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

N. J. DeCesare1, M. Hebblewhite1, H. S. Robinson1 & M. Musiani2

1 Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, College of Forestry and Conservation, University of Montana, Missoula, MT, USA
2 Faculty of Environmental Design, University of Calgary, Calgary, AB, Canada

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 (Chaneton & 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 (Kareiva et al., 2007; Shapira, Sultan & Shanás, 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 (Molén, Almaraz & Sánchez-Zapata, 2008), Allee effects (Angulo et al., 2007),
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 mechanisms 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 ρR, and source of predation niches, ρP. We liken ρR to overlap in resource preference often modeled in habitat suitability studies (Hirzel & LeLay, 2008), and ρP 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 ρP > 0, including completely disproportionate predation among prey species (ρP = 1) and disproportionate selection for one species (ρP < 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
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 sympathy 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 dependant 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 dispensatory 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>
<thead>
<tr>
<th>Declining species</th>
<th>Alternate prey</th>
<th>Shared predator</th>
<th>Role of declining prey</th>
<th>$\rho^R$</th>
<th>$\kappa_1/\kappa_2$</th>
<th>Ultimate cause</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Island fox</td>
<td>Feral pig</td>
<td>Golden eagle</td>
<td>2</td>
<td>None</td>
<td>High</td>
<td>Species introduction</td>
<td>Roemer et al. (2001), Angulo et al. (2007)</td>
</tr>
<tr>
<td>Cascade frogs</td>
<td>Trout</td>
<td>Garter snake</td>
<td>2</td>
<td>None</td>
<td>High</td>
<td>Species introduction</td>
<td>Pope et al. (2008)</td>
</tr>
<tr>
<td>Macquarie Island</td>
<td>Rabbit</td>
<td>Feral cat, weka</td>
<td>2</td>
<td>None</td>
<td>High</td>
<td>Species introduction</td>
<td>Taylor (1979)</td>
</tr>
<tr>
<td>Parakeet</td>
<td>Rabbit</td>
<td>Feral cat, weka</td>
<td>2</td>
<td>High</td>
<td>High</td>
<td>Species introduction</td>
<td>Smith &amp; Quin (1996)</td>
</tr>
<tr>
<td>Conilurine rodents</td>
<td>Rabbit</td>
<td>Feral cat, fox</td>
<td>2</td>
<td>None</td>
<td>High</td>
<td>Species introduction</td>
<td>Norbury (2001)</td>
</tr>
<tr>
<td>Skinks</td>
<td>Rabbit</td>
<td>Feral cat, ferret</td>
<td>2</td>
<td>None</td>
<td>High</td>
<td>Species introduction</td>
<td>Baldi et al. (2004), Novaro &amp; Walker (2005)</td>
</tr>
<tr>
<td>Guanaco</td>
<td>Sheep, hare, red</td>
<td>Cougar</td>
<td>2</td>
<td>High</td>
<td>High</td>
<td>Species introduction</td>
<td>Van Duyne et al. (2009)</td>
</tr>
<tr>
<td>Przewalski horse</td>
<td>Livestock, red</td>
<td>Cougar</td>
<td>2</td>
<td>Moderate</td>
<td>High</td>
<td>Species introduction</td>
<td>Kinley &amp; Apps (2001)</td>
</tr>
<tr>
<td>Woodland caribou</td>
<td>Deer, elk, moose</td>
<td>Wolf</td>
<td>2</td>
<td>Low</td>
<td>High</td>
<td>Human disturbance</td>
<td>Wittmer et al. (2007)</td>
</tr>
<tr>
<td>Woodland caribou</td>
<td>Moose</td>
<td>Wolf</td>
<td>2</td>
<td>Low</td>
<td>Moderate</td>
<td>Human disturbance</td>
<td>Robinson et al. (2002), Robinson (2009)</td>
</tr>
<tr>
<td>Mule deer</td>
<td>White-tailed deer</td>
<td>Cougar</td>
<td>2</td>
<td>Low</td>
<td>Moderate</td>
<td>Human disturbance</td>
<td>Cooley et al. (2008)</td>
</tr>
<tr>
<td>Vancouver island</td>
<td>Black-tailed deer</td>
<td>Cougar, wolf</td>
<td>2</td>
<td>Low</td>
<td>Moderate</td>
<td>Human disturbance</td>
<td>Bryant &amp; Page (2005)</td>
</tr>
<tr>
<td>Sierra Nevada bighorn sheep</td>
<td>Mule deer</td>
<td>Cougar</td>
<td>2</td>
<td>Low</td>
<td>Low</td>
<td>Human disturbance</td>
<td>Gibson (2006)</td>
</tr>
<tr>
<td>Roan antelope</td>
<td>Wildebeest, zebra</td>
<td>Lion</td>
<td>2</td>
<td>High</td>
<td>High</td>
<td>Human subsidy</td>
<td>Harrington et al. (1999)</td>
</tr>
<tr>
<td>Desert tortoise</td>
<td>Human (garbage)</td>
<td>Common raven</td>
<td>2</td>
<td>None</td>
<td>High</td>
<td>Human subsidy</td>
<td>Kristan &amp; Boorman (2003), Kristan et al. (2004)</td>
</tr>
<tr>
<td>Seabirds</td>
<td>Human (fish discards)</td>
<td>Gull</td>
<td>2</td>
<td>None</td>
<td>High</td>
<td>Human subsidy</td>
<td>Oro &amp; Martinez-Abrain (2007), Sanz-Aguir et al. (2009)</td>
</tr>
<tr>
<td>Elk</td>
<td>Bison</td>
<td>Wolf</td>
<td>1</td>
<td>Moderate</td>
<td>Low</td>
<td>Predator reintroduction</td>
<td>Garrott et al. (2009)</td>
</tr>
</tbody>
</table>
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 by pigs were implicated in immediate crashes of fox populations.

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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, Bourman & 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 & Boorman, 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 & Boorman (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 & Martinez-Abrain, 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 c. californiana (Gibson, 2006); Vancouver Island marmots Marmota vancouveresris (Bryant & Page, 2005); Roan antelope Hippotragus equinus (Harrington et al., 1999); multiple conilonure rodent species (Smith & Quin, 1996); Cascades frogs Rana cascadae (Pope et al., 2008); the now extinct Macquarie Island parakeet Cyanoramphus novaevandiae 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 dispensatory 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 Duyn 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 depensatory predation upon the endangered Przewalski horse. In another system, Garrott et al. (2009) recently predicted that depensatory 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 depensatory 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 depensatory. 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 & Martinez-Abrain, 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 exploitive 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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