The effect of feral cats on the population viability of black-vented shearwaters (*Puffinus opisthomelas*) on Natividad Island, Mexico

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Abstract

Insular breeding seabirds are likely to be particularly vulnerable to introduced mammalian predators because they often lack behavioural, morphological and life-history defenses against predation. We studied the life-history of the black-vented shearwater (*Puffinus opisthomelas*) on Natividad Island, Baja California Sur, Mexico, to examine its vulnerability to introduced feral cats. Using an allometric equation, we estimated that feral cats consumed 328 g of food day^{-1} to satisfy their nutritional requirements. We used stable isotope analysis of cat scat to estimate that 90% of the cats' diet was composed of shearwaters. Using data from our focal species and from the closely related manx shearwater (*Puffinus puffinus*), we created a demographic model to evaluate the effects of cat population size on the annual growth rate (λ) of the shearwater. The annual growth rate for black-vented shearwaters was estimated to be 1.006 in the absence of cat predation. With predation, we estimated that annual growth rate declined approximately 5% for every 20 cats in a population of 150,000 birds. Persistence times of bird colonies decreased both with an increase in the size of the feral cat population and with a decrease in the size of the initial bird population.

INTRODUCTION

Life-history characteristics such as low annual productivity, long reproductive cycles, delayed reproductive maturity and low adult mortality (Warham, 1990; Russell, 1999) make seabird populations particularly vulnerable to introduced predators at their colonies (Moors & Atkinson, 1984). Feral cats (*Felis catus*), in particular, have wreaked havoc on insular seabird colonies. Using a variety of techniques, researchers have estimated cat mortality for Marion Island (450,000 seabirds annually, Van Aarde, 1980), Macquarie Island (47,000 Antarctic prions, *Pachyptila vittata*, and 110,000 white-headed petrels, *Pterodorma lessonii*, annually, Jones, 1977), and Kerguelen Island (1.2 million seabirds annually, Pascal, 1980). This level of mortality is likely to have dramatic effects on the population viability of seabird breeding colonies. For example, on the Crozet

Islands, cats are probably responsible for the local extinction of ten petrel species in the last century (Derenne & Mougin, 1976). Despite the well-documented negative effects of cat predation in seabird colonies, there has been little work evaluating the viability of seabird populations that are exposed to these predators.

The Pacific islands off the Baja California peninsula support 17 species of breeding seabirds. Feral cats occur or have occurred on all nine islands or island groups in the region (Donlan *et al.*, 1999; Tershy *et al.*, in press) and have caused several seabird extirpations (McChesney & Tershy, 1998) and the extinction of the Guadalupe storm petrel (*Oceanodroma macrodactyla*, Jehl & Everett, 1985). The black-vented shearwater (*Puffinus opisthomelas*) is endemic to this region and is likely to be particularly vulnerable to introduced predators because (1) it breeds in a geographically restricted range, (2) all breeding sites are easily accessible to predators, (3) it has already been extirpated, probably by feral cats, from several breeding locales, and (4) it shares all of its main breeding locations with permanent human inhabitants and, prior to recent removal programmes,

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introduced mammals (Everett, 1988; Keitt, 1998).

In this paper we develop a model to evaluate the degree to which feral cat predation can reduce black-vented shearwater annual population growth rate (λ) and colony persistence times. While we recognize there are shortcomings to the approach we use and that we have relied on many assumptions to generate our model, our goals are to (1) stimulate discussion on the effects of introduced predators on seabird islands, and (2) provide data that are of use for land managers evaluating the costs and benefits of removing introduced predators from islands.

STUDY AREA

Natividad Island (27.92°N, 115.15°W) is a desert island located 5 km north of Punta Eugenia, Baja California Sur, Mexico. The island is 6 km long and 2.5 km wide at its maximum, with an area of 1000 ha. Natividad Island is the northwesternmost corner of the recently formed *Reserva de la Biosferá 'El Vizcaíno'*, the largest protected area in Mexico. Population estimates from 1997 indicate that 75,000 pairs of black-vented shearwaters breed on Natividad Island, approximately 95% of the world's population (Keitt, Tershy & Croll 2000*b*). The shearwater colony covers the southwest end of the island, an area of 250 ha.

Black-vented shearwaters are nocturnal, burrow-nesting birds that forage in the near shore waters of the southwestern United States and northwestern Mexico (Keitt, Tershy & Croll 2000*a*). The shearwaters attend the Natividad Island colony for 10 months of the year. Reproduction takes 4 months from egg laying to fledging and during this time the eggs and chicks are safe from cat predation in their burrows. Cats feed on adult and immature birds as they socialize on the ground or as they come and go from their nesting burrows (Keitt, 1998; Keitt *et al.*, 2000*b*).

Domestic cats were reported as feral on Natividad Island as early as 1922 by Anthony (1925) and subsequently by Bancroft (1927), Banks (1964), Delong & Crossin (1968) and Jehl (1973; 1984). Seasonal fishermen, who were reported using the island as early as the 1920s (Lamb, 1927), probably introduced cats to the island. It appears that the cat population decreased significantly or was extirpated between the late 1960s when Jehl (1984) reported feral cats as abundant and the early 1990s when island residents reported reintroducing cats to control the native deer mouse (*Peromyscus maniculatus*) population. We observed feral cats to be abundant on the island in 1997 and 1998.

METHODS

In order to quantify the rate of shearwater predation by cats we used two methods: (1) a direct count of shearwater mortality using carcass deposition rates; (2) an energetic approach whereby cat consumption was estimated from an allometric equation for eutherian mammals. We used these data to estimate how many

shearwaters an individual cat needs to consume each month to satisfy field metabolic rates. To estimate the population level effects of cat predation we developed a population matrix model for the black-vented shearwater. We then incorporated additional mortality from predation into the model to investigate how varying cat populations could affect annual population growth and colony persistence times.

Effects of cat predation

To assess current levels of shearwater mortality from feral cats on Natividad Island we performed weekly counts of carcasses in four 100 m × 200 m plots. Once counted, carcasses were removed from the plot. Because the colony is flat, with no plant cover to hide shearwater carcasses, it was possible to count dead shearwaters simply by walking through the colony. We calculated average mortality (number of dead birds deposited day^{-1} m^{-2}) in each of the plots and extrapolated to the whole colony by multiplying mortality × colony area.

We obtained cat population numbers from a removal programme conducted after our research was finished. Using the cat population we calculated the monthly shearwater mortality per cat. We were unable to determine cause of mortality when counting shearwater carcasses and some of the carcasses were probably birds that were not depredated by cats. Therefore, the mortality estimates from these plots should be considered the upper limit of mortality due to cat predation.

We also estimated cat-induced mortality using an energetic approach. We calculated daily biomass consumption based on field metabolic rate, estimated how much of a cat's diet came from shearwaters, and used these data to calculate how many shearwaters were consumed each month per cat.

Daily consumption of biomass (b) by a feral cat was estimated using the allometric equation (Nagy, 1987):

$$b = 3.35 \bullet (\text{predator weight})^{0.813} \bullet \frac{2.86}{18} \qquad (1)$$

This equation provides an estimate for the biomass needed to maintain a free-living eutherian mammal for 1 day. In this formulation, 2.86 is included to account for the 65% water content of prey items (K. Nagy, pers. comm.) and 18 is the estimated mean metabolizable energy contents of the prey in kilojoules of metabolizable energy per gram of dry matter (Nagy, 1987). We estimated the average cat weight to be 2.7 kg based upon field observations of 149 insular feral cats by B. M. Fitzgerald (King, 1990). We were unable get weight measurements for the cats on Natividad Island.

We assumed a cat satisfies 90% of its energy needs from shearwaters. We based this upon evidence from our stable isotope analysis and from the literature. We used stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) to assess relative marine versus terrestrial input to cat diet (Schoeninger & Deniro, 1984; Kelly, 2000). Cat scat was opportunistically collected around the island and subsequently dried and ground in the lab. Feathers of shearwaters were also

collected for analysis. Isotope values were determined using a Carlo Erba Model NA 2500 elemental analyzer coupled to a Finnigan Delta Plus isotopic ratio mass spectrometer at the Colorado Plateau Stable Isotope Laboratory, Northern Arizona University.

Several studies from Marion Island have indicated that feral cats' diet consisted primarily of seabirds on that island. Van Aarde (1980) found that petrels accounted for 87% of the total weight of the stomach contents of cats. In addition, Van Aarde (1980) found that petrels occurred in 97.4% of cat stomachs inspected from Marion Island in 1975. Van Rensburg (1985) estimated that petrels contributed almost 93% of the total energy requirements of feral cats on Marion Island, while house mice (*Mus musculus*) contributed only 4%.

Based on field observations we estimated that cats eat 50% of the weight of a black-vented shearwater, leaving behind bones, feathers and other parts. Black-vented shearwaters weigh on average 408 g (Table 1) so we estimated a cat consumes 200 g of tissue per shearwater. We used the calculated cat metabolic demand and shearwater weight to calculate the mean monthly consumption of shearwaters by cats. Minimum and maximum estimates are from the 95% confidence limits provided by Nagy (1987):

$$n_c = \frac{b \bullet 30 \text{ days}}{200 \text{ } g/\text{bird}} \quad (2)$$

Demographic model

We used life-history data on survivorship, age at first breeding and reproductive success (defined as the proportion of eggs laid that produced fledged chicks) for the closely related manx shearwater (*Puffinus puffinus*) (Table 1) to parameterize a population matrix model (Caswell, 1989). The black-vented shearwater was, until recently, considered a subspecies of the manx shearwater (Keitt *et al*., 2000*b*).

Table 1. Demographic parameters and their sources used in the population projection matrix and predation rate calculations

Parameter	Mean	SD	N	Source	Species[1]
POPULATION MATRIX					
Population size (pairs)	76,570	18,411		Keitt, 1998	BVSH
Adult survival[2]	90%	6	6	Perrins *et al*., 1973	MASH
	93–96%			Harris, 1966	MASH
Survival to age at first breeding	32%			Brooke, 1990	MASH
% Adults breeding each year	80%			Brooke, 1990	MASH
Reproductive success	70%	11.5	5	Brooke, 1990	MASH
PREDATION					
Colony attendance	10 mo.			Keitt, 1998	BVSH
Reproductive cycle	4 mo.			Keitt, 1998	BVSH
Shearwater weight	408 g	44	258	Keitt, 1998	BVSH
Period immature birds spend on colony	Age 3–2mo. Age 4–4 mo. Age 5–4 mo.			Brooke, 1990	MASH

[1]BVSH = black-vented shearwater, MASH = manx shearwater.
[2]We combined these estimates and used 92% adult survival in the model.

The model consists of five age classes of subadults (aged 1 to 5 years) and one class of breeding adults (6 years and older). The model iterates across years and population numbers change with time as a function of reproduction (F_i) and survivorship (S_i) values for each age class i. Reproduction, F_i, is estimated as the product of the proportion of adults breeding in any one year (0.80), clutch size (1.0), survival from laying to fledging (0.70), immature survival from fledging to age class 1 (0.743), and proportion of eggs laid that produce females (0.50). We ran the simulation using females only and assumed that the sex ratio was 50:50 and that predation rate was equal for both sexes. Initial population vectors were assigned according to the stable age distribution. The proportion of the population assigned to each age class was: (1) = 0.12; (2) = 0.091; (3) = 0.067; (4) = 0.062; (5) = 0.056; (6) = 0.60.

Table 2 shows the form of the population projection matrix.

In order to assign survivorship for each immature age class we used data on survivorship to age at first breeding (0.32). Most mortality of immature birds occurs in the first year after fledging (Brooke, 1990) and survivorship of birds 3 years and older should approach that of adults (Russell, 1999). We assumed survivorship for age classes 3–4, 4–5 and 5–6 was equal to adults (0.92). We then calculated survivorship for age classes 0–1, 1–2 and 2–3 as:

$$S_i = \sqrt[3]{\frac{0.32}{0.92}} \quad (3)$$

Incorporating cat predation into the demographic model

We defined X_i as the probability of a shearwater in age class (i) being eaten by a cat. We calculate X_i as:

$$X_i = \frac{1}{N_i} \sum_{t=1}^{T_i} n_c \bullet \frac{N_i}{\sum_{j=3}^{6} N_j} \quad (4)$$

Where N_i is the number of individuals in age class i and T_i is the number of months an individual in age class i

Table 2. Population projection matrix used to simulate population growth of black-vented shearwaters on Natividad Island. Parameters in parentheses are used to incorporate cat predation into the model

	Immature classes				Breeding adults
year 1	year 2	year 3	year 4	year 5	year 6+
0	0	0	0	0	$F = 0.201$
$S_1 = 0.743$	0	0	0	0	0.00
0	$S_2 = 0.743$	0	0	0	0.00
0	0	$S_3 = 0.92 \bullet (1-X_3)$	0	0	0.00
0	0	0	$S_4 = 0.92 \bullet (1-X_4)$	0	0.00
0	0	0	0	$S_5 = 0.92 \bullet (1-X_5)$	$S_{adult} = 0.92 \bullet (1-X_6)$

X_i is defined in equation (4) in the text and represents annual mortality due to cat predation for age class i.

is on the colony. This is a weighted rate of consumption, where we are assuming birds are eaten in proportion to their availability at the colony. Thus, $(1 - X_i)$ is the probability that an adult is not eaten in a given year. We assumed adults were on the colony for months 1–10, age class 4 and 5 birds were on the colony for months 1–4, and age class 3 birds were present for months 1 and 2 (Table 1). Survivorship in the matrix was then multiplied by the probability of surviving cat predation for age classes 3–6.

To account for the reproductive failure due to the loss of either parent during the 4 month reproductive period, Reproduction (F) was multiplied by $(1 - X_6)^2$, with $T_6 = 4$. We assumed that reproduction occurred during months 1–4; thus survival of reproductive birds was affected by the presence of the younger age classes.

In the description above we assume that cats depredated adult and immature birds equally. Thus, predation rate on all age classes is assigned proportionally according to the number of birds in each age class. We also ran the model using the assumption that cats were twice as likely to depredate immature birds as adult birds, thereby decreasing the number of adult birds consumed. We initiated the model runs from the stable age structure in the absence of cat predation. We calculated persistence times by iterating the matrix model until the population went extinct for populations that had a growth rate less than 1.

RESULTS

Shearwater mortality

Using data from our mortality plots we estimated the total number of birds killed per week in the colony at 236 ($\pm$ 85), or 1012 month^{-1}. Predation rate was slightly higher in the early stages of the breeding season in 1997, perhaps because immature birds were more common on the surface of the colony at this time. The cat removal programme indicated a population of 25 cats. If 25 cats were responsible for 1012 dead birds month^{-1} then each cat killed 40.5 birds month^{-1}.

Using the energetic model, we calculated that a 2.7 kg free-ranging cat needs to consume 328 g of food per day (minimum 190 g day^{-1}, maximum 452 g day^{-1}). Results from stable isotope values show a clear marine signature in the cat diet (Table 3) indicating that cats receive a substantial portion of their diet from black-vented shearwaters. Assuming that 90% of the cat's diet consisted of black-vented shearwaters, we calculated

Table 3. Stable isotope signatures of feral cat scat ($n=7$) and black-vented shearwaters ($n=2$). Carbon and nitrogen values are very similar for both cat scat and shearwater feathers, indicating that a large percentage of the cat's diet comes from shearwaters. Data are presented as mean (SE)

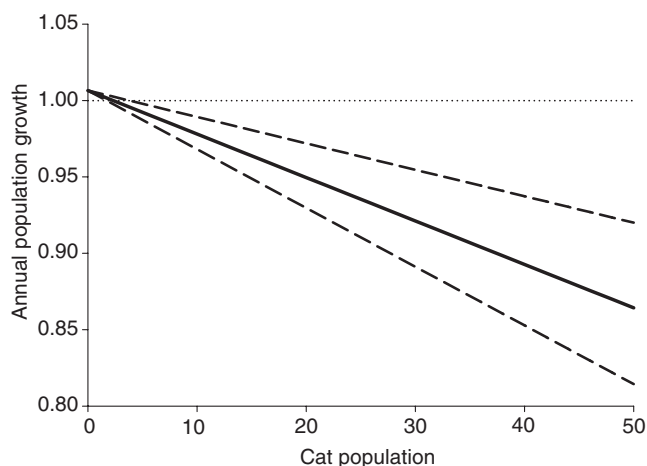|	δ ^{13}C	δ ^{15}N
Feral cat	−17.7 (0.44)	19.3 (1.49)
Shearwater	−16.5 (0.06)	16.9 (0.31)

Fig. 1. Annual population growth, λ, ($\pm$ 95% confidence intervals) for a population of 150,000 black-vented shearwaters as a function of the number of cats on the colony. Horizontal dotted line represents a stable population.

that a feral cat on Natividad Island consumed 295 g of shearwater day^{-1}. Finally, assuming that a cat eats 50% of a black-vented shearwater, or approximately 200 g per bird killed, we estimated that a cat must eat 1.5 black-vented shearwaters day^{-1} or 45 birds month^{-1} to meet its metabolic requirements.

Demographic model

Our baseline model, without cat predation, predicted an annual population growth rate of 1.006 for the black-vented shearwater. This is consistent with small annual population growth and is characteristic of long-lived species such as seabirds (Russell, 1999).

Annual population growth declines with increasing cat predation (Fig. 1). A theoretical population of 20 cats on Natividad Island, assuming a bird population of 150,000, would cause an approximate 5% annual decrease in population growth during the first year. Subsequent population growth rates would decrease even more as the cats consumed a constant number, but an increasing fraction of the existing birds.

Persistence time for the shearwater colony decreased both with increased predation level (i.e., more cats) and with a smaller initial bird population size. On Natividad Island, a population of 20 cats would lead to a persistence time of only 21 years for a population of 150,000 birds (Fig. 2). When we made immature birds twice as likely to be depredated as adults there was virtually no change in the persistence times.

DISCUSSION

We found feral cats to be a serious threat to the population viability of black-vented shearwaters on Natividad Island. In our simulations, even relatively small cat populations lead to dramatic reductions in annual population growth of shearwaters. Using plots to estimate mortality rates we calculated that one cat
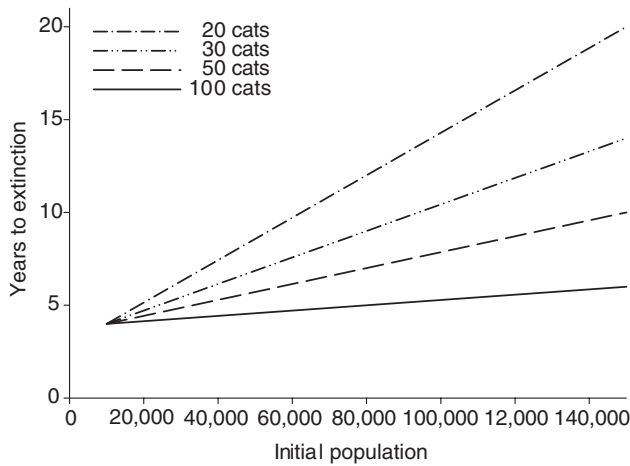
Fig. 2. Estimated years to extinction for bird colonies of sizes 10,000 to 150,000 birds with predation by 100, 50, 30 and 20 cats.

depredates 40.5 shearwaters per month. Using an energetic approach we calculated a monthly mortality rate of 45 shearwaters per cat. The similarity in these two independent mortality assessments suggests that they are realistic estimates of cat-induced mortality. Our stable isotope data suggest that cats met a large percentage of their dietary needs with shearwaters. This is similar to published data that suggests cats in seabird colonies meet between 90 and 95% of their dietary needs with seabirds (Van Aarde, 1980; Van Rensburg, 1985).

Shearwater mortality

There are several estimates for the daily food requirements of feral cats available in the literature, and our estimate of 328 g day^{-1} falls somewhere in the middle of these. Apps (1983) estimated mean food intake of feral cats on Dassen Island off the South African coast. Apps used two methods to estimate food intake: intake of caged feral cats and data from scat collection. The caged cats ate an average of 490 g day^{-1} and the scat data provided an estimate of 547 g day^{-1}. Liberg (1984) determined the absolute intake of feral cats in southern Sweden to be 294 g day^{-1}. Van Aarde (1980) estimated caloric requirements for cats on Marion Island to be approximately 600,000 kJ year^{-1} for females and 486,000 kJ year^{-1} for males. Using the conversion of 18.0 kJ of metabolizable energy per gram of dry matter (Nagy, 1987) and the 65% water content of seabirds, those numbers are equivalent to 260 and 210 g day^{-1} for females and males, respectively. Van Aarde admits these estimates are absolute minimums because he used data on laboratory, not free-living, animals.

We were able to obtain two independent population numbers for cats on Natividad Island. The first number of 25 feral cats in the shearwater colony came from a cat-removal programme initiated after our research was complete (Wood *et al.*, in press). A second estimate can be calculated based upon our mortality plot data and energetic model. Assuming a predation rate of 45 shearwaters month^{-1} cat^{-1} and a mortality rate of 1012 birds

month^{-1}, we calculated a cat population of 22.5 individuals. Again, the similarity of these results suggests that our mortality estimates are realistic.

Cats on Natividad Island are not limited to black-vented shearwaters as a prey source but we assumed that they met 90% of their energy requirements from shearwaters. Shearwaters on Natividad are easy prey for cats and are most likely a preferred food for feral cats on the island. This is supported by the findings of Bloomer & Bester (1990) on Marion Island, where seabirds were the preferred prey item and frequency of occurrence in the diet reflected seasonal abundance of the prey items.

Demographic model

Because certain life-history data are not available for black-vented shearwaters, we used life-history parameters measured for manx shearwaters to build a population projection matrix. While the manx shearwater inhabits more temperate latitudes, many life-history parameters for black-vented shearwaters, such as duration of incubation and chick-rearing periods, are almost identical to those of the manx shearwater (Keitt *et al.*, 2000*b*). In addition, Ainley, Telfer & Reynolds (1997) estimate the survivorship of the similarly sized, tropical Townsend's and Newell's shearwaters (*Puffinus auricularis townsendi, P. a. newelli*) at 0.90, very close to the survivorship of 0.92 we used in the population model. Skira (1991) reported the adult survivorship of another *Puffinus* shearwater, the short-tailed shearwater (*P. tenuirostris*), as 0.92.

We assumed birds aged 3 and older had annual survivorship equivalent to adults and that predation rate was proportional to the number of birds in each age class. For nocturnal, burrow-nesting seabirds such as the black-vented shearwater, it has been suggested that immature birds are more likely than breeders to be depredated by introduced predators (Harris, 1966). Because immature birds spend more time socializing on the colony surface outside of protective burrows it is reasonable to assume they would be more likely to be depredated by cats. We were unable to age the carcasses we collected in the mortality plots and thus were unable to assess relative mortality on the different age classes. However, the outcome of the model was virtually unchanged when we ran the model using the assumption that immature birds were twice as likely to be depredated as breeders. In fact, persistence times tended to decrease slightly with increased predation on immature birds and a proportional decrease in predation on adult birds. This result was unexpected because we assumed that as cats favoured immature birds there would be a concomitant increase in reproductive success of adults that led to longer persistence times.

Persistence times for all of the situations we modelled were surprisingly short. Even with 150,000 birds and 20 cats, persistence time was less than 25 years. As formulated, the model assumes per capita cat consumption remains the same as the shearwater population decreases. Clearly as the shearwater population becomes much

smaller the cat population will either decrease, or the cats will have to supplement their diet with other items. Actual persistence times for shearwaters will depend on the ability of the cats to catch shearwaters at low densities and/or to maintain their population by supplementing their diet with alternative prey items.

Implications for seabird conservation

There are many factors that affect the severity of predation on seabirds at their colony and it is important that land managers understand the ramifications of differing scenarios on the viability of these populations (see Moors & Atkinson, 1984).

Availability of prey throughout the year can greatly affect how many cats survive from year to year. Although black-vented shearwater attendance at the colony declines during the non-breeding season (September through November), they can be found at the colony virtually year round (Keitt *et al.*, 2000*b*). This year-round attendance provides a consistent prey base that may help maintain the island's cat population. A contrasting example is Ascencion Island in the Indian Ocean, where the seabirds are absent for more than 3 months per year. Cats are unable to maintain a large population, and cat predation on the remaining bird species is kept at a sustainable level (Stonehouse, 1962). Jones (1977) and Corbett (1979) found similar effects of seasonal food availability on cat populations on Macquarie Island and in Scotland, respectively. In contrast, Apps (1983) found that rabbits on Dassen Island provided a year-round food base which maintained high cat populations and led to increased predation on penguins. Perhaps more importantly, these secondary prey items could maintain the cat population as bird populations near extinction.

It is likely that on Natividad Island other factors have limited the cats' ability to consume black-vented shearwaters. Although we do not know the historical black-vented shearwater population on Natividad Island, because cats were first reported on the island almost 100 years ago, it is likely the population has been greatly reduced. However, because there were over 75,000 breeding pairs of shearwaters on Natividad Island in 1997, it is unlikely that the shearwater population has been declining at a rate equivalent to the output of our model for 20 cats. It is possible that dogs brought to the island by fishermen as early as the 1920s may have controlled cat populations. In fact, it was widely believed by island residents that, in the 1980s, dogs on the island killed all the cats. Clearly, interactions such as these can greatly affect how quickly cat populations reduce seabird populations.

In conclusion, the black-vented shearwater's characteristics of almost year-round attendance at the colony, long incubation period, slow chick growth rate, restricted breeding range, naivety with terrestrial predators and low fecundity increase their vulnerability to cat predation. Because black-vented shearwaters share similar life-history characteristics with most Procellariiform seabirds (Warham, 1990), our model may accurately represent the expectations for other seabird species experiencing cat predation.

REFERENCES

Ainley, D. G., Telfer, T. C. & Reynolds, M. H. (1997). Townsend's and Newell's shearwater (*Puffinus auricularis*). In *The Birds of North America*, No. 297. Poole, A. & Gill, F. (Eds). Philadelphia, PA: Academy of Natural Sciences and Washington, D.C.: American Ornithologists' Union.

Anthony, A. W. (1925). Expedition to Guadalupe Island, Mexico, in 1922. The birds and mammals. *Proc. Calif. Acad. Sci.* **14**: 277–320.

Apps, P. J. (1983). Aspects of the ecology of feral cats on Dassen Island, South Africa. *S. Afr. J. Zool.* **18**: 393–399.

Bancroft, G. (1927). Notes on breeding and insular birds of central lower California. *Condor* **29**: 188–195.

Banks, R. C. (1964). Birds and mammals of the voyage 'Gringa'. *Trans. San Diego Soc. Nat. Hist.* **13**: 177–184.

Bloomer, J. P. & Bester, M. N. (1990). Diet of a declining feral cat *Felis catus* population on Marion Island [Antarctic]. *S. Afr. J. Wildl. Res.* **20**: 1–4.

Brooke, M. (1990). *The manx shearwater*. London: T. & A. D. Poyser.

Caswell, H. (1989). *Matrix population models: construction, analysis, and interpretation*. Sunderland, MA: Sinauer Associates.

Corbett, L. C. (1979). *Feeding, ecology and social organisation of wild cats (**Felis silvestris**) and domestic cats (**Felis catus**) in Scotland*. PhD thesis, University of Aberdeen.

Delong, R. L. & Crossin, R. S. (1968). Status of seabirds on Islas de Guadalupe, Natividad, Cedros, San Benitos, and Los Coronados. Unpubl. manuscript, Pacific Ocean Biological Survey Project, USMNH, Washington, DC.

Derenne, P. & Mougin, J. L. (1976). Données écologiques sur les mammifères introduits de l'Ile aux Cochons, Archipel Crozet. *Mammalia* **40**: 21–52.

Donlan, C. J., Tershy, B. R., Keitt, B. S., Wood, B., Sanchez, J. A. & others (1999). Island conservation action in northwest Mexico. In *Proceedings of the Fifth California Islands Symposium*: 330–338. Browne, D., Haney, H. & Mitchell, K. (Eds). Sponsored by the US Minerals Management Service, Pacific OCS Region, 770 Paseo Camarillo. Camarillo, CA: Santa Barbara Museum of Natural History.

Everett, W. T. (1988). Biology of the black-vented shearwater. *Western Birds* **19**: 89–104.

Harris, M. P. (1966). Age of return to the colony, age of breeding and adult survival of manx shearwaters. *Bird Study* **13**: 84–95.

Jehl, J. R., Jr. (1973). Studies of a declining population of brown pelicans in northwestern Baja California. *Condor* **75**: 69–79.

Jehl, J. R., Jr. (1984). Conservation problems of seabirds in Baja California and the Pacific Northwest. In *Status and conservation of the world's seabirds*: 41–48. Croxall, J. P., Evans, P. G. H. & Schreiber, R. W. (Eds). Cambridge: ICBP Techincal Publication 2.

Jehl, J. R., Jr. & Everett, W. T. (1985). History and status of the avifauna of Isla Guadalupe, Mexico. *Trans. San Diego Soc. Nat. Hist.* **20**: 313–336.

Jones, E. (1977). Ecology of the feral cat, *Felis catus* (L), (Carnivora: Felidae) on Macquarie Island. *Aust. Wildl. Res.* **4**: 249–262.

Keitt, B. S. (1998). *Ecology and conservation biology of the black-vented shearwater (**Puffinus opisthomelas**) on Natividad Island, Vizcaino Biosphere Reserve, Baja California Sur, Mexico*. Msc thesis, University of California, Santa Cruz.

Keitt, B. S., Croll, D. A. & Tershy, B. R. (2000a). Dive depth and diet of the black-vented shearwater. *Auk* **117**: 507–510.

Keitt, B. S., Tershy, B. R. & Croll, D. A. (2000b). Black-vented shearwater (*Puffinus opisthomelas*). In *The birds of North America*. Poole, A. & Gill, F. (Eds). Philadelphia, PA: Academy of Natural Sciences and Washington, DC: American Ornithologists' Union.

Kelly, J. F. (2000). Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Can. J. Zool.* **78**: 1–27.

King, C. M. (1990). *The handbook of New Zealand mammals*. Auckland: Oxford University Press.

Lamb, C. C. (1927). The birds of Natividad Island, lower California. *Condor* **29**: 67–70.

Liberg, O. (1984). Food habits and prey impact by feral cats and house-based domestic cats (*Felis catus*) in a rural area in southern Sweden. *J. Mammal.* **65**: 424–432.

McChesney, G. J. & Tershy, B. R. (1998). History and status of introduced mammals and impacts to breeding seabirds on the California Channel and northwestern Baja California Islands. *Col. Waterbirds* **21**: 335–347.

Moors, P. J. & Atkinson, I. A. E. (1984). Predation on seabirds by introduced animals, factors affecting its severity. *International Council for the Preservation of Birds Technical Publication* **2**: 667–690.

Nagy, K. A. (1987). Field metabolic rate and food requirement scaling in mammals and birds. *Ecol. Monogr.* **57**: 111–128.

Pascal, M. (1980). Structure et dynamique de la population de chats harets de l'archipel des Kerguelen. *Mammalia* **44**: 161–82.

Perrins, C. M., Harris, M. P. & Britton, C. K. (1973). Survival of Manx shearwaters (*Puffinus puffinus*). *Ibis* **115**: 335–348.

Russell, R. W. (1999). Comparative demography and life history tactics of seabirds: implications for conservation and marine monitoring. *Amer. Fish. Soc. Sym.* **23**: 51–76.

Schoeninger, M. J. & Deniro, M. J. (1984). Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. *Geochimica et Cosmochimica Acta* **40**: 625–639.

Skira, I. (1991). The short-tailed shearwater: a review of its biology. *Corella* **15**: 45–52.

Stonehouse, B. (1962). Ascension Island and the British Ornithologists Union centenary expedition. *Ibis* **103b**: 124–161.

Tershy, B. R., Donlan, C. J., Keitt, B. S., Croll, D. A., Sanchez, J. A., Wood, B., Hermosillo, M. A., Howald, G. R. & Biavaschi, N. (in press). Island conservation in northwest Mexico: a conservation model integrating research, education, and exotic mammal eradication. In *Turning the tide: the eradication of invasive species*. Veitch, C. R. & Clout, M. N. (Eds). Auckland: Invasive Species Specialist Group of the World Conservation Union (IUCN).

Van Aarde, R. J. (1980). The diet and feeding behaviour of feral cats, *Felis catus*, on Marion Island. *S. Afr. J. Wildl. Res.* **10**: 123–128.

Van Rensburg, P. J. J. (1985). The feeding ecology of a decreasing feral house cat *Felis catus* population at Marion Island Sub-Antarctic. In *Antarctic nutrient cycles and food webs*: 620–624. Siegfried, W. R., Condy, P. R. & Laws, M. A. (Eds). Wilderness, South Africa: Springer-Verlag.

Warham, J. (1990). *The petrels: their ecology and breeding systems*. San Diego: Academic Press.

Wood, B., Tershy, B. R., Hermosillo, M. A., Donlan, C. J., Sanchez, J. A., Keitt, B. S., Croll, D. A., Howald, G. R. & Biavaschi, N. (in press). Removing cats from islands in northwest Mexico. In *Turning the tide: the eradication of invasive species*. Veitch, C. R. & Clout, M. N. (Eds). Auckland: Invasive Species Specialist Group of the World Conservation Union (IUCN).