Peer Reviewed: Student Commentary

The Role of Lethal Control in Managing the Effects of Apparent Competition on Endangered Prey Species

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Abstract

*Apparent competition is the process by which one prey species may indirectly cause the decline in another species by sustaining a common predator. I argue apparent competition caused Sierra Nevada bighorn sheep (*Ovis canadensis californiana*) and Channel Island fox (*Urocyon littoralis*) population declines in the mid-1990s. In the Sierra Nevada, mountain lions (*Puma concolor*) are believed to have caused bighorns to abandon their winter ranges, thus indirectly contributing to population declines. In the Channel Islands, golden eagle (*Aquila chrysaetos*) predation is thought to have reduced 3 resident fox populations by over 95%. I argue, in both cases, native predators are the primary cause of the declines. Additionally, I argue these predators are primarily sustained by hyperabundant alternative prey species. In such cases direct management, to include lethal control of predators and hyperabundant alternative prey, may be necessary to restore these endangered bighorn and fox populations.* (WILDLIFE SOCIETY BULLETIN 34(4):1220–1224; 2006)

Key words

apparent competition, Channel Island fox, endangered species management, hyper-predation, lethal control, Ovis canadensis californiana*, Sierra Nevada bighorn sheep,* Urocyon littoralis.

Apparent competition is the process by which one prey species indirectly causes the decline in another prey species by sustaining a common predator (Holt 1977). In this manner a native predator may suppress a population if it is bolstered by a hyperabundant (unnaturally over-abundant) alternative prey species. I argue that apparent competition caused Sierra Nevada bighorn sheep (*Ovis canadensis californiana*) and Channel Island fox (*Urocyon littoralis*) population declines. If this is the case, direct management to include lethal control of both native predators and hyperabundant prey may be necessary to restore these populations to viable levels. In this paper I present the following arguments to justify the need for direct management: 1) predation by mountain lions (*Puma concolor*) and golden eagles (*Aquila chrysaetos*) was the primary cause of these declining bighorn and fox populations, respectively, and 2) these 2 predators are primarily supported by hyperabundant alternative prey species: mule deer (*Odocoileus hemionus*) in the Sierra Nevada and pigs (*Sus scrofa*), deer fawns, and carrion from deer and elk (*Cervus elaphus*) in the Channel Islands.

Sierra Nevada Bighorn Declines

The decline in Sierra Nevada bighorn populations is believed to be a consequence of altered habitat selection. Sierra Nevada bighorns normally occupy low elevations during the winter; however, beginning in the 1980s these bighorns wintered at higher elevations. In the mid-1990s these higher elevations experienced heavy snows and severe cold. All 5 Sierra Nevada bighorn herds on Mt. Langley, Mt. Baxter, Mt. Williamson, Wheeler Ridge, and in Lee Vining Canyon collapsed, and 12 fatalities occurred in a single avalanche in the Wheeler Ridge herd. As a result the total population of bighorns in the Sierra Nevada plummeted from an estimated 310 individuals in 1986 to just 100 individuals in 1995 (U.S. Fish and Wildlife Service [USFWS] 2003).

The reason all 5 Sierra Nevada bighorn populations abandoned their winter ranges almost simultaneously is a mystery, although several hypotheses attempt to explain this behavior. One possibility is that helicopter harassment during reintroduction programs triggered the bighorns' alteration in habitat selection. However, this argument may be invalid for the following reasons: 1) previous reintroduction events caused no winter range avoidance, 2) Mt. Baxter sheep wintered on low-elevation ranges immediately following this harassment, and 3) other herds not used for reintroduction also abandoned their winter ranges (Wehausen 1996).

A second hypothesis is that poor forage due to a drought from 1987–1992 caused the bighorns to abandon their winter ranges (B. Pierce, California Department of Fish and Game [CDFG], personal communication). However, this hypothesis is contradicted by the following facts: 1) winter range abandonment preceded the drought, 2) a drought from 1976–1977 caused no winter range abandonment, and 3) after the 1987–1992 drought, bighorns did not return to their winter ranges, even during heavy winters in 1993 and 1995 (Wehausen 1996).

A third possible explanation is that policies of fire suppression in the Sierra Nevada since the beginning of the 20th century led to the deterioration of the bighorns' winter ranges and caused their range shift. Bighorn sheep require a visually open habitat in order to detect and evade predators, and the accumulation of vegetation may have caused bighorns to abandon their winter ranges (Krausman and Shackleton 2000). However, this hypothesis seems unlikely because bighorns did not abandon their winter ranges until the 1980s, probably well after any unfavorable impacts of fire suppression appeared in their habitat.

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Channel Island Fox Population Declines

In the Channel Islands, the 3 island fox subspecies on San Miguel (*U. l. littoralis*), Santa Rosa (*U. l. santarosae*), and Santa Cruz (*U. l. santacruzae*) are preyed on by golden eagles, which colonized the northern Channel Islands in the mid-1990s. An infrequent island visitor before its recent colonization, the golden eagle is considered a native predator. Golden eagles reduced the fox population by over 95% on the 3 northern Channel Islands where it occurs (National Park Service [NPS] 2003). On Santa Cruz, golden eagles caused 19 of 21 known fox mortalities between 1993 and 1995, and 25 of 29 documented mortalities between 2000 and 2004, and on San Miguel, golden eagles caused 5 of 7 known fox mortalities between 1998 and 1999 (Roemer et al. 2001, NPS 2003, 2004).

The reason golden eagles colonized the northern Channel Islands in the mid-1990s is uncertain. Before their arrival, golden eagles likely were deterred from nesting on the Channel Islands due to the lack of conspecific attraction (D. Van Vuren, University of California at Davis, personal communication). Because golden eagles did not originally inhabit the Channel Islands, individuals that visited the islands were less likely to find mates, which may have discouraged their continued stay. Several theories have been suggested to explain golden eagle colonization of the northern Channel Islands.

The predominant hypothesis is that resident bald eagles (*Haliaeetus leucocephalus*) prevented golden eagles from colonizing the northern Channel Islands until 1960, when dichlorodiphenyltrichloroethane (commonly known as DDT) contamination caused the extirpation of bald eagles and allowed their territorial competitors to establish residence (NPS 2003, 2004). This theory assumes bald eagles to be competitively superior to golden eagles and to have, thus, prevented earlier colonization. I could find no evidence of this in the literature. This hypothesis also would fail to explain the 3-decade lag between the extirpation of bald eagles and the arrival of golden eagles.

A second hypothesis explaining golden eagle colonization is their protection in the second half of the 20th century. In 1962 the Bald and Golden Eagle Protection Act was amended to protect golden eagles and thereafter facilitated recovery throughout the Southwest (B. Latta, Santa Cruz Predatory Bird Group, personal communication). Additionally, increasing urbanization in southern California may have displaced some individual golden eagles from their habitats on the mainland to the Channel Islands (Roemer et al. 2001). The combination of an increasing golden eagle population and displacement in southern California may have expedited colonization on these offshore islands.

An Alternative Hypothesis: Apparent Competition

I argue that apparent competition may have caused the collapse of the Channel Island fox and Sierra Nevada bighorn populations. The presence of hyperabundant mule deer in the Sierra Nevada and feral pigs and other introduced herbivores (e.g., mule deer, elk) in the Channel Islands may have supported large populations of mountain lions and golden eagles, respectively, and thereby indirectly contributed to the decline in Sierra Nevada bighorn and Channel Island fox populations.

Sierra Nevada Bighorns

Predation by mountain lions provides a compelling argument for the Sierra Nevada bighorn's range shift. Immediately prior to and coincident with their winter range avoidance, Wehausen (1996) found 49 bighorns killed by mountain lions on the Mt. Baxter winter ranges between 1974 and 1988. During this period mountain lion predation on this herd began to increase exponentially (Fig. 1). The 49 lion kills documented represent 80% of winter range mortalities and 71% of all known mortalities for the Mt. Baxter herd, prior to the severe winters in the 1990s (Wehausen 1996). Other herds in the Sierra Nevada may have been particularly vulnerable to mountain lion predation because their populations were considerably smaller than the Mt. Baxter herd, and 3 other herds recently were reintroduced and were in unfamiliar territory (Krausman et al. 1999, Sawyer and Lindzey 2002). These 2 conditions existed in the re-established Lee Vining herd, where 9 of 10 radiocollared sheep that died between 1986 and 1989 were killed by mountain lions (L. Chow, U.S. Geological Survey-Biological Resource Division, personal communication). This frequent mountain lion predation would represent a major threat to Sierra Nevada bighorns had they remained in their low-elevation winter ranges. Because of the coincident timing and high intensity of mountain lion predation, I argue apparent competition may best explain the Sierra Nevada bighorn's winter range abandonment. Additionally, I believe the threat posed by mountain lions to the Sierra Nevada bighorn may be explained by apparent competition with deer, the lion's primary prey species.

Data from buck harvests and lion depredations in California's Mono and Inyo Counties, where all of the Sierra bighorns reside, suggest a strong relationship between increasing deer and lion populations and decreasing bighorn populations (Mohr et al. 2003, CDFG 2005; Fig. 2). Buck

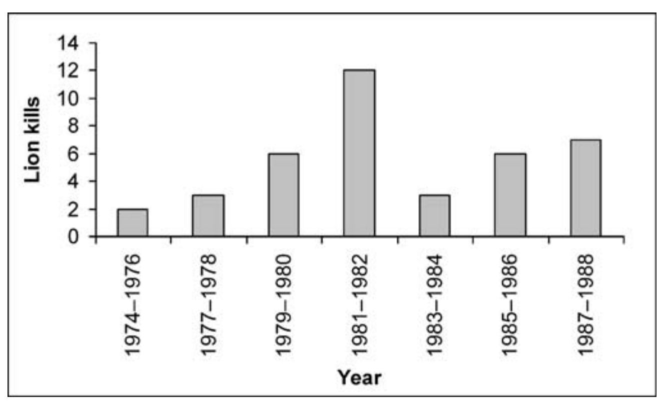

Figure 1. Bighorns in the Mt. Baxter herd killed by mountain lions (1974–1988; J. Wehausen, University of California White Mountain Research Station, unpublished report).

harvests, as an indicator of total deer population, are used to track deer populations and set harvest regulations in several states (Rupp et al. 2000). These data show that during the mid- and late 20th century, Sierra Nevada deer numbers irrupted to 3–4-times historic levels, possibly due to fire suppression and the spread of livestock, 2 conditions that favor deer populations (Berger and Wehausen 1991, Mohr et al. 2003). Mountain lion populations did not respond to the increasing deer populations because they were hunted and bountied throughout the state of California before receiving protection in 1972 (Torres et al. 1996). While the protection of mountain lions may have factored in their population increase by itself, the presence of a hyper-abundant deer population certainly sustained their expansion. Thus, by supporting an expanding mountain lion population, deer may have indirectly pushed bighorn sheep to the brink of extinction by means of apparent competition.

Sierra Nevada deer population declines during the 1987–1992 drought may have caused mountain lions to prey more heavily on bighorn sheep (Fig. 3). In Round Valley, bordering the Sierra Nevada on the east, estimated deer numbers declined from 5,247 in 1986 to 939 individuals in 1991 (B. Pierce, CDFG, unpublished data). Round Valley's lion population also decreased, but only after a lag of almost a decade, again suggesting that deer sustained the high densities. During this lag mountain lions may have preyed more frequently on bighorn sheep and contributed to their winter range avoidance, thereby indirectly causing the observed collapse in sheep numbers.

I believe mountain lion predation provides the best explanation for the Sierra Nevada bighorn's winter-range abandonment and probably indirectly caused the decline in all 5 remaining bighorn herds due to winter mortality. Additionally, because mountain lion numbers expanded due to a hyperabundant deer population, I contend that they indirectly caused the collapse of Sierra Nevada bighorn populations through apparent competition.

Channel Island Fox

I argue the presence of hyperabundant alternative prey species provides the most credible explanation for the golden eagle's colonization of the northern Channel Islands. Golden eagles may subsist on live feral pigs and deer fawns; additionally, the culling and eradication of introduced sheep, deer, and elk populations may provide enough carrion to support a nesting golden eagle population. Watson et al. (1992) found golden eagles to be highly dependent on carrion and, in the late 20th century, the eradication of tens of thousands of sheep on the northern Channel Islands would have provided a substantial food source for golden eagles and may, thereby, have contributed to their colonization (NPS 2004). Additionally, invasive deer and elk persist on Santa Rosa and are culled each winter, providing an estimated 200–500 deer carcasses alone, which may help support golden eagles (NPS 2003, USFWS 2004).

In addition to these sources of carrion, thousands of introduced pigs on Santa Cruz, now a primary prey source for golden eagles, may have enticed transient golden eagles to colonize these islands in the 1990s (Roemer et al. 2001, 2002, Courchamp et al. 2003, Roemer and Donlan 2004). However, both piglet and deer fawn remains were found in golden eagle nests on the northern Channel Islands (NPS 2003, 2004). Although these alternative prey species occupied the northern Channel Islands since the mid-19th century, golden eagles did not arrive until over a century later. I argue that because golden eagles were found to be the exclusive factor in the decline in the northern island fox populations and were sustained by pigs and other invasive herbivores, this also is a case of apparent competition.

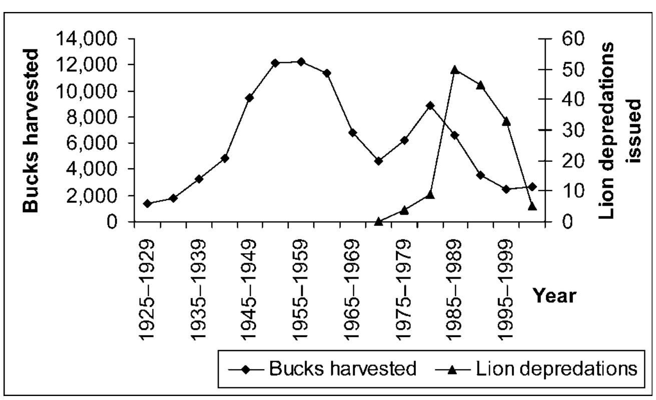

Figure 2. Buck harvests and mountain lion depredations plotted over 5-year intervals in Mono and Inyo Counties, California, USA (1925–2004; Mohr et al. 2003, California Department of Fish and Game 2005).

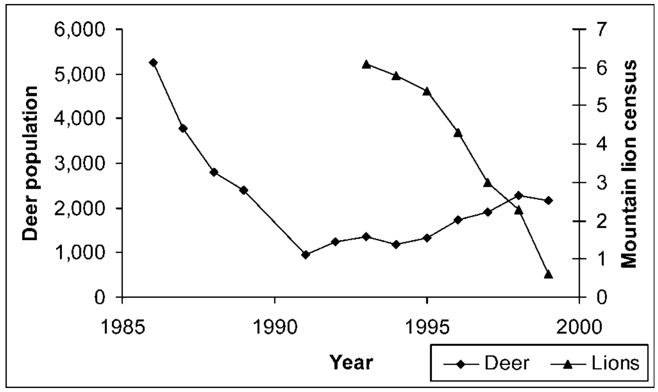

Figure 3. Deer and mountain lions in Round Valley (1985–2000; B. Pierce, California Department of Fish and Game, unpublished data). The mountain lion graph plots the average number of mountain lions observed during winter flights.

Management Implications

I contend the evidence presented suggests that the endangered bighorns and foxes suffered from the effects of apparent competition involving alternative prey populations and a common predator. Despite this parallel, key differences exist in the current recovery plans for these 2 animals. In the Sierra Nevada, predator control has been implemented to protect the endangered bighorns (USFWS 2003); however, I argue alternative prey species should also be regulated as part of a long-term solution. In contrast, in the Channel Islands, alternative prey species control has been adopted to protect the endangered foxes without the initiation of lethal predator control (T. Coonan, NPS, personal communication). Thus, I contend current management actions may be insufficient to protect and recover these species. I believe a synthesis of these 2 policies may be needed to recover these endangered species.

This synthesis must include management of the hyperabundant alternative prey species, which I have identified as the root of the species' declines. Though the Sierra Nevada management has not yet addressed this essential issue, authorities in the Channel Islands are currently implementing a pig eradication program on Santa Cruz in order to deter further colonization by golden eagles. This management action presents another critical question to this case study: how will pig eradication impact the northern Channel Island ecosystem and its endangered fox populations? One possible outcome is the disappearance of golden eagles from the northern Channel Islands. However, pig eradication will supply an abundant source of carrion that may help sustain continued golden eagle presence for 2–4 years, the estimated duration of the eradication program (NPS 2004). Additionally, golden eagles may subsist on the carrion and fawns of Santa Rosa's deer and elk populations. The eradication of these invasive ungulates is scheduled to begin in 2008 and to last 3 years (USFWS 2004).

Another possible result of pig eradication is the decline or even extirpation of fox populations due to prey switching by golden eagles, as shown in Courchamp et al.'s (2003) theoretical model. Like the case in the Sierra Nevada, the decline of alternative prey populations may exacerbate the situation for the endangered Channel Island fox. These arguments suggest that pig eradication may have serious ill effects on the island fox populations. The continued presence of golden eagles on the northern Channel Islands threatens to eliminate the unwary fox populations wavering on the brink of extinction. Because of the substantial risks involved, golden eagle removal should precede the completion of the pig eradication.

The second strategy to protect these endangered species is to control the predators that are driving these bighorns and foxes toward extinction. I believe this action should assume highest priority because in both situations only a handful of predators potentially could extinguish these endangered species. In the Sierra Nevada, individual mountain lions may have triggered bighorns to abandon their winter ranges (J. Wehausen, University of California White Mountain Research Station, unpublished report). Similarly, in the Channel Islands, a few golden eagles could decimate fox populations on all 3 northern islands (Roemer et al. 2001). Thus, these predator populations must be closely monitored to ensure that certain individuals do not cause the extinction of their endangered prey species.

Even though the Sierra Nevada and Channel Islands case studies both involve conflicts between protected predators and endangered species, lethal predator removal has been implemented only for mountain lions. This controversial policy coincides with the gradual recovery of bighorn populations in the Sierra Nevada, from an estimated 250 animals in 2001 to 350 animals today (USFWS 2003; J. Wehausen, personal communication). However, this policy alone may not guarantee the Sierra Nevada bighorn's long-term persistence, because mountain lions continue to threaten these bighorns. Between 2003 and 2005, 3 mountain lions were removed after killing several bighorn sheep in the Wheeler Ridge herd (B. Pierce, personal communication). While predator control has lately proven effective in protecting the Sierra Nevada bighorns, further actions including deer regulation may be necessary to ensure this animal's long-term survival.

In contrast to the Sierra Nevada, Channel Islands management has pursued golden eagle removal by live-capture and relocation, even though lethal predator control may be necessary for the survival of island foxes. Since November 1999, 38 golden eagles have been captured from Santa Cruz Island and translocated to northeast California (T. Coonan, personal communication). However, an estimated 2–4 golden eagles remain on Santa Cruz, and 3 remain on Santa Rosa that killed 5 foxes between late 2004 and early 2005 (T. Coonan, personal communication). These golden eagles endanger the estimated 100 wild foxes that remain on Santa Cruz and the scant 10 wild foxes on San Miguel and 8 on Santa Rosa (T. Coonan, personal communication). Because these remaining golden eagles have proven difficult to capture, lethal removal should be considered (Courchamp et al. 2003).

The Bald and Golden Eagle Protection Act provides exceptions for the recovery of endangered species. Golden eagles may be killed "for the scientific or exhibition purposes of public museums, scientific societies, and zoological parks, or for the religious purpose of Indian tribes, or…for the protection of wildlife or…agricultural or other interests in any particular locality," (16 United States Code 668a). Because golden eagles can be killed to protect livestock, their lethal removal to save an endangered species should be considered. Furthermore, this act specifies that golden eagles may be removed to protect wildlife, and the endemic island fox, an animal threatened with immediate extinction by golden eagles, certainly qualifies for this action.

I contend that lethal control of threatening predator populations and the regulation of alternative prey species should be combined to address these crises. However, managing agencies have only adopted one of these 2 steps. This combined approach, addressing both predators and alternative prey species, has been suggested by a number of studies (Courchamp et al. 1999, 2003, Ernest et al. 2002, Rubin et al. 2002). The Sierra Nevada and Channel Islands provide an interesting lesson for conservation biology: when protected predators threaten endangered prey species, predator control should be combined with the regulation of alternative prey species to ensure the persistence of endangered prey populations. I believe this dual tactic could help restore sustainable wild populations of bighorn sheep and foxes to the Sierra Nevada and Channel Islands, respectively. By applying the lessons from the Sierra Nevada and Channel Islands case studies, conservation teams may ensure the protection of endangered prey populations threatened by apparent competition.

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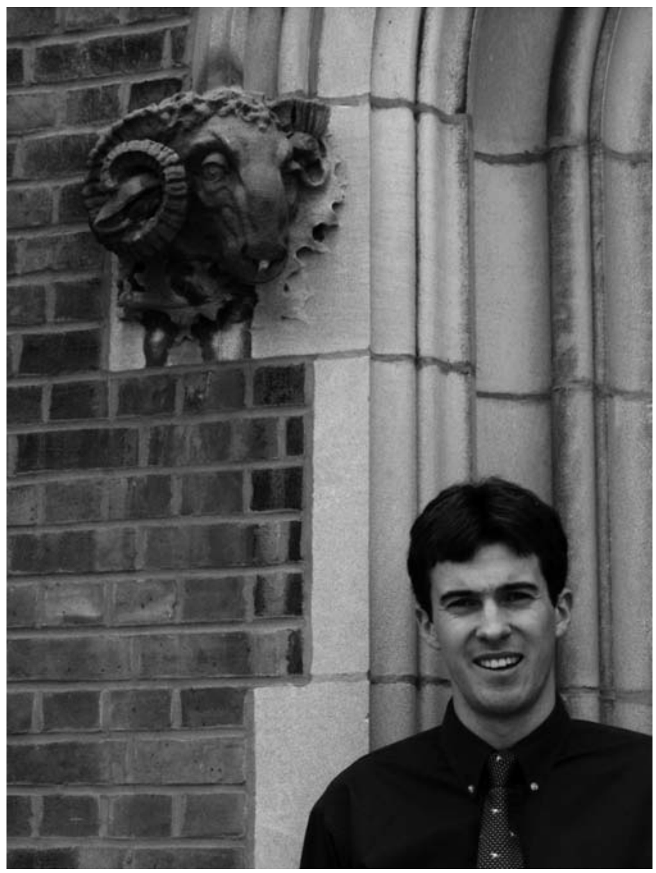

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