

Feral cat diet and impact on sooty terns at Juan de Nova Island, Mozambique Channel

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Keywords

seabird; Tropical Island; alien predator; matrix model; biological invasion.

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Abstract

Feral cat *Felis catus* predation on seabirds has been well documented; however, details regarding shifts in feral cat diet in relation to seabird availability, seabird predation rate and impact on seabird population dynamics are scarce. Here, we present data documenting a seasonal shift in feral cat diet at Juan de Nova Island, Mozambique Channel. We also quantify sooty tern *Sterna fuscata* predation by feral cats and examine the impact on sooty terns over both the short term (by removing individual cats from sub-colonies) and over the longer term by highlighting their influence on population growth rate (λ) using a deterministic matrix model. Cat diet shifted dramatically from insects, rats and mice outside the tern breeding season to primarily terns when terns were breeding. The predation rate of sooty terns at Juan de Nova was estimated at 5.94 terns cat⁻¹ day⁻¹, with a proportion of these (22%) being killed without being consumed ('surplus kills'). When only one cat was removed from each sub-colony, tern predation declined tenfold in the short term. From our matrix model, the annual growth rate for sooty terns was 1.01 in the absence of cat predation. It remained above one until a predation impact equivalent to approximately three times the estimated cat density (12.04 per km²) was incorporated. Our results demonstrate that cats preferentially predate and have an impact on breeding sooty terns at Juan de Nova, and that an increase in cat density could lead to negative effects on population growth, despite the large breeding tern population.

Introduction

Cat predation is a major threat to seabird populations because most seabirds have not co-evolved with terrestrial predators and thus do not possess behavioural, morphological or life-history traits that allow them to persist in the presence of terrestrial predators (Moors & Atkinson, 1984; Savidge, 1987; Peck & Congdon, 2005). Consequently, evidence for the extirpation of seabird populations, and even species, by cats is mounting (e.g. Derenne & Mougin, 1976; Moors & Atkinson, 1984; Fitzgerald & Veitch, 1985; Nogales *et al.*, 2004). Despite this, detailed information on the impact of cats, the temporal dynamics of predation and the viability of seabird populations sustaining cat predation is scarce (but see Ashmole, Ashmole & Simmons, 1994; Keitt *et al.*, 2002; Keitt & Tershy, 2003; Martínez-Gómez & Jacobsen, 2004).

The islands in the Mozambique Channel are important because they offer seabirds a suitable breeding habitat and are located near areas where oceanographic conditions combine to encourage productivity regimes upon which seabirds rely during breeding (Jaquemet *et al.*, 2005). As a result, this region has the largest number of breeding sooty terns *Sterna fuscata* in the world as well as important breeding colonies of other species (e.g. tropic birds, boobies,

frigate birds, etc.) (Le Corre & Jaquemet, 2005). Seabird populations in this region have been in decline since the 18th century, the putative result of human activities (either directly or indirectly) (Feare, 1978, 2003; Le Corre, 2001).

Juan de Nova Island is a small (4.4 km²) coralline atoll situated 285 km east of Mozambique and 150 km west of Madagascar (latitude 17°03'S, longitude 42°45'E) and is a designated wildlife sanctuary. The island is uninhabited, except for a contingent of 14 French military personnel. Sooty terns arrive to breed at Juan de Nova *en masse* during August/September, and depart immediately after breeding (March/April), thereby providing potential predators either a clear abundance or a total lack of sooty terns (Le Corre & Jaquemet, 2005). Cats have been recorded on the island from the early 20th century (Benson *et al.*, 1975). The impact that they have on sooty terns and other native fauna remains unknown. Juan de Nova is distinct among the islands in the region in that only two species of seabird breed on the island: the sooty tern *S. fuscata*, with ~2000 000 breeding pairs, and the crested tern *Sterna bergii*, with ~250 breeding pairs (Le Corre & Jaquemet, 2005).

This paper addresses a number of issues pertaining to the feeding ecology and impact that feral cats have on breeding sooty terns at Juan de Nova Island. Firstly, we document the diet of cats at Juan de Nova, both within and outside the

sooty tern breeding season, from scat and stomach contents. We then estimate the population size of feral cats, based on trapping and spotlighting data, and determine the rate of cat predation on sooty terns using carcass deposition rates. As we simultaneously trapped cats and monitored tern predation, we were also able to assess the effect of cat removal on predation rates over a daily temporal scale, something that has not been documented previously. Finally, we develop a simple age structured deterministic model to examine the influence that cat predation has on sooty tern population growth rate (λ) at Juan de Nova, and discuss the implications of our results for sooty tern conservation and management.

Materials and methods

This study was carried out between 2002 and 2006. At Juan de Nova Island, sooty terns breed during the austral summer in two sub-colonies located far from human settlement at the Eastern and Western points of the island (Fig. 1) (Jaquemot, Le Corre & Quartly, 2007). As Juan de Nova is remote, access is limited by the availability of military aircraft, and so data collection was necessarily opportunistic. Cat scats (for diet analysis) were collected from December 2002 to February 2003 (chick rearing stage). A small number were also obtained in February 2004. This gave a total of 27 cat scats that were used to determine the diet of feral cats when sooty terns were present. Cat scats were also obtained during a 2-day trip in May 2006 and a 6-week visit in July/August of the same year (before terns arrived to breed). Seventy-seven scats were obtained in total from these latter two trips. From these samples, we were able to determine cat diet when sooty terns were not present.

Cat scat rapidly decomposes when not protected (i.e. when it is exposed to the elements) (Sanchez *et al.*, 2004). In fact, Sanchez *et al.* (2004) recorded a median persistence

time of 30 days for cat scat. This fact, taken together with the time of scat collection, and the arrival/departure time of sooty terns at Juan de Nova, meant that we were confident that our results on the temporal dynamics of cat predation would not be biased by 'remnant' scats being included in the wrong category. Moreover, the small number of scats (<10) that had been exposed for some time (based on whitening and poor condition) could not be analysed and so were discarded.

In addition to the scat samples, 26 cats were trapped during the July/August 2006 trip and their stomach contents were examined. Of these, four cats were trapped within 16 days after the arrival of sooty terns, thus allowing us to examine whether, and how quickly, a diet shift towards terns occurred.

Cat diet analysis

Protocols for dietary analysis from cat scats and stomach contents have been described in detail elsewhere (Nogales *et al.*, 1988; Tidemann, Yorkston & Russack, 1994). The frequency distributions of prey types from within and outside of the sooty tern breeding season were compared using χ^2 analysis. This and all other analyses were conducted using the statistical package JMP 4.0.2 (SAS Institute, 2000).

Cat population size and predation rate

Before we arrived at Juan de Nova in July/August 2006, 17 cats had been shot by the military during the previous month. The size of the remnant cat population was estimated from trapping and spotlighting data. Cats were trapped over a period of 6 weeks. Ten traps per night were placed throughout the island and their location was marked with GPS (Fig. 1). Traps were re-located where night-time

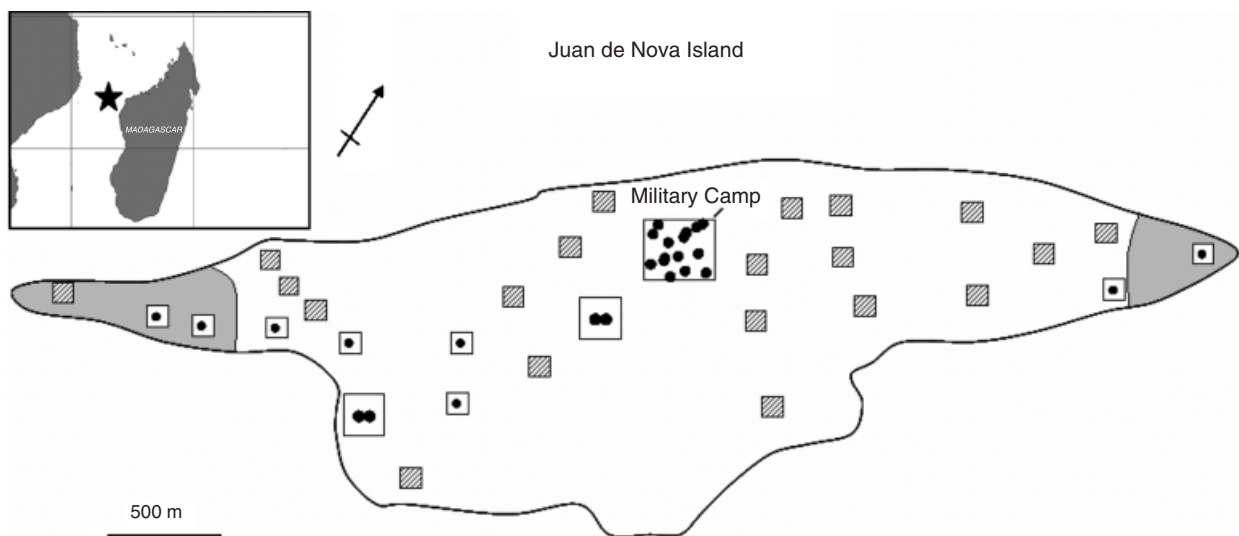


Figure 1 Map of Juan de Nova Island, Mozambique Channel showing the placement of cat *Felis catus* traps (squares) and cat captures (squares with black dots) in July/August 2006. Hashed squares indicate trap placement without cat capture. The two tern *Sterna fuscata* sub-colonies are shaded grey.

spotlight observations indicated that cats were present in new locations. We used a simple exponential smoothing model, as implemented in JMP, to generate the 95% confidence limits of the cat population based on our cumulative histogram of cat captures (Quinn & Keough, 2003). The exponential smoothing algorithm calculates a prediction based on exponentially weighted averages over time (Quinn & Keough, 2003). This method can be used on time series data to estimate population sizes or fluctuations (Lele, Taper & Gage, 1998).

In addition to this method, we conducted transect surveys at night (spotlighting) in order to validate the statistical approach described above. Spotlight transect surveys were conducted at least once per week throughout the trapping period using the method of Read & Bowen (2001). Transects were conducted along a 1.5 km transect in the middle of the island, and on the paths leading to each of the tern sub-colonies (each 0.8 km in length). Surveys were conducted on foot by two people simultaneously, with each person walking a different transect. It was assumed that cats/eye-shine could be seen at a distance of 100 m (Read & Bowen, 2001). An estimate of the cat population was obtained by extrapolating the average density of cats observed within the combined transect area (0.62 km²) to the area of the island as a whole (i.e. 4.4 km²).

Predation of sooty terns was measured during the last 16 days of this period after sooty terns had arrived *en masse* for breeding/pair formation. We used the method of Keitt *et al.* (2002) to quantify predation. We conducted daily counts of tern carcasses in two 200 m × 200 m plots at the Eastern and Western points of Juan de Nova (one in each sub-colony). Carcasses were removed from the plots each day and the cause of death was determined. Three categories were used to sort carcasses: (1) evidence of cat predation (puncture wounds to the neck and chest from cat incisors) and consumption of at least some of the carcass, (2) evidence of cat predation (as above) but no evidence of consumption, (3) no damage to the carcass (i.e. not predated by a cat). Totals for the second category are conservative as scavenging by Pied Crows *Corvus albus* and Hermit Crabs (*Pagurus* sp.) was observed in the field. Average mortality was calculated from the sum of the number of dead birds in categories (1) and (2)

day⁻¹ m⁻². As plot nest density mirrors that of the sub-colonies (Jaquemet *et al.*, 2007), we extrapolated this to the scale of the whole colony by multiplying mortality \times colony area (Keitt *et al.*, 2002).

Effect of cat removal

As we simultaneously removed cats while documenting tern predation during the visit in July/August 2006 (during the pre egg-laying period), we were also able to directly assess the short-term effect of cat removal on sooty tern mortality. This was done by comparing the mean numbers day⁻¹ m⁻² of predated terns in both plots (combined) before cat removal versus the number after the removal of two cats (one from each sub-colony) using a Welch ANOVA. This analysis allows for unequal variances between the two sample periods (Quinn & Keough, 2003).

Demographic model

We used a deterministic matrix model (no year-to-year variation in parameters, Caswell, 1989) to examine the impact of cats on sooty terns, parameterized with life history, survivorship and reproductive success data collated by Feare (1976, 2003) and Feare & Doherty (2004) for sooty terns in the Seychelles (Table 1). A deterministic model was used because our main aim was to determine the effects of cat density (Starfield, 1997). The model was not designed to estimate minimum viable populations or population persistence times (Caswell, 1989; Jones, 2002). Only females are considered in the simulations, with demographic parameters adjusted accordingly. Our model assumes five age classes of pre-breeders and one for birds (≥ 6 years of age) that breed. The model iterates across breeding seasons (years), changing as a function of survivorship (S) for each class and reproductive success (F):

$$F = \beta \times f \times FS \times \alpha$$

where (β) is the proportion of adult females that breed, (f) is fecundity (eggs per female per year⁻¹), (FS) is fledging success (fledglings per egg) and (α) is the sex ratio at birth

Table 1 Demographic parameters used in the deterministic population model, variation (where available) and the original source of the estimates

Parameter	Estimate	Variation	Reference
Population size	2 000 000 (pairs)	1 550 747–424 437 (range)	Le Corre & Jaquemet (2005)
Adult females breeding each year	100%		Feare (1976)
Fledging success (fledglings per egg)	0.58	0.03 (SE)	Feare (2003)
Fecundity (eggs per female per year)	1.00		Feare (1976)
F	0.29		Feare (1976)
S_1	0.83		Feare (1976)
S_2	0.83		Feare (1976)
S_3	0.85		Feare (1976)
S_4	0.85		Feare (1976)
S_5	0.90		Feare & Doherty Jr. (2004)
S_6	0.91	0.01 (SE)	Feare & Doherty Jr. (2004)
Colony attendance	210 days	180–243 (range)	Le Corre & Jaquemet (2005)

(assumed to be balanced). Consequently, S_1 represents survival from fledging to 1-year-old birds (Table 1).

To incorporate cat predation into the model, we assumed that cats would kill birds randomly with respect to sex. We assumed that only breeding birds (i.e. ≥ 6 years of age) were predated by cats because (1), nests are on the ground and incubating adults are in constant attendance and (2), the proportion of non-breeders at colonies is predicted to be minimal and so predation by cats on this class would be extremely small relative to that of breeders (Feare, 1976). Chick death due to adult mortality was incorporated into the model by multiplying reproductive success (F) by the probability of an adult tern surviving cat predation $1 - (1 - S_6)^2$ (Keitt *et al.*, 2002). Even though chick predation by cats has been observed in great numbers (S. Jaquemet, pers. obs.), we did not incorporate it into the model because quantitative estimates are unavailable, and the temporal and spatial variability of chick predation makes using an estimate from the literature too speculative (Ashmole, 1963; Ratcliffe, Hughes & Roberts, 1999). This necessarily makes our model more conservative. Monte Carlo simulations were used to generate 95% confidence intervals for population growth rates (Alvarez-Buylla & Slatkin, 1993). We ran 10 000 simulations for each projected matrix and incorporated variation in breeding success calculated by Feare & Doherty (2004) for sooty terns from the Seychelles. Breeding success varied according to a normal distribution. We stress that confidence intervals generated by Monte Carlo simulations only pertain to uncertainty in breeding success, and are therefore very conservative.

We evaluated the extent to which the annual growth rate was affected by changes in adult survival and reproductive success while keeping all other parameters unchanged. This was done in separate simulations by measuring the effect of reductions in adult survival and reproductive success of 5%. We also calculated elasticity values (% variance in λ explained by breeding success and survival). Matrix analyses were performed and elasticity was calculated using PopTools 2.7.5 (<http://www.cse.csiro.au/poptools>) (Hood, 2006).

Results

Cat diet analysis

A total of 104 cat scats and 26 cat stomachs containing the remains of 302 prey items were collected and analysed in the lab (Table 2). The frequencies of prey items present in scats/stomachs during the tern breeding period versus the non-tern breeding period are presented in Fig. 2. There was a significant difference between the two periods in the frequency of prey items ($\chi^2 = 152.47$, d.f. = 6, $P < 0.001$). Outside the tern breeding period, the majority of prey items were insects, rats and mice (Fig. 2). Most insects were *Gromphadorhina* sp. (Blaberidae, 62%) as well as grasshoppers (Acrididae, 20%). Mantidae (4.6%) and other families made up the remainder (Table 2). Sooty terns were present in low

numbers and the few that we recorded were from older scats, presumably from when terns were present (Fig. 2).

Scats and stomachs collected during the tern breeding period contained mostly tern remains (Fig. 2). Rats, mice, insects and reptiles were also present, but at a low frequency (Fig. 2, Table 2). Of the four cat stomachs collected after the arrival of the sooty terns, three contained a minimum of two terns and the fourth contained the remains of a guinea fowl *Numida meleagris* (Table 2).

Cat population size

We trapped and removed 26 cats from Juan de Nova Island over a period of 41 days. The number of cats trapped per night was high at the beginning of the trapping period, but levelled off after the first 7 days (Fig. 3). The majority of these (15) were caught in the vicinity of the military camp (a source of human refuse) (Fig. 1). Four were caught in the tern sub-colonies, with the rest caught at various locations around the island (Fig. 1). A total of 17 cats were shot by military personnel before the commencement of trapping (see 'Materials and Methods'). This means that 43 cats were removed during the period June–August 2006. A simple exponential smoothing model applied to our data gives an upper 95% confidence limit of 53 cats (12.04 per km²), suggesting that presently, a maximum of 10 cats remain at Juan de Nova. Our spotlighting data supported the statistical approach by suggesting that Juan de Nova Island had a cat population density of 11.4 cats per km² (50 cats), and that seven cats now remain.

Cat predation rate

During the 16 days that we monitored predation at Juan de Nova, 122 sooty tern carcasses were removed from our two plots within the two tern sub-colonies (Fig. 4). Eighty-nine (73%) of these carcasses showed evidence of cat predation and consumption, 27 (22%) were killed without being consumed and six (5%) showed no evidence at all of cat predation (Fig. 4). After two cats were removed (16/8/07), the majority of kills were predated and consumed (30; 89%) compared with predation without consumption (4; 11%). No carcasses were without evidence of cat predation during this time. To our knowledge, this is the first time that cat predation on seabirds without consumption ('surplus killing') has been quantified.

Using the data from our plots, and extrapolating for the entire colony, we estimate that 416 (± 154) sooty terns per week were killed by the maximum of ten cats remaining on the island during the time that our plots were being monitored. This equates to 5.94 (± 2.2) terns cat⁻¹ day⁻¹. When we multiply the predation rate by 53 (our estimate of the maximum cat population before our arrival), we obtain a figure of 2205 terns week⁻¹ (0.1% of the breeding population) that could be killed by cats at Juan de Nova during a breeding season. It must be noted, however, that this estimate is generated from an assumption that ten cats remain. This is the maximum number of cats left on

Table 2 Diet composition of *Felis catus* on Juan de Nova Island, expressed as the number of individual prey items per category, a proportion of the total number of items and the frequency of occurrence

	<i>n</i> (prey items)	Proportion of total (%)	Frequency of occurrence (%)
Scats (104 scats)			
Birds			
<i>Sterna fuscata</i>	30	12	29
<i>Foudia madagascariensis</i>	2	1	2
Unknown	7	3	7
Mammals and reptiles			
<i>Rattus rattus</i>	79	32	66
<i>Mus musculus</i>	57	23	38
<i>Cryptoblepharus boutoni</i>	4	2	2
<i>Hemidactylus mabouia</i>	1	0	1
Invertebrates			
<i>Gromphadorhina</i> sp.	30	12	16
Elateridae	3	1	2
Mantidae	3	1	3
Acrididae	17	7	16
Vespidae	1	0	1
Pentatomidae	1	0	1
Unknown	6	2	6
Human refuse	6	2	6
Total	247		
Stomachs (26 stomachs)			
Birds			
<i>Sterna fuscata</i>	7	13	15
<i>Numida meleagris</i>	1	2	4
Mammals and reptiles			
<i>Rattus rattus</i>	7	13	27
<i>Mus musculus</i>	8	15	31
<i>Cryptoblepharus boutoni</i>	3	5	12
Invertebrates			
<i>Gromphadorhina</i> sp.	24	44	19
Mantidae	1	2	4
Acrididae	1	2	4
Human refuse	3	5	12
Total	55		

Juan de Nova, and so the predation rate is likely to be conservative.

Effect of cat removal

The sooty tern predation rate during the first four days of tern arrival at Juan de Nova increased incrementally to a clear peak on the fourth day (Fig. 4). On the fifth day (16/8/06), two cats were caught in cages that were set within each of the two tern sub-colonies (Fig. 4). The average (\pm SE) rate of cat predation across both sub-colonies before cat removal was $0.420 \text{ terns km}^{-2} \pm 0.12$. After cat removal, the predation rate declined to $0.036 \pm 0.01 \text{ terns km}^{-2}$: a >tenfold decrease. This decrease was significant (Welch ANOVA; $F_{1,4; 12} = 9.41$, $P = 0.03$). When the rate was adjusted to only include carcasses that were predated and consumed, a similar result was obtained (before cat removal; mean = $0.329 \pm 0.09 \text{ terns km}^{-2}$, after cat removal; mean = $0.032 \text{ terns km}^{-2} \pm 0.01$: Welch ANOVA; $F_{1,4; 12} = 9.24$,

$P = 0.03$). The predation rate remained low for the remainder of the period (Fig. 4).

Demographic model

The basic matrix population model (without cat predation incorporated) predicted an annual population growth rate of 1.01. This is a small annual growth rate consistent with that seen in other species of seabird (Keitt *et al.*, 2002; Awkerman *et al.*, 2006). As expected, population growth declines with an increase in cat predation (Fig. 5). However, the number of cats required to cause a population growth rate of <1 is much larger than our maximum estimated cat population of 53. In fact, the model suggests that a minimum of 120 cats are required for this to occur (Fig. 5). For the range of values tested in the sensitivity analysis, adult survival rate had a stronger impact on the population growth rate than did reproductive success (Fig. 6). This was confirmed by the elasticity values (adult survival, 0.53, reproductive success, 0.06).

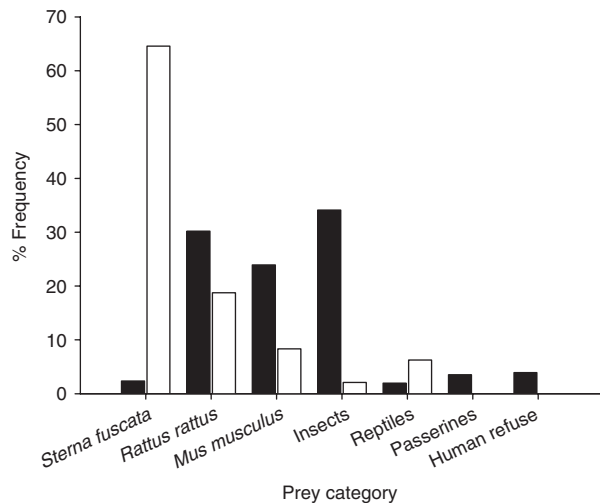


Figure 2 Frequency (%) of occurrence of prey items found in the scat and stomachs of feral cats *Felis catus* collected at Juan de Nova Island both outside (black bars) and during the sooty tern *Sterna fuscata* breeding season (white bars).

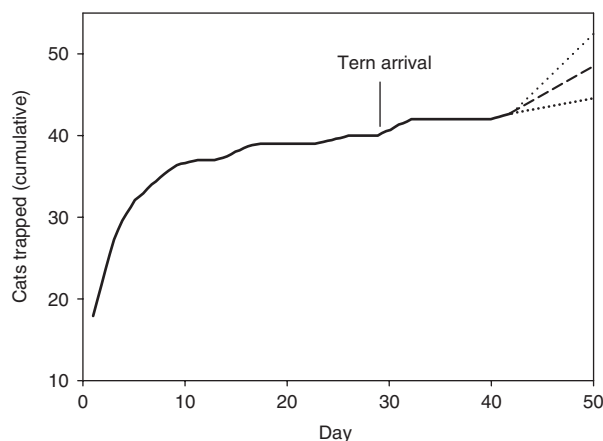


Figure 3 Cumulative plot of number of cats *Felis catus* caught over time. The plot begins at 17 because this number of cats was removed by military personnel just before the start of the trapping campaign. A simple exponential smoothing model was applied to the data and the upper and lower 95% confidence intervals generated (dashed line).

Discussion

Cat diet analysis

Due to the nature of our data, we are unable to exclude the possibility that seasonal (year to year) changes in prey availability have influenced the results of the cat dietary analysis. Specifically, seasonal fluctuations in rat or mice availability could impact sooty tern predation rates. However, mice and rat systematic trapping conducted during the different field sessions did not show any major changes in rat or mice density (D. R. Peck *et al.* unpubl. data). Nonetheless, the dietary analysis confirms, as in many previous

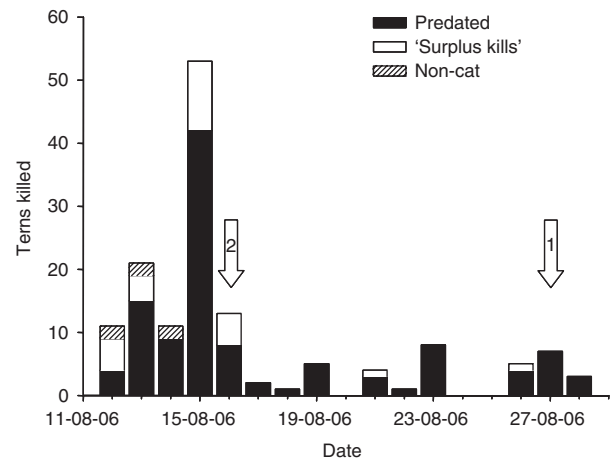


Figure 4 Proportion of predated (and consumed) sooty terns versus 'surplus kills', and those that died from unknown causes (non-cat). The plot shows changes in the proportions of these categories over time. Total numbers of terns from both sub-colonies are shown. The arrows indicate when and the number of cats removed from the two sub-colonies combined.

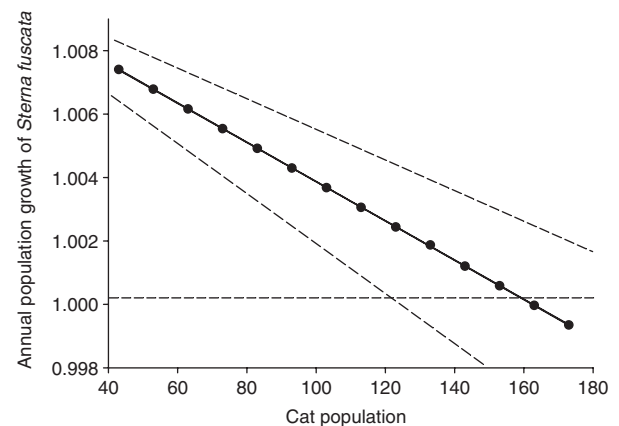


Figure 5 Matrix population model showing population growth (λ) (\pm 95% confidence interval), for the population of two million female sooty terns *Sterna fuscata* as a function of the number of cats at Juan de Nova Island. The horizontal dotted line represents a stable population.

studies, that cats are generalist predators that consume a wide range of prey types (Nogales & Medina, 1996; Lozano, Moleon & Virgos, 2006; Medina & García, 2007; Bonnaud *et al.*, 2007). We appear to observe a clear shift in the diet of feral cats at Juan de Nova synchronous with the arrival of sooty terns. When terns are available, they are eaten in preference to other prey items (Fig. 2). Outside of the tern breeding period, a wider variety of prey items are consumed that includes human refuse (Fig. 2). It has been suggested that this 'opportunistic' feeding behaviour facilitates the settlement and the persistence of feral cat populations on islands with seasonal food resources (Apps, 1986; Pontier *et al.*, 2002). This seems to be the case for the cats at Juan de

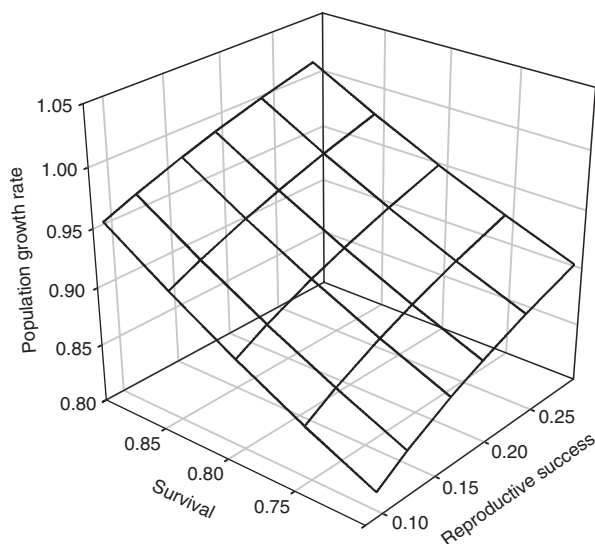


Figure 6 Sensitivity analysis of the deterministic matrix model for sooty terns *Sterna fuscata*: the effect of changing reproductive success and adult survival on the population growth rate (λ).

Nova Island, although, as mentioned above, further data (within year) are required to explore this possibility fully.

The effect of cat removal

It has been highlighted that both acute (short-term) and chronic (long-term) characteristics of invasive mammal predation need to be understood for effective management practices (Strayer *et al.*, 2006; Williamson, 2006). As cats were simultaneously removed while predation on sooty terns was quantified at Juan de Nova, we had the unique opportunity to examine the acute impact of cat predation on seabirds: something that has not been attempted previously.

We observed a clearly defined arrival, *en masse*, of sooty terns at Juan de Nova Island on 12/8/06. Simultaneously, large numbers of sooty terns were found predated by cats in our plots (Fig. 4). The pattern we observed of predation rate peak and decline is interesting and could be the result of either (1) a decline in cat predation because the 'surplus killing' of so much accessible prey declines after four days and consequently predation levels off or (2), predation rate decline because two cats were removed from the sub-colonies. A third possibility is that our results reflect a combination of these two, and we believe this to be likely based on the following arguments.

Surprisingly, few studies have mentioned the phenomenon of 'surplus killing' in cats (but see Stuart, 1986; Short, Kinnear & Robley, 2002) and to our knowledge, none have directly quantified it. Our data indicate that this not only occurs, but that it declines with time, as evidenced by the decreasing numbers of surplus kills towards the end of the study period (Fig. 4). Thus, there is some evidence that our temporal pattern of predation rate change confirms the first hypothesis (above).

However, the large change in predation rate that clearly occurred after 16/8/06 cannot simply be explained by the proportion of surplus killing declining with time because even without the surplus kills included, a tenfold decrease was observed (refer results) (Fig. 4). Thus, the removal of two cats significantly and immediately reduced the number of dead sooty terns in our plots. Removing another cat on 27/8/06 may also have had an effect on tern predation, but as monitoring stopped after this time, we cannot comment further (Fig. 4).

Removing cats from seabird colonies has previously been shown to drastically reduce predation rates over annual temporal scales (Cooper *et al.*, 1995; Keitt & Tershy, 2003; Rodríguez, Torres & Drummond, 2006). In the current paper, we present the effects of cat removal within a season, and when cat density was low, thereby allowing us to highlight the fact that the removal of one cat can drastically reduce seabird mortality rates over short temporal scales. Of course, we have no way of knowing whether predation increased after we stopped monitoring our plots. However, it would seem likely that as cats moved into vacant territories, predation would again increase.

Demographic model

We recognize the limitations of our deterministic modelling approach because certain life-history data are unavailable, and predation rates are subject to various processes (see above) (Caswell, 1989; Mills, Doak & Wisdom, 1999; Doherty *et al.*, 2004; Ezard, Becker & Coulson, 2006). Moreover, even though both techniques for estimating cat density were similar, it is likely that we have underestimated the cat density at Juan de Nova during the period of tern predation. This may be because of individual variation in cat behaviour in relation to our ability to spot individuals at night and in the likelihood of certain cats (e.g. older or more experienced ones) being trapped (Read & Bowen, 2001; Say, Gaillard & Pontier, 2002). Thus, the results of our modelling must be interpreted cautiously. However, as management decisions are often required before reliable long-term data can be collected for more complex model development, deterministic models serve a crucial function.

Our modelling shows that even under scenarios of extremely high predation (i.e. >120 cats), the sooty tern population at Juan de Nova Island may still be able to persist (Fig. 5). However, the cat population at Juan de Nova is far from dense. Our estimate of around 12 per km² is 20-times smaller compared with the largest recorded feral cat density of 243 per km² at Cousine Island in the Seychelles (Laboudallon, 1987; Parr *et al.*, 2000). Moreover, our estimate was taken at the very start of the tern breeding season when cat numbers are predicted to be at their lowest because terns were unavailable for ~5 months. Thus a seasonally dependant population of 120 cats (~37 per km²) is not unrealistic, especially in light of the fact that cats are known to rapidly increase in numbers (via. immigration and reproduction) when preferred prey densities are high (Pech *et al.*, 1992).

Our cat predation and demographic modelling results seem counter-intuitive in that the removal of one cat lowers the predation rate 10 fold and yet a threefold increase of the current cat population is required for the model to produce a population decline. Although predation rate and population growth are related, it must be noted that the matrix model calculates λ by taking into account population size and life-history parameters in addition to predation rate. Thus, although predation may have a large initial impact, over longer periods, population size and life-history parameters may regulate population growth to some extent.

Management/conservation implications

Our study revealed that human refuse, insects, introduced rats and introduced mice provide a food resource outside of the tern breeding season, which probably facilitates the persistence of the cat population at Juan de Nova Island. This scenario maintains breeding season predation on sooty terns (a process known as 'hyperpredation'; Holt, 1977; Courchamp, Langlais & Sugihara, 2000). We have also shown that cats switch from insects and rats to sooty terns, and start to preferentially predate them immediately they become available. Removal of rats and mice could minimize the hyperpredation effect. However, to do this successfully would require information on rat and mouse densities and their trophic ecologies before being attempted (Rodriguez *et al.*, 2006). This is clearly a research/management priority.

Soulé *et al.* (1988) and more recently Courchamp, Langlais & Sugihara (1999a,b) described the possibility that removing a super-predator (cats) may lead to an increase in secondary predation (e.g. by rats) that could ultimately increase negative effects on the target species (the so-called 'mesopredator release effect'). However, these predictions are based on differential equation models that do not take into account the age structure of the target species and the differences of sensitivity in the growth rate (λ) to changes in survival or breeding success. Our matrix population model clearly shows that sooty terns, as with all long-lived seabirds, are more sensitive to changes in adult survival than to changes in breeding success (Fig. 6). Although rats have been known to predate adult seabirds, they likely only predate eggs and chicks in large numbers (Croxall & Rothery, 1991). Therefore, they are predicted to reduce breeding success, and have a weaker effect on adult survival. On the other hand, our results clearly show that cats have a strong impact on adult survival. Consequently, we believe that for sooty terns, the eradication of cats should not lead to a mesopredator release effect. This is not to say, however, that other species may not be affected. Therefore, maintaining adult sooty tern survival (by eradicating cats) should be a management priority, as highlighted by studies on other seabird species (e.g. Martínez-Gómez & Jacobsen, 2004).

In relation to other seabird species, it is also notable that sooty terns at Juan de Nova are seasonal, highly synchronized breeders. They could therefore 'swamp' the cat population during their breeding season, especially given the large population size. However, species that breed all year

round or for extended periods (or in low numbers) would suffer persistent predation. These species (e.g. Audubon's shearwater, red and white-tailed tropic birds) are perhaps more vulnerable to the effects of chronic cat predation than the synchronous breeders, and could thus return to breed once all cats have been removed from Juan de Nova Island. To conclude, we recommend that a review of the current impact of feral cats on sooty terns and other seabird species elsewhere in the western Indian Ocean be undertaken, especially if population sizes are small and/or the species concerned breeds asynchronously.

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