *et al.*, 2005; Sanz-Aguilar *et al.*, 2009). These 'symptomatic' approaches to management directed at predation risk and competition can be a quick fix for species recovery, though 'systemic' management of the ultimate cause for decline (human disturbance) may be necessary for long-term recovery (Lessard *et al.*, 2005; Sinclair & Byrom, 2006). For example, while predator removal may be an effective short-term means of releasing pressure from endangered prey (Lessard *et al.*, 2005; Sanz-Aguilar *et al.*, 2009), concurrent primary prey control or habitat management is required to address asymmetry among competing prey species (Courchamp *et al.*, 2003; Lessard *et al.*, 2005; Gibson, 2006; Oro & Martínez-Abraín, 2007). Conversely, eradication of competing prey without predator control may, in fact, enhance predation upon endangered prey by generalist predators (Courchamp *et al.*, 2003), a management paradox in need of further research. Both cost and effectiveness vary with control strategy (Baxter *et al.*, 2008), and complete eradication of predator or primary prey populations may be unreachable without isolation from sources of immigration (Morrison *et al.*, 2007). Thus methods to address predation levels may provide short-term relief, but ultimately the source of asymmetry among competing prey should be resolved. Human alteration of global ecosystems has shifted the emphases of conservation from 'equilibria' and 'climax communities' to adaptive management in the face of regime shifts (Chapman, 2006; deYoung *et al.*, 2008; Contamin & Ellison, 2009). In this light, we encourage adaptive management practices that acknowledge short-term uncertainty without being paralyzed by it, while setting in place long-term platforms for monitoring and scientific inference to best address the ultimate sources of change.

Conclusions

Our review clearly identified the role of apparent competition in species declines across taxa. While scenarios may have distinct causes and unique qualities, we encourage the recognition of apparent competition dynamics as a mechanism of decline in multiple-prey systems. We have shown that asymmetry among prey species can exist in apparent competition under shared predation just as previously shown for exploitative competition for shared resources. Continued research linking hypothesized mechanisms of asymmetry to empirical results will strengthen the theoretical foundation from which to base recovery programs for many endangered species. Ultimate causes may include introduced species,

ecosystem disturbance or climate change, each resulting in increased primary prey and predator populations to the detriment of endangered prey species. We have identified a number of recognizable symptoms of asymmetry in apparent competition dynamics, and we encourage future research and adaptive management directed toward the refinement of indicators for prey endangerment in such systems. Finally, as the measures employed in real-world conservation biology depend upon consensus of a majority of stakeholders (Van Dyke, 2008), the ethics, practicality and long-term sustainability of managing for a given species using control of its predators or prey competitors should be carefully evaluated. While short-term management may be required to avoid imminent extinction, we propose adaptive conservation efforts directed at long-term results.

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