

# Induced changes in island fox (*Urocyon littoralis*) activity do not mitigate the extinction threat posed by a novel predator

Brian R. Hudgens · David K. Garcelon

Received: 29 June 2009 / Accepted: 16 August 2010  
© Springer-Verlag 2010

**Abstract** Prey response to novel predators influences the impacts on prey populations of introduced predators, bio-control efforts, and predator range expansion. Predicting the impacts of novel predators on native prey requires an understanding of both predator avoidance strategies and their potential to reduce predation risk. We examine the response of island foxes (*Urocyon littoralis*) to invasion by golden eagles (*Aquila chrysaetos*). Foxes reduced daytime activity and increased night time activity relative to eagle-naïve foxes. Individual foxes reverted toward diurnal tendencies following eagle removal efforts. We quantified the potential population impact of reduced diurnality by modeling island fox population dynamics. Our model predicted an annual population decline similar to what was observed following golden eagle invasion and predicted that the observed 11% reduction in daytime activity would not reduce predation risk sufficiently to reduce extinction risk. The limited effect of this behaviorally plastic predator avoidance strategy highlights the importance of linking behavioral change to population dynamics for predicting the impact of novel predators on resident prey populations.

**Keywords** Behavioral plasticity · Extinction risk · Predator avoidance · Matrix model · Species recovery

---

Communicated by Peter Banks.

---

B. R. Hudgens (✉) · D. K. Garcelon  
Institute for Wildlife Studies,  
PO Box 1104, Arcata, CA 95518, USA  
e-mail: hudgens@iws.org

D. K. Garcelon  
e-mail: garcelon@iws.org

## Introduction

Predicting the consequences of species interactions is a long-standing ecological challenge, one that has become increasingly important as human activities bring together species with little or no evolutionary history. Introduced predators pose one of the most persistent, potent, and pervasive threats to island populations (Clavero and Garcia-Berthou 2005). Deliberate introduction of predators as biological control agents or fur-bearing animals often wreaks havoc on native prey species (Salo et al. 2007; Kauhala 1996; Simberloff and Stiling 1996). In addition, many prey species are faced with novel predators as species ranges shift due to global climate changes and human impacts on the landscape (Gompper 2002; Roemer et al. 2002). The impact of a novel predator on prey populations may be mitigated or exacerbated by predator effects on prey behavior. Prey may adapt new foraging strategies to reduce predation risk, such as increasing vigilance (Berger et al. 2001), utilizing different habitats (Lima and Bednekoff 1999; Werner et al. 1983), or shifting daily activity patterns (Holomuzki 1986; Lima and Bednekoff 1999). Because behavioral adaptations can occur on an ecological time scale, they have the potential to mitigate impacts of novel predators on resident prey species. However, this potential may be limited by evolutionary constraints or ecological costs (Werner et al. 1983), which in turn limit the population-level effect of adaptive behavioral change. Because of such limitations, the impact of a novel predator depends not only on prey behavioral responses, but also on the link between those responses and population consequences.

Understanding the consequence of novel predators on prey behaviors can be informed by ecological and evolutionary prey responses to the loss of major predators. Many prey species expand their activities to new spatial or temporal

habitats in the absence of predators. A comparison of the activity patterns of the island fox (*Urocyon littoralis*) and the mainland grey fox (*U. cinereoargenteus*) from which it evolved provides a good example. Grey foxes are almost completely nocturnal on the southern California mainland (Kavanau and Ramos 1975) where there is significant predation risk from bobcats and coyotes (Farias et al. 2005), and, perhaps most significantly with respect to activity patterns, golden eagles (Geffen and MacDonald 1993). In contrast, island foxes have evolved for the past 10,000–16,000 years off the California coast (Wayne et al. 1991) and, in the absence of significant predation risk, are active at all times of day and night (Crooks 1994; Crooks and Van Vuren 1995).

A recent invasion of golden eagles (*Aquila chrysaetos*) to the Channel Islands presents a unique opportunity to evaluate not only prey behavioral response to a novel predator, but also the population-level consequences of that response. Although bald eagles (*Haliaeetus leucocephalus*) inhabited the island until the 1950s (Kiff 1980), these scavengers mainly fed on fish and birds; land mammals as a group represented only 1% of their diet (Collins et al. 2005). In contrast, golden eagles are proficient hunters of land mammals, which comprised nearly 60%—island foxes alone comprised 7.2%—of the diet of golden eagles resident to the Channel Islands (Collins and Latta 2009). In the face of this novel and effective predator, island fox populations rapidly declined to less than 10% (Roemer et al. 2002) of the pre-invasion population peak estimated at approximately 1,500 adult foxes (Roemer et al. 1994), leading to the species being listed under the Endangered Species Act (United States Fish Wildlife Service 2004). Fox populations continued to decline through 2003 (Bakker et al. 2005). From 2003 to 2005 the minimum number of island foxes known alive on Santa Cruz island increased for the first time since before 1999 from 56 to 104 animals (Schmidt et al. unpublished data), coinciding with the most dramatic reduction in eagle numbers on the island (from 14 at the end of 2002 to 3 at the end of 2005), resulting from eagle removal efforts commencing in 1999 (Coonan et al. 2005).

Predation-risk theory (Lima and Bednekoff 1999) and studies on closely related species (Geffen and MacDonald 1993; Kavanau and Ramos 1975) suggest that island foxes should respond to golden eagle invasion by increasing foraging efforts at night when predation risk remains low, while decreasing daytime activity when predation risk is high. If these responses reflect behavioral plasticity in daily activity patterns, island foxes should revert to more diurnal habits as predation pressure is alleviated following golden eagle removal. A sufficiently strong behavioral shift could mitigate the extinction threat posed by golden eagles by reducing predation pressure on the fox to sus-

tainable levels. However, island fox behavioral response to golden eagle invasion may have been limited by other evolutionary or ecological pressures, such as failure to recognize the eagle predator archetype (Cox and Lima 2006), limited behavioral plasticity, low standing genetic variation, or constraints imposed by foraging requirements. Such limitations could result in a behavioral response that, though noticeable, is not sufficient to mitigate the impact of golden eagles on island fox populations, exemplifying what Banks and Dickman (2007) called level III prey naïveté.

In this paper we compare fox activity patterns following the invasion of a novel predator, the golden eagle, to observations reported by Crooks (1994) prior to the arrival of golden eagles on the islands and document a shift in island fox activity patterns towards greater nocturnal habits. We also document a reversion toward more diurnal habits in individual foxes over the course of golden eagle removal efforts. We then demonstrate that although there was a substantial behavioral response consistent with predator avoidance, it was not sufficient to offset the severe predation pressure imposed by golden eagles on a time scale relevant to fox conservation.

## Methods

Between January 2003 and April 2005 we radio tracked a total of 99 wild-born adult island foxes (37 male and 62 female) on Santa Cruz Island, CA (34°0'N, 119°45'W). Island foxes were radio collared during annual population surveys conducted from 2003 to 2005, supplemented by targeted efforts to trap known animals not captured during population surveys. Foxes were tracked for an average of 13.6 months each ( $\pm 9.3$  months SD; range 1–871 days). We used transmitter collars from two manufacturers (Holohil Systems Ltd., Carp, Ontario, Canada, and Advanced Telemetry Systems, Isanti, MN), equipped with mortality sensors. Activity monitoring was conducted as part of the effort to collect data on island fox survival. We collected a total of 9,814 activity checks (Table 1). Activity checks occurred an average of 3.5 days apart. Checks were made using a telemetry receiver (Model R-1000, Communications Specialists, Orange, CA) and a three-element yagi antenna. Each time a telemetry signal was received, field personnel would listen for 2 min to determine if the transmitter was moving. When the polarity of the transmitting antenna changes with respect to the receiving antenna, the tone of the signal modulates and can be detected by the operator. When the animal is stationary, there is no modulation. For the animal to be considered “active,” a modulating signal had to be heard for half of the 2-min period.

## Fox activity 2003–2005

We first separated the 24-h day into dawn, daytime, dusk, or nighttime hours, and recorded which observations occurred during each of these periods. Except as noted below, dawn and dusk were designated as 1 h before and after civil twilight on the day of observation; daytime hours were designated as between 1 h after morning civil twilight to 1 h before evening civil twilight; and nighttime hours were designated as 1 h after evening civil twilight to 1 h before morning civil twilight. Civil twilight times for Santa Cruz Island were taken from a US Navy database (<http://aa.usno.navy.mil/data/>). Too few observations were taken in the dawn hours to allow for meaningful comparisons, so we excluded these observations from further analyses.

For each individual, we determined the proportions of observations taken during a given time period when it was active. Observations for which activity could not be determined or from dead animals were excluded from analyses. To ensure independence between the mean and variance of proportional data, we applied an arcsine-square root transformation before analyses (Sokal and Rohlf 1995). Differences in activity patterns between daytime, dusk, and nighttime periods were analyzed with a repeated measures ANOVA and paired *t* tests, as appropriate, using individuals as the repeated measure. Differences in activity patterns across years were analyzed by within-subject tests of a repeated measures ANOVA for relative daytime and nighttime activity. Relative daytime (nighttime) activity was calculated as the proportion of daytime (nighttime) observations in which a fox was active divided by the sum of the proportions of daytime, dusk, and nighttime observations in which a fox was active. Only foxes for which we had observations for all three periods for all 3 years ( $n = 17$ ; Table 1) were used to examine differences in activity patterns across years. We present analyses for both relative daytime and nighttime activity even though the method used to calculate these values introduces some degree of correlation between them. Analyses were conducted using SAS software (SAS 8.2; SAS Institute).

**Table 1** Number of activity checks conducted by year and time period

Year	Day	Dusk	Night
2003	1,024	91	56
2004	2,679	976	2,034
2005	1,126	593	1,235
2003–2005	1,919	570	897

The *last row* indicates the number of activity checks during each time period from animals followed in all three time periods for all 3 years of the study

## Shift in activity patterns 1992 versus 2003–2005

To determine if island foxes had shifted activity patterns since 1992, a time prior to the regular occupation of the island by golden eagles, we compared the proportion of animals that were active during daytime and nighttime hours to that reported by Crooks (1994). Both studies took place in areas of the island with moderate to heavy vegetative cover (K. Crooks, personal communication). We re-analyzed our data to conform to Crooks' methods. Crooks (1994) conducted a total of 592 diurnal activity checks and 614 nocturnal activity checks from 12 foxes between January and November 1992. Following Crooks (1994), we defined daytime hours as the period between 07:00 and 19:00 h, and nighttime hours as the period between 19:00 and 07:00 h for purposes of this comparison. For each of these periods we calculated the numbers of observations taken when animals were active or inactive. There was less than a 1% difference between activity patterns of the fox population (i.e., the overall fraction of observations that animals were active) and individual activity patterns (i.e., the mean relative activity of individual foxes) for the same time periods. We compared these numbers to those reported by Crooks using a chi-square test.

## Estimated impact of behavioral shift

To determine the potential for observed behavioral modifications to mitigate the extinction risk posed by eagles, we evaluated a three-stage matrix model (Table 2). We compared predicted population growth rates of baseline and reduced mortality models. The baseline model assumed mean survivorship and fecundity values from 1993 through 1999 taken from Roemer (1999). This period encompasses the invasion and population peak of golden eagles on Santa Cruz Island (Coonan et al. 2005). We made the simplifying

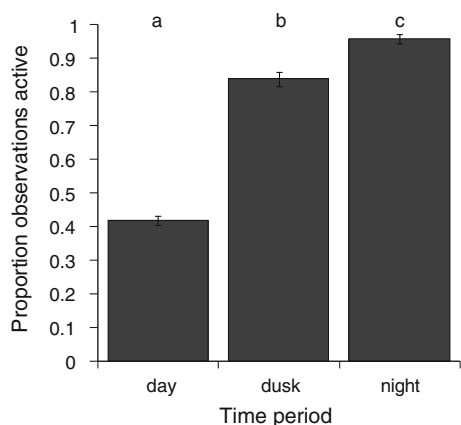
**Table 2** Stage-based transition matrices used to predict island fox population growth

	Pup	Yearling	Adult
Baseline matrix			
Pup <sup>a</sup>	0	0.28	0.66
Yearling <sup>b</sup>	0.22	0	0
Adult <sup>c</sup>	0	0.51	0.43
Reduced mortality matrix			
Pup <sup>a</sup>	0	0.28	0.66
Yearling <sup>b</sup>	0.3058	0	0
Adult <sup>c</sup>	0	0.5639	0.4927

<sup>a</sup> Number of female pups produced/female fox multiplied by pup survivorship

<sup>b</sup> Annual survivorship for yearling foxes

<sup>c</sup> Annual survivorship for adult foxes



**Fig. 1** Diurnal differences in activity patterns of radio-collared island foxes (*Urocyon littoralis*) on Santa Cruz Island, CA. Each bar represents the fraction of all observations of the 99 animals tracked from 2003 to 2005 taken during that time period (defined relative to civil twilight as described in the text) during which an animal was active. Error bars indicate  $\pm 1$  SE. Significantly different activity levels (paired  $t$  test,  $P < 0.05$ ) among periods are indicated by differing letters above bars

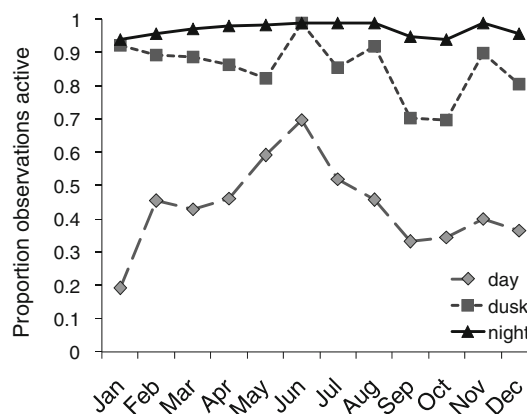
assumption that a reduction in diurnal activity resulted in an equivalent proportional reduction in age-specific mortality. For example, a 5% (absolute) reduction in diurnal activity from 50 to 45% would represent a 10% proportional reduction, resulting in a proportional reduction in age-specific mortality by 10% (e.g., from 80 to 72%) in the reduced mortality model. Predicted population growth rates for models assuming full eagle predation (baseline model) and reduced mortality (modified model) were calculated as the dominant eigenvalues of the corresponding transition matrices. We determined the minimum impact that a behavioral response would need to have on age-specific mortality rates to prevent population decline as rates that resulted in a predicted population growth rate of one (i.e., a stable population).

## Results

### Fox activity 2003–2005

While island foxes were active throughout a 24-h day, they were least likely to be active during daytime hours, and most likely to be active during nighttime hours (repeated measures ANOVA  $F_{2,186} = 528$ ,  $P < 0.001$ ; Fig. 1). Foxes were less than half as likely to be active during the daytime as during dusk or nighttime (Fig. 1). Peak activity periods occurred in May and June, and then declined through the fall and winter months (Fig. 2). There was no clear pattern in the relative activity rates during different periods of the day throughout the year.

Between 2003 and 2005, island foxes became more active in general, particularly during the daytime and dusk



**Fig. 2** Seasonal activity patterns of radio-collared island foxes (*Urocyon littoralis*) on Santa Cruz Island, CA. Lines represent the proportion of observations which foxes were active during each time period taken during the calendar month averaged over 99 animals tracked between 2003 and 2005

hours (Fig. 3b). We only had data for all three periods of the day for all 3 years for 17 foxes. During this interval, individual foxes became more diurnal, increasing their daytime activity and decreasing their nighttime activity relative to their overall activity level (daytime:  $F_{1,32} = 4.98$ ,  $P < 0.02$ ; nighttime:  $F_{1,32} = 12.78$ ,  $P < 0.001$ ; Fig. 3b).

### Shift in activity patterns 1992 versus 2003–2005

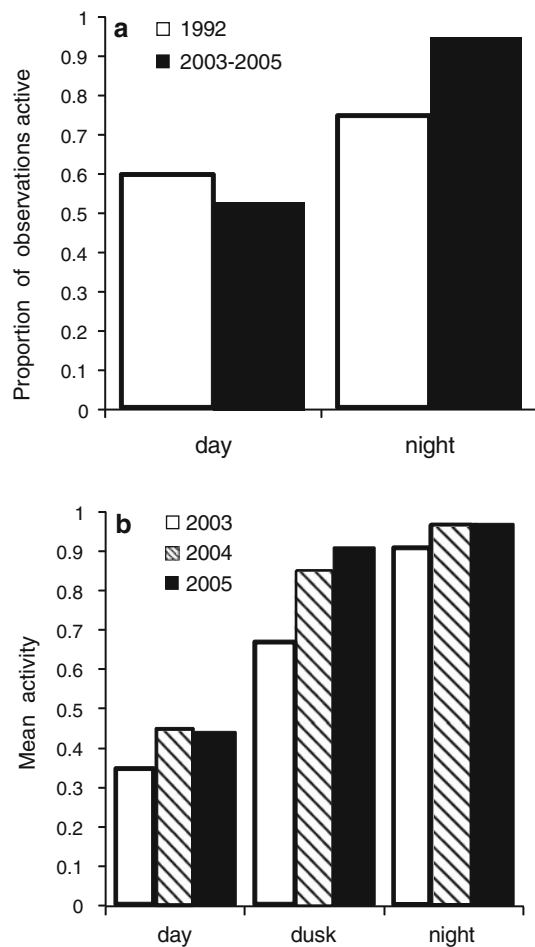
Island foxes have become less diurnal since golden eagles invaded Santa Cruz. Island foxes in this study were 7% less likely to be active during the daytime and 20% more likely to be active at nighttime than eagle-naïve island foxes studied by Crooks in 1992 ( $\chi^2 = 11.3$ ,  $P < 0.001$ ; Fig. 3a). These changes correspond to an 11.7% proportional reduction of diurnal activity and 26.7% proportional increase in nocturnal activity between 1992 and 2003–2005.

### Estimated impact of behavioral shift

The baseline model predicted a deterministic population decline of 36% per year, comparable to the observed decline from 1993 through 1999 (Roemer et al. 2002). The reduced mortality model still predicted a 26% annual population decline. In order to prevent a population decline, a behavioral response to golden eagle predation would have to reduce age-specific mortalities by 44% from the baseline mortalities used in the model.

## Discussion

Island foxes were less likely to be active during the daytime and more likely to be active at night during our study than



**Fig. 3** Changes in fox activity through time. *Top panel (a)* shows proportion of all observations from active foxes in 1992 ( $n = 12$ ) and 2003–2005 ( $n = 99$ ) active in the daytime and nighttime as defined by Crooks (1994) (i.e., day = 07:00–19:00, night = 19:00–07:00). *Bottom panel (b)* shows mean ( $\pm 1$  SE) activity levels during different periods of the day (defined relative to civil twilight as described in the text) of individual foxes tracked continuously from 2003 to 2005 ( $n = 17$ ). Activity levels refer to the proportion of activity checks of an individual fox during each time period that it was active

they were in 1992 before exposure to golden eagles. Increased diurnal activity by individual foxes throughout a period of golden eagle removal indicates that this response is at least partially driven by behavioral plasticity. The small magnitude of the observed behavioral modification limits its potential to mitigate the extinction threat posed by golden eagles.

Factors other than eagle predation that may have influenced fox activity have also changed in the decade separating our study from Crooks (1994), including severely reduced fox density (Coonan et al. 2005), removal of feral grazers and associated changes in vegetation (Cohen et al. 2009), and fluctuations in the numbers of fox prey species. A similar reduction in island fox densities caused by disease on Santa Catalina Island (Timm et al. 2009) did not

result in a decline in diurnal activity (Swarts et al. 2009), and recovery of vegetation following removal of feral grazers would have been continuing from 2003 to 2005, when island foxes in our study were reverting to increased diurnality. While we cannot rule out prey availability as a contributing factor, foxes have been commonly observed during the daytime on San Clemente Island through dramatic fluctuations in rodent densities (BH personal observation).

Our results are consistent with theoretical predictions on predator avoidance (Lima and Bednekoff 1999) and observations in other species. Eagle predation risk is associated with reduced activity in minks (Salo et al. 2008), and predation risk has been associated with changes in diurnal activity in guppies (Fraser et al. 2004), salmon (Metcalf et al. 1998) and rats (Fenn and MacDonald 1995). Although shifting circadian patterns to avoid predation has been well documented in many systems, island fox response to golden eagles presented here and by Swarts et al. (2009) represents the first example we are aware of demonstrating shift in daily activity patterns as a result of a novel predator.

In contrast to Swarts et al. (2009), we find strong evidence that changes in diurnal activity in response to golden eagle invasion represents a behaviorally plastic response to predation pressure. Since Swarts et al. (2009) included the same 2003–2005 dataset, the differences likely stem from how these data were analyzed. We specifically analyzed changes in the relative amounts of diurnal activity of individual foxes in response to reduced predation pressure from 2003 to 2005, providing a more powerful test of intragenerational response by eliminating nuisance sources of variation such as differences in the overall activity and diurnality of individual foxes, and annual differences in overall activity, while the analysis used by Swarts et al. (2009) provided a more powerful test to determine seasonal and pre- versus post-golden eagle invasion effects. We note, however, that their choice of seasons (differences between December–April and May–November) did not follow the patterns of fox behavior. Because these seasons did not correspond to a part of the fox annual cycle tied to activity, such as the pup-rearing season (May–July) versus the rest of the year, fox activity varied greatly within each of the periods they examined (Fig. 2), reducing their ability to detect seasonal effects.

Behaviorally plastic response to predation pressure is likely a common phenomena in nature and has been observed in a wide variety of other systems. Examples include ungulates, which adapted more vigilant behaviors after witnessing predation of young at the invasion front of reintroduced carnivores (Berger et al. 2001); larval salamanders, which became more active at night when exposed to predatory dytiscid beetles (Holomuzki 1986); and a diurnal population of rats, which reverted to nocturnal

behaviors when experimentally protected from nocturnal red foxes (Fenn and MacDonald 1995).

We cannot rule out evolutionary adaptation or other mechanisms contributing to the observed reduction in diurnal activity observed in our study. Indeed, it seems likely that golden eagles may have effected adaptive evolutionary changes in island fox behaviors. Daytime activity levels were positively associated with eagle mortality risk for radio-collared animals between 1993 and 1994 (Roemer et al. 2002). Golden eagles killed 73% of the foxes in that study, representing strong selective pressure favoring predator avoidance. In contrast, eagles killed only 14.1% (14/99) of our study animals, and we did not find higher daytime activity levels in eagle-killed versus surviving foxes (mean percent daytime observations active  $\pm$  SD: foxes killed by eagle =  $33 \pm 4.9\%$ , foxes not killed by eagles =  $43 \pm 1.5\%$ ). The lack of relationship between diurnal activity and eagle predation is perhaps due to reduced golden eagle numbers, the elimination of island foxes genetically predisposed to relatively higher diurnal tendencies, increased eagle vigilance in the modern island fox population, elimination of island foxes from high-risk areas of the island, or a greater reduction in diurnal activity in areas of a fox's home-range exposed to eagles (e.g., diurnal activity may be associated with higher vegetative cover).

Island foxes in this study exemplified a type 3 prey naïveté, exhibiting an appropriate predator avoidance behavior but still being overwhelmed by a novel predator (Banks and Dickman 2007). Consequently, golden eagle removal was a necessary component to successful recovery efforts (Coonan and Schwemm 2009). Island fox (log) survivorship on the northern Channel Islands between 1999 and 2003 was tightly correlated with the number of eagles remaining on the island ( $r^2 = 0.997$ ; calculated from Coonan et al. 2005), further suggesting a relatively small population-level benefit realized from behavioral modification. The importance of such behavioral changes for prey conservation may not, however, be in preventing population extinction in the absence of conservation efforts, but in buying time for enacting conservation measures. Even a small reduction in population decline due to behavioral modification can increase the chances that these conservation efforts might succeed.

The demands associated with breeding often drive animals to adopt behaviors that increase predation risk (Rohr et al. 2003). Unfortunately for island foxes, the period when increased diurnal activity is most beneficial—when feeding young pups—corresponds to the time when eagles are most actively hunting to feed their own young. One-third of known eagle predation events on island foxes between 2001 and 2006 occurred during May and June (Schmidt et al. unpublished data), corresponding to the peak provisioning period of golden eagle chicks (Collopy 1984). This high-risk

period coincides with increased island fox activity as their pups approach independence. Additional limits on a behavioral response to novel predators include prey nutritional state (Metcalf and Steele 2001), physiological traits (Benard 2006) and other constraints allowing only partial adoption of a strategy for all individuals. Ultimately, the population consequences of a particular predator avoidance strategy depend on limits to how that strategy affects the mean fitness of individuals in the population.

Predator avoidance strategies in response to novel predators may also influence interactions between prey and other species within ecological communities. For example, the island skunk, endemic to Santa Cruz Island, is nearly completely nocturnal, presumably to reduce interactions with the competitively superior foxes (Crooks and Van Vuren 1995). As foxes recover following golden eagle removal from the island, their increased nocturnal behaviors may exacerbate the negative impact of increasing numbers of foxes on skunk populations (Roemer et al. 2002) by increasing the per capita effects of foxes on skunks through increased interactions or by increasing the dietary overlap as foxes spend less time foraging on diurnal prey. As was the case for island fox population response to golden eagles, the influence of increased island fox nocturnality on island skunk populations would appear to be rather limited compared to the influence of reduced fox numbers, as indices of island skunk populations increased 17-fold following golden eagle invasion (Roemer et al. 2002).

We do not mean to imply that behavioral responses generally do not influence population processes; rather, that the links between prey behavioral responses and population processes are complex and need to be considered explicitly if we are to understand the population and community consequences of prey facing novel predators. While prey behavioral responses to novel predators may well influence its population response, it is not sufficient to study anti-predator behaviors without the context of how changes in those behaviors affect prey population dynamics.

**Acknowledgments** We thank R. Wolstenholme, J. Fox, A. Blackford, J. Chelko, C. Newman, Z. Smith, K. Kapheim, G. Cline, R. Rumelhart, S. Krause, and G. Schmidt for their efforts in collecting and managing activity data. D. Van Vuren, The Nature Conservancy, National Park Service, and US Navy provided logistical support. The manuscript was improved by comments from K. Crooks, T. Coonan, B. Cypher, M. Potter, and J. Young. Data collection was funded by The Nature Conservancy. This study complied with the current laws of the United States of America and state of California.

## References

- Bakker VJ, Garcelon DK, Aschehoug ET, Crooks KR, Newman C, Schmidt GA, Van Vuren DH, Woodroffe R (2005) Current status of the Santa Cruz Island fox (*Urocyon littoralis santacruzae*). In:

- Garcelon DK, Schwemm CA (eds) Proceedings of the sixth California Islands symposium. Institute for Wildlife Studies, Arcata, pp 275–298
- Banks PB, Dickman CR (2007) Alien predation and the effects of multiple levels of prey naiveté. *Trends Ecol Evol* 22:229–230
- Benard MF (2006) Survival trade-offs between two predator-induced phenotypes in Pacific treefrogs (*Pseudacris regilla*). *Ecology* 87:340–346
- Berger J, Swenson JE, Persson I-L (2001) Recolonizing carnivores and naive prey: conservation lessons from Pleistocene extinctions. *Science* 291:1036–1039
- Clavero M, Garcia-Berthou E (2005) Invasive species are a leading cause of animal extinctions. *Trends Ecol Evol* 20:110–110
- Cohen B, Cory C, Menke J, Hepburn A (2009) A spatial database of Santa Cruz Island vegetation. In: Damiani CC, Garcelon DK (eds) Proceedings of the seventh California Islands symposium. Institute for Wildlife Studies, Arcata, CA, pp 229–244
- Collins PW, Latta BC (2009) Food habits of nesting Golden Eagles (*Aquila chrysaetos*) on Santa Cruz and Santa Rosa islands, California. In: Damiani CC, Garcelon DK (eds) Proceedings of the Seventh California Islands Symposium. Institute for Wildlife Studies, Arcata, pp 255–268
- Collins PW, Guthrie DA, Rick TC, Erlandson JM (2005) Analysis of prey remains excavated from an historic bald eagle nest site on San Miguel Island, California. In: Garcelon DK, Schwemm CA (eds) Proceedings of the sixth California Islands symposium. Institute for Wildlife Studies, Arcata, CA, pp 103–120
- Collopy MW (1984) Parental care and feeding ecology of golden eagle nestlings. *Auk* 101:753–760
- Coonan TJ, Schwemm CA (2009) Factors contributing to success of island fox reintroductions on San Miguel and Santa Rosa Islands, California. In: Damiani CC, Garcelon DK (eds) Proceedings of the 7th California Islands symposium. Institute for Wildlife Studies, Arcata, pp 363–376
- Coonan TJ, Rutz K, Garcelon DK, Latta BC, Gray MM, Aschehoug ET (2005) Progress in island fox recovery efforts on the north Channel Islands. In: Garcelon DK, Schwemm CA (eds) Proceedings of the sixth California Islands symposium. Institute for Wildlife Studies, Arcata, pp 263–274
- Cox JG, Lima SL (2006) Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. *Trends Ecol Evol* 21:674–680
- Crooks KR (1994) Comparative ecology of the island spotted skunk and the island fox of Santa Cruz Island, California. M.S. Thesis. University of California, Davis
- Crooks KR, Van Vuren D (1995) Resource utilization by two insular endemic mammalian carnivores, the island fox and island spotted skunk. *Oecologia* 104:301–307
- Farias V, Todd KF, Wayne RK, Sauvajot RM (2005) Survival and cause-specific mortality of gray foxes, *Urocyon cinereoargenteus*, in southern California. *J Zool* 2006:249–254
- Fenn MGP, MacDonald DW (1995) Use of middens by red foxes: risk reverses rhythms of rats. *J Mammal* 76:130–136
- Fraser DE, Gilliam JF, Akkara JT, Albanese BW, Snider SB (2004) Night feeding by guppies under predator release: effects on growth and daytime courtship. *Ecology* 85:312–319
- Geffen E, MacDonald DW (1993) Activity and movement patterns of Blanford's foxes. *J Mammal* 74:455–463
- Gompper ME (2002) Top carnivores in the suburbs? Ecological and conservation issues raised by colonization of north eastern North America by coyotes. *Bioscience* 52:185–190
- Holomuzki JR (1986) Predator avoidance and diel patterns of micro-habitat use by larval tiger salamanders. *Ecology* 67:737–748
- Kauhala K (1996) Introduced carnivores in Europe with special reference to central and northern Europe. *Wildlife Biology* 2:197–204
- Kavanau JL, Ramos J (1975) Influences of light on activity and phasing of carnivores. *American Naturalist* 109:391–418
- Kiff LF (1980) Historical changes in resident populations of California Islands raptors. In: Power DM (ed) The California Islands: proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History, Santa Barbara, pp 651–673
- Lima SL, Bednekoff PA (1999) Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *American Naturalist* 153:649–659
- Metcalfe NB, Steele GI (2001) Changing nutritional status causes a shift in the balance of nocturnal to diurnal activity in European minnows. *Funct Ecol* 15:304–309
- Metcalfe NB, Fraser NHC, Burns MD (1998) State-dependent shifts between nocturnal and diurnal activity in salmon. *Proceedings of the Royal Society B: biological sciences* 265:1503–1507
- Roemer GW (1999) The ecology and conservation of the island fox (*Urocyon littoralis*). Ph.D. Dissertation. University of California, Los Angeles
- Roemer GW, Garcelon DK, Coonan TJ, Schwemm C (1994) The use of capture recapture methods for estimating, monitoring, and conserving island fox populations. In: Halvorson WL, Garcelon DK (eds) The fourth California Islands symposium: update on the status of resources. Santa Barbara Museum of Natural History, Santa Barbara, pp 387–400
- Roemer GW, Donlan CJ, Courchamp F (2002) Golden eagles, feral pigs, and insular carnivores: how exotic species turn native predators into prey. *Proc Natl Acad Sci USA* 99:791–796
- Rohr JR, Madison DM, Sullivan AM (2003) On temporal variation and conflicting selection pressures: a test of theory using newts. *Ecology* 84:1816–1826
- Salo P, Korprimaki E, Banks PB, Nordstrom M, Dickman CR (2007) Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B* 274:1237
- Salo P, Nordstrom M, Thomson RL, Korprimaki E (2008) Risk induced by a native top predator reduces alien mink movement. *J Anim Ecol* 77:1092–1098
- Simberloff D, Stiling P (1996) Risks of species introduced for biological control. *Biol Conserv* 78:185–192
- Sokal R, Rohlf F (1995) *Biometry*, 3rd edn. W.H. Freeman and Company, New York
- Swarts HM, Crooks KR, Willits N, Woodroffe R (2009) Possible contemporary evolution in an endangered species, the Santa Cruz Island fox. *Anim Conserv* 12:120–127
- Timm SF, Muson L, Summers BA, Terio KA, Dubovi EJ, Rupprecht CE, Kapil S, Garcelon DK (2009) A suspected canine distemper epidemic as the cause of a catastrophic decline in Santa Catalina Island foxes (*Urocyon littoralis catalinae*). *J Wildl Dis* 45:333–343
- United States Fish Wildlife Service (2004) Endangered and threatened wildlife and plants; listing the San Miguel Island Fox, Santa Rosa Island Fox, Santa Cruz Island Fox, and Santa Catalina Island Fox as endangered. *Fed Regist* 69:10335–10353
- Wayne RK, George SB, Gilbert D, Collins PW (1991) A morphologic and genetic study of the island fox, *Urocyon littoralis*. *Evolution* 45:1849–1868
- Werner EE, Gilliam JF, Hall DJ, Mittelbach GG (1983) An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540–1548