Removing Protected Populations to Save Endangered Species

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Conservation of species threatened with imminent extinction may require drastic measures that can be emotionally charged, politically unsavory, and legally challenging. A complex example relates to the decline of the island fox (*Urocyon littoralis*), endemic to the California Channel Islands, off the coast of the United States.

The island fox exists as six subspecies, each found on a separate island. Serious population crashes recently occurred on three islands after colonization by golden eagles (*Aquila chrysaetos*). Preying mainly on abundant feral pigs (*Sus scrofa*), eagles reached numbers sufficient to drive the unwary fox toward extinction (*1*). Two subspecies are now extinct in the wild, and a third, endemic to Santa Cruz Island, dropped from approximately 1500 to fewer than 100 in less than a decade (*2*). Efforts to protect foxes by translocating golden eagles have been successful (31 eagles have been translocated since 1999, with an associated increase in fox survival), but efforts to remove the last 7 to 10 eagles have failed, preventing fox recovery (*3*).

In the next few months, a plan to eradicate feral pigs will begin (*4*). This action will help restore the island's natural vegetation, and might also help fox recovery by removing the eagles' prey base. To assess this strategy, we investigated the effect of different levels of pig and eagle control on fox persistence (Fig. 1). Modifying a preexisting model of interacting dynamics (*1*, *5*), we simulated fox population sizes after 6 years, the projected time to pig eradication (*3*, *4*). Unexpectedly, pig control leads to decline or extinction of the fox population if eagle control is insufficient. This counterintuitive result occurs because eagle predation on foxes increases as pig availability declines. Congruent with this, fox recovery is directly proportional to the intensity of eagle removal.

Our model suggests that, had the eagle translocations not occurred, pig eradication could trigger deterministic fox extinction (Fig. 1C). After the translocations, pig eradication might ultimately facilitate fox recovery through eagle disappearance (Fig. 1D). However, fox numbers may first decline to <30 individuals, at which point population viability analysis predicts a high extinction probability (*5*): Demographic and environmental stochasticity, additional sources of food, Allee effects, and disease epizootics all are expected to increase the probability of fox extinction. Our parsimonious model predicts that foxes are highly sensitive to predation by eagles and warns of the potentially disastrous effect of removing pigs while eagles remain. Because eagle eradication is doubtful by translocation alone, other means should be pursued, including lethal removal, if the fox is to be saved.

The advocated removal of a magnificent bird of prey has significant legal challenges. In the United States, the Migratory Bird Treaty Act and the Bald Eagle and Golden Eagle Protection Act both prevent take of golden eagles except under special circumstances granted by the Secretary of the Interior.

This exemplifies how solving conservation problems is often more complex than redressing its primary cause (here, pigs). As often, biodiversity managers are now faced with a difficult dilemma. This time, it is associated with a paradox: the protection of the island fox, an endangered species, depends upon complete removal, by any and all means, of a small population of golden eagles, a protected species.

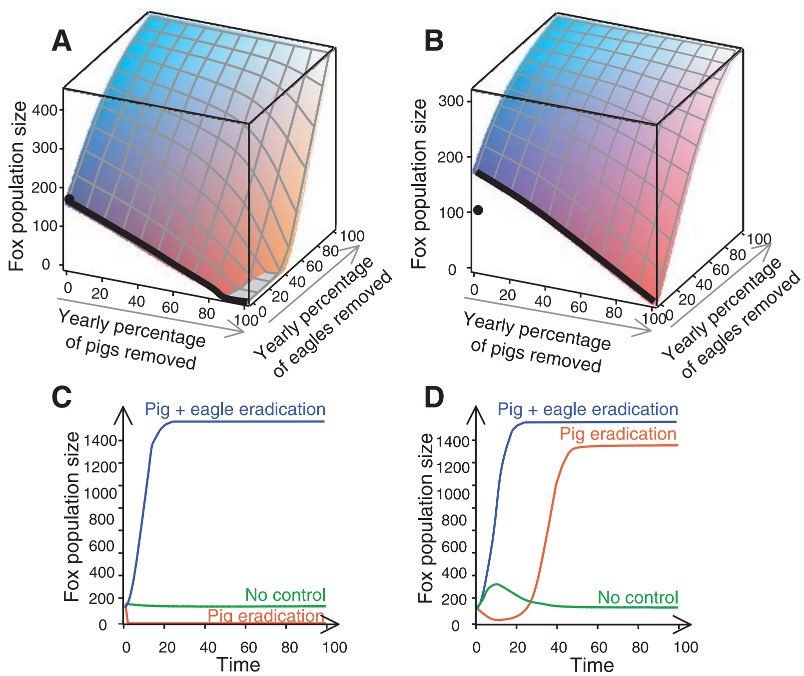

Fig. 1. Three-dimensional plot showing fox population size after 6 years of controlling pigs and/or eagles. (**A**) Initial conditions (solid circle) taken from (*1*): 25 eagles, 154 foxes, and 7561 pigs. (**B**) Conservative 2003 levels: 10 eagles, 100 foxes, and 1000 pigs. Controlling pigs only (black line) can result in fox extinction [gray area in (A)]. (**C** and **D**) Change in fox population size over 100 years following eradication of pigs only (red line), of pigs and eagles (blue line), and no control of either species (green line).

References and Notes

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5. Materials and methods are available as supporting material on *Science* Online.
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Supporting Online Material
www.sciencemag.org/cgi/content/full/302/5650/1532/DC1
Materials and Methods
References

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Supplementary online material:

We used a simple predator-prey model, where one predator (golden eagle = E) has the choice between two prey (fox = F, and piglet = P).

$$\begin{cases} \dfrac{dF}{dt} = r_f F\left(1 - \dfrac{F}{K_f}\right) - \mu_f \dfrac{\phi F}{\phi F + P} EF \\ \dfrac{dP}{dt} = r_p P\left(1 - \dfrac{P}{K_p}\right) - \mu_p \dfrac{P}{\phi F + P} EP - \omega P \\ \dfrac{dE}{dt} = \dfrac{\mu_f \lambda_f \phi F^2 + \mu_p \lambda_p P^2}{\phi F + P} E - \nu E - \delta E \end{cases}$$

Each prey population *i* is characterized by its intrinsic growth rate (r_i), its carrying capacity (K_i), a predation rate by eagles (μ_i), and a term of eagle preference for foxes (ϕ) relative to piglets. Eagle mortality rate is ν and the rate at which prey *i* are turned into new predators is given by λ_i. The control of pigs and eagles are given by ω and δ, respectively. Parameter estimates are the same as in (*S1*). Simulations are based on varying the intensity of ω and δ (from zero to 100%) for six years, the projected time to complete pig eradication (*S2, S3*), or for 100 years.

The model assumes a simple response from the eagle: after their primary prey is reduced or eradicated, eagles feed more heavily on foxes. This simple, linear response likely has more complex dynamics, especially if other species are considered. Alternative prey might be expected to lessen the eagle's impact on the fox, but our previous work suggests that foxes and piglets were the eagles' principle prey (*S1*). Alternative prey also might increase eagle survival and persistence, thereby leading to higher, long-term eagle predation on the fox. Other factors not considered in this model, including stochastic variation in vital rates, environmental perturbation, Allee effects, disease introduction and the presence of pig carcasses left over from the eradication all are expected to further increase the probability of fox extinction. Models accounting for the presence of pig carcasses or of an Allee effect in foxes (not shown) showed increased extinction risks.

Moreover, comparative estimates of the persistence of fox populations of different size suggest that the risk of extinction increases with declining population size and disease severity (*S4*). At a population size of $\geq$ 200 foxes extinction risk is only 1% in 50 years. When population size declines to 50 individuals extinction risk increases to 20% and at 20 animals it increases to nearly 60%. Population declines due to catastrophic events have actually occurred. Between 1998 and 1999, the Santa Catalina Island fox population was reduced by approximately 90% owing to a canine distemper virus epizootic (*S5*). Any deterministic decline of an island fox population would therefore raise the probability of stochastic extinction to unacceptable levels.

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S2. T. Coonan, K. Rutz. *Island Fox Captive Breeding Program 2002 Annual Report* (National Park Service, Channel Islands National Park, Ventura, Calilfornia, 2003).
S3. U.S. National Park Service. *Santa Cruz Island Primary Restoration Plan* (2002; www.nps.gov/chis/restoringsci/island.html).
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S5. S. Timm *et al*. *Island Fox Recovery Efforts on Santa Catalina Island, California*. (Santa Catalina Island Conservancy, Avalon, California, 2002).

(ESRF), FEDERATION OF EUROPEAN CHEMICAL SOCIETIES (FECS), FEDERATION OF EUROPEAN MATERIALS SOCIETIES (FEMS), FEDERATION OF EUROPEAN MICROBIOLOGICAL SOCIETIES (FEMS), FEDERATION OF EUROPEAN NEUROSCIENCE SOCIETIES (FENS), FEDERATION OF EUROPEAN PHARMACOLOGICAL SOCIETIES (EPHAR), MARIE CURIE FELLOWSHIP ASSOCIATION (MCFA), "SAUVONS LA RECHERCHE" (SLR).

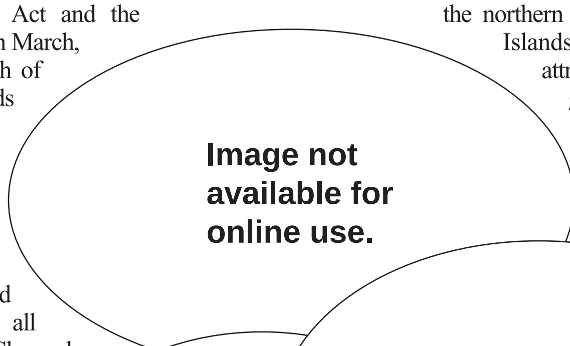
Predators and Prey in the Channel Islands

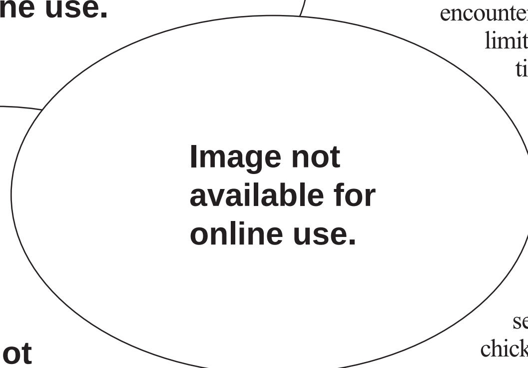
IN THEIR BREVIA, "REMOVING PROTECTED populations to save endangered species" (28 Nov., p. 1532), F. Courchamp *et al.* use a predator-prey model on Santa Cruz Island to make the case for lethal removal of golden eagles (*Aquila chrysaetos*) from Channel Islands National Park. In the model, as nonnative feral pigs (*Sus scrofa*) are removed, eagles increasingly target native foxes (*Urocyon littoralis*) and could drive them to extinction if mitigating measures are not taken. But in fact, some of the underlying factors in this model do not represent actual conditions.

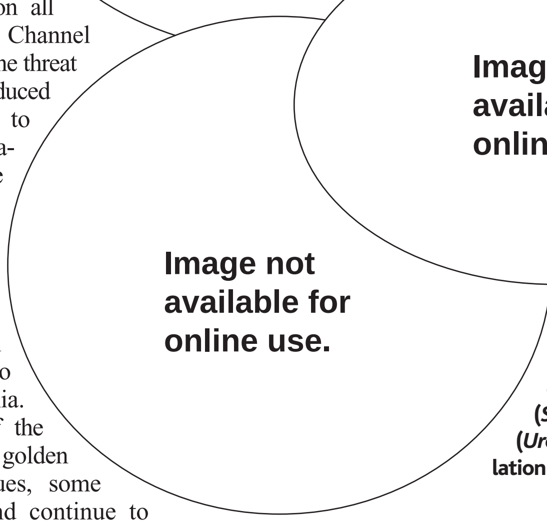
Eagles are protected under the Bald and Golden Eagle Protection Act and the Endangered Species Act. In March, the fox subspecies on each of the northern Channel Islands were listed as endangered, and measures to prevent fox extinction and ultimately provide for recovery are being taken. Between 1999 and 2002, foxes were captured and brought into captivity on all three of the northern Channel Islands, to be held until the threat from eagles is further reduced or eliminated, and to increase wild fox populations through captive breeding and release. A working group of 90 professionals advises the fox recovery effort. Since 1999, 35 golden eagles have been captured and relocated to northern California. Despite employment of the most effective known golden eagle capture techniques, some eagles evade capture and continue to breed and prey on foxes.

Running a captive breeding program on three island locations is not without its own risks, particularly from disease, loss of genetic variation, and changes in behavior. For those reasons, and to learn more about the efficacy of restoration in the face of a novel predator, foxes were released from the breeding facilities on Santa Cruz and Santa Rosa Islands starting in December 2003. On Santa Cruz, five of the nine foxes released were killed by golden eagles, and the remaining four were returned to captivity. On Santa Rosa, one of the released foxes died of eagle predation, seven remain in the wild, and a pair of the released foxes has produced two pups. Captive-bred foxes seem much more susceptible to eagle predation. In contrast, annual survivorship of the remaining wild foxes on Santa Cruz was 80% in 2003, as determined by radiotelemetry.

Even with a high population of pigs present, the island foxes released from captivity experienced a high predation rate, suggesting that they were the preferred food for some eagles or the more accessible food in some areas. Moreover, the removal of the pigs on Santa Cruz is necessary for the recovery of nine endangered or threatened plants. Bald eagles (*Haliaeetus leucocephalus*), which were the dominant raptor species on the islands until the 1950s, coexisted with abundant fox populations. They have recently been reintroduced to Santa Cruz Island. Mature bald eagles and the absence of all feral prey should make the northern Channel Islands less attractive to golden eagles.







In the California Channel Islands, golden eagles (*Aquila chrysaetos*) prey on feral pigs (*Sus scrofa*) and island foxes (*Urocyon littoralis*). The fox population is in decline.

CREDIT: JEFF VANUGA/CORBIS; CLIVE DRUETT, PAPILIO/CORBIS; KENNAN WARD/CORBIS

Island foxes were brought into captivity because of predation by golden eagles. Because foxes are successfully breeding in captivity, the immediate threat of extirpation is low, even with pig removal. Although Courchamp *et al.*'s model therefore has limited application, the policy issue of lethally removing a protected predator is entirely relevant to fox recovery. Such lethal removal of golden eagles may be the only management action which, in the end, permits recovery of island foxes. It can now be reviewed and evaluated under the process by which federal agencies safeguard species and landscapes.

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IN THEIR BREVIA "REMOVING PROTECTED populations to save endangered species" (28 Nov., p. 1532), F. Courchamp *et al.* describe a remarkable ecological scenario from California's Channel Islands, where the introduction of pigs enabled colonization by golden eagles, resulting in the decline of an endemic island fox via eagle predation. Courchamp *et al.* predict that without the complete removal of eagles, eradication of pigs would amplify threats posed by the eagles to the foxes. They have called the actual and predicted dynamics of this system "unexpected" and "unique" (*1*). Although highly illuminating, this example may represent a special case of a scenario more common than the authors appreciate.

The original human settlers of Polynesia encountered islands with rich avifaunas, limited reptile and bat faunas, and plentiful inshore marine resources (*2*, *3*). These resources alone were probably insufficient to sustain resident human populations (*3*). Instead, humans spread throughout Polynesia by transporting horticulture and animal husbandry from Near Oceania, introducing many plants and several animals (pigs, dogs, and chickens) throughout the Pacific (*3*). Subsequently, pigs were the only large nonhuman mammal in Pacific ecosystems, existing on various islands in domesticated and feral states. They were certainly exploited for food, but the extent to which humans relied on them is uncertain (*4*, *5*). Nevertheless, they were intentionally translocated throughout Polynesia in tandem with human expansion (*4*) and may have played a role in successful human establishment throughout the region.

Anthropogenic impacts of human colonization and expansion in the Pacific ultimately resulted in the extinction of thousands of native insular bird and reptile species (*2*). In potentially assisting human colonization, pigs may have played an indirect role in these declines. Interestingly, some islands where pigs were introduced but later became extinct (*4*) suffered extremely high levels of avifaunal extinction (*6*). The situation in the Channel Islands may represent an analogous case, singularly unique in that the apex predators in this case are golden eagles rather than humans.

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Response

DRATCH *ET AL.* ARGUE THAT OUR MODEL OF apparent competition involving golden eagles, feral pigs, and critically endangered island foxes "has limited application," because "underlying factors… do not represent actual conditions." We contend that its implications for island fox conservation are crucial.

Our model—like all models—is an abstraction that cannot predict what will happen, but only suggests what may happen. Our model was derived from another that accurately depicted fox decline following golden eagle colonization (*1*). We took great care to parameterize it to reflect conditions both before and after the translocation of golden eagles. Hence, our model was based on the best available data. We acknowledge that our formulation ignored the recent reintroduction of bald eagles, but we caution that deterrence of golden eagles by bald eagles is speculative (*2*). Although we support bald eagle reintroduction, we do not believe that decisions concerning fox recovery should hinge on the assumption that this undocumented management action will work.

Although we are reassured by the persistence of foxes in captivity and acknowledge the National Park Service's (NPS) efforts in averting extinction, captive populations are no substitute for wild ones. Further, the NPS has delayed several conservation measures that could have improved the chances of recovery (*3*), and the recent unsuccessful releases of captive foxes on Santa Cruz Island described by Dratch *et al.* were conducted against the advice of the "working group of 90 professionals" (*4*). Finally, the NPS already had information on the "efficacy of restoration in the face of a novel predator." In 2002, they released three captive-borne foxes on Santa Cruz Island and two were killed by golden eagles (*3*). Such decisions point to the need for the NPS to base resource management in the National Parks on sound science (*5*).

We have previously advocated—with great regret—the lethal removal of golden eagles that have proven too elusive to capture (*6*). We are encouraged that Dratch *et al.* agree that this measure may be necessary, but we are concerned that they may not view this action as urgent. Whether pig eradication alone will prompt the extinction or recovery of wild foxes can only be known for certain by trying it—our research shows that the risk of extinction is high. The precautionary principle therefore suggests that immediate, and complete, removal of golden eagles is the measure needed to spur recovery of the critically endangered island fox.

Helgen suggests that domestic/feral pigs "may have played a role in successful human establishment" throughout Polynesia and "may have played an indirect role" in the declines of insular bird and reptile species via apparent competition. We find Helgen's hypothesis both clever and thought provoking, but we also note that apparent competition is difficult to elucidate and often overlooked as an important process in communities and ecosystems (*7*, *8*). We considered the case on the Channel Islands to be "unique" because we were able to show that apparent competition was responsible for the trophic reorganization of this vertebrate community and that it ultimately led to the near extinction of an endemic insular carnivore (*1*). In contrast, although it is highly likely that pigs played some role in the extinctions of insular fauna in the Polynesian region, it is difficult to be sure whether these past extinction events were due to apparent competition, or to direct effects such as predation and habitat modification (*9–11*).

The value of our study was essentially threefold: We were able to reveal the mechanism responsible as it occurred, we linked this mechanism with a loss in biodiversity that resulted from the introduction of an exotic species, and we then projected possible effects of management actions. The community reorganization was "unexpected": No one predicted that golden eagles would colonize the islands as a consequence of the pigs' presence. Our model projections were likewise "unexpected": Removing pigs at first seemed a logical solution to the problem, yet our model suggested that this might cause eagles to focus more on the remaining foxes, increasing the latter's probability of extinction.

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CORRECTIONS AND CLARIFICATIONS

Letters: "The health benefits of eating salmon" by C. M. Rembold (23 July, p. 475). The credit for the image accompanying this letter was inadvertently omitted. The credit should be Pat Wellenbach/AP.

TECHNICAL COMMENT ABSTRACTS

COMMENT ON "Observation of the Inverse Doppler Effect"

Evan J. Reed, Marin Soljacic, Mihai Ibanescu, John D. Joannopoulos

Seddon and Bearpark (Reports, 28 November 2003, p. 1537) presented a creative and exciting observation of a reversed Doppler effect when an electromagnetic shock propagates through a transmission line. We find that the physical origin of this anomalous effect is fundamentally different from the one suggested by Seddon and Bearpark (that $v_{phase}v_{group} < 0$) but that the experimental results can be properly validated with the correct theory.

Full text at www.sciencemag.org/cgi/content/full/305/5685/778b

RESPONSE TO COMMENT ON "Observation of the Inverse Doppler Effect"

N. Seddon, T. Bearpark

We thank Reed *et al.* for their comments and alternative interpretation of the experimentally observed inverse Doppler shift. However, we believe that the wave propagation and reflection processes presented in the original paper accurately describe the physical mechanisms in this experiment.

Full text at www.sciencemag.org/cgi/content/full/305/5685/778c