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Trophic roles of black rats and seabird impacts on tropical islands: Mesopredator release or hyperpredation?

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A B S T R A C T

Rats contribute to the decline of tropical seabird populations by affecting their breeding success through direct predation of eggs and chicks. When they coexist with other predators, invasive rats may also generate indirect interactions via the changes they impose on the structure of communities and trophic interactions following invasion ('hyperpredation process'), or when apex predators are eradicated from the ecosystem ('mesopredator release effect'). Understanding these effects is necessary to implement restoration operations that actually benefit threatened seabird populations. We investigated these processes on two French tropical seabird islands of the western Indian Ocean, Europa and Juan de Nova, where black rats coexist with two different apex predator species (introduced cats and potentially native barn owls). The parallel use of several methods (diet analysis, stable isotopes, seabird monitoring) to identify trophic roles of rats revealed that the direct impact of rats on seabirds was particularly high on Europa where only rats and owls occur, with high consumption of chicks resulting in low breeding success for several seabird species. We also suggested that hyperpredation associated with top-down regulation of cats is occurring on Juan de Nova, although territoriality of cats may buffer this process. Conversely we found evidence that mesopredator release effect is unlikely, irrespective of the apex predator identity. Considering the most likely effects on both islands we provided recommendations on eradication priorities to mitigate the risk of local extinction that seabirds are currently facing.

1. Introduction

The introduction of rats on islands has been identified as one of the main threats to seabird breeding populations (Croxall et al., 2012). There is an extensive literature documenting the negative direct impacts of rats on seabirds. Jones et al. (2008) identified 94 studies showing a direct impact of invasive rats (*Rattus rattus*, *Rattus exulans*, *Rattus norvegicus*) on seabirds (115 cases of predation on 61 islands, involving 75 species of seabirds). Rats can prey upon eggs and chicks of many families of seabirds as well as adults of some species of small size (e.g. storm petrels) (Jones et al., 2008; Pickup, 1999; Seto and Conant, 1996; Tomkins, 1985).

Invasive rats may also generate negative indirect impacts via the changes they impose on the structure of communities and trophic interactions following invasion, or when apex predators are eradicated from the ecosystem (Fig. 1). In particular mesopredator release effect (a specific case of intraguild predation) and hyperpredation process may occur depending on the functional role of

rats in the invaded ecosystem. Intraguild predation occurs when two predators are simultaneously involved in a predatory relationship while competing for a shared prey (Holt and Polis, 1997; Polis and Holt, 1992). Generally one predator (i.e. apex predator) preys upon the other (i.e. mesopredator) through an asymmetrical intraguild predation (Holt and Polis, 1997). In this configuration both predators have an important impact on the common prey and mesopredator release (e.g. release of rats) may occur after removal of the apex predator (e.g. cats) resulting in an increase of the negative impact on native species (Fig. 1) (Courchamp et al., 1999). Hence mesopredator release effect requires two conditions: (1) the negative effect of rats on seabird population growth rate after the removal of the apex predator must outweigh the initial cumulative impacts of both predators, and (2) mesopredator population dynamics must be regulated by the apex predator (i.e. top-down regulation) (Courchamp et al., 1999). Although mesopredator release effect has often been discussed in the field of conservation, there are few documented examples (Nishijima et al., 2014). On Little Barrier Island (New Zealand), cats and rats preyed upon petrels and cats also preyed upon rats. After the eradication of cats, breeding success of petrels considerably decreased, and improved

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only after the eradication of rats (Rayner et al., 2007). Rats are likely to have caused this decrease in breeding success of petrels, although no evidence of simultaneous increase in the rat population could be made (Girardet et al., 2001). In addition, although the breeding success decreased indirectly due to the elimination of cats, an increase in survival of adult birds and population growth rate probably also concomitantly occurred (Le Corre, 2008). Alternatively, rats may act as alternative prey for the apex predator and indirectly impact native seabirds through apparent competition (Bate and Hilker, 2012; Courchamp et al., 2000). Apparent competition applies to those situations in which two prey species have a negative indirect effect on one another resulting from interactions with a common predator (Holt, 1977; Holt and Lawton, 1994). Thus, as in the case of a ‘real’ competition between the two prey species, the increase of the size of one population causes the decrease of the other, while these two species are not necessarily exploiting the same resource (hence the term “apparent” competition). Apparent competition on islands has been studied in the particular case where the main prey species is native and the secondary prey is an introduced species (Courchamp, 1999), a process called hyperpredation (Smith and Quin, 1996) (Fig. 1). In this process, an introduced prey adapted to predation (e.g. rats) and with high growth rate and behavioural anti-predator strategies, promotes apex predator numbers (e.g. cats), which in turn increases the impact on native prey (e.g. seabirds). Therefore, the possibility of complex and indirect interactions resulting from the introduction or removal of a predator must be the subject of special attention when planning the eradication of invasive rodents.

In this paper, we investigated the trophic roles of black rats (*R. rattus*) on tropical islands. In particular we compared direct and indirect effects they generate on breeding populations of seabirds. Trophic roles of rats and their consequences on seabirds were studied with a combination of methods (diet analysis, stable isotopes, seabird monitoring) on two contrasted French tropical islands lying in the Indian Ocean. These data also meet the current need of documenting the effects of invasive rats on native communities on tropical islands (Townsend et al., 2006; Varnham, 2010). The results may inform local stakeholders on eradication priorities for the restoration of these islands. The understanding of these interactions also has a global scope in terms of conservation, as the predator associations described here are relatively common on islands.

2. Material and methods

2.1. Study sites

Europa (2223 ha; 22°210S, 40°210E) and Juan de Nova (561 ha; 17°030S, 42°450E) are two tropical islands lying in the Mozambique Channel (between the East African coast and Madagascar), administered since 2007 by TAAF (Terres Australes et Antarctiques Françaises) (Fig. 2). The climate is characterized by the alternation of a warm and wet season (austral summer, between November and March) and a dry and cooler season (austral winter between April and October). Black rats have been introduced to both islands before the mid-19th century (Russell et al., 2011b). Europa supports high rat densities (10–80 rats ha⁻¹) whereas rat densities are intermediate on Juan de Nova (10–35 rats ha⁻¹) (Russell et al., 2011a). On Europa, the large lagoon supports an additional 3-ha islet at the northern entrance, where rats are also present. Cats (*Felis catus*, <80 individuals in 2006) and mice (*Mus musculus*) have also been introduced on Juan de Nova and a small population of barn owls (*Tyto alba*, <15 pairs) breeds on Europa but their status (native or introduced) is uncertain (Russell and Le Corre, 2009). Cats were heavily controlled on Juan de Nova between 2006 and 2011 but not eradicated (123 cats removed and less than 10 cats left in 2011). These islands are major breeding sites for seabirds (Table 1) and turtles (*Chelonia mydas*, *Eretmochelys imbricata*) (Le Corre and Jaquemet, 2005). In particular, very large colonies of sooty terns (*Onychoprion fuscatus*) breed during summer on Juan de Nova (450,000 pairs) and during winter on Europa (760,000 pairs). They are also home to several other native species, including reptiles, songbirds and shorebirds, and are stopping points for many migratory species. Fieldwork consisted of 1 or 2 months long visits (at least once a year between 2006 and 2013) to these remote islands occupied year-round by military detachments (15 people).

2.2. Diet of black rats

Black rats were trapped in summer and winter between 2006 and 2013 on both islands. On each island trapping sessions were carried out inside and outside sooty tern colonies (within 1 km of the colony) when terns were breeding (during summer on Juan de Nova and during winter on Europa), and only outside tern colonies when terns were absent. No other seabird bred inside and outside tern colonies on Juan de Nova but a few breeding pairs of

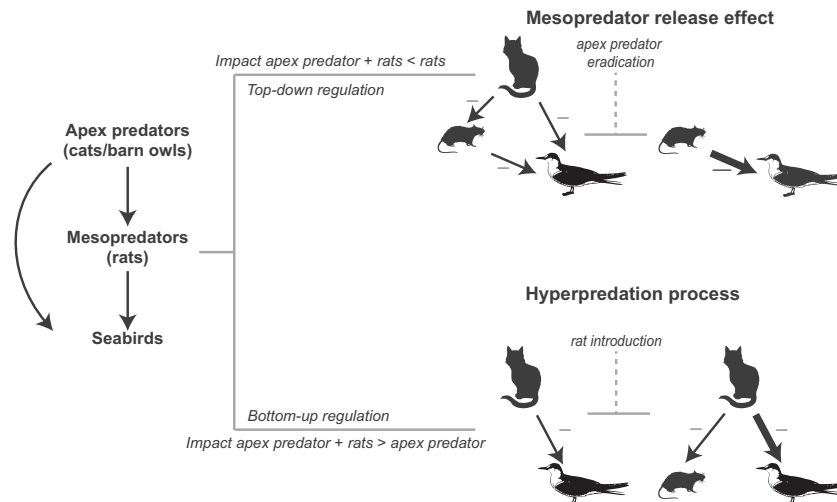


Fig. 1. Schematic representations of mesopredator release effect and hyperpredation process. In a bottom-up driven system (hyperpredation process) rat population is regulated by trophic resources whereas in a top-down driven system (mesopredator release effect) abundance of rats is regulated by apex predators.

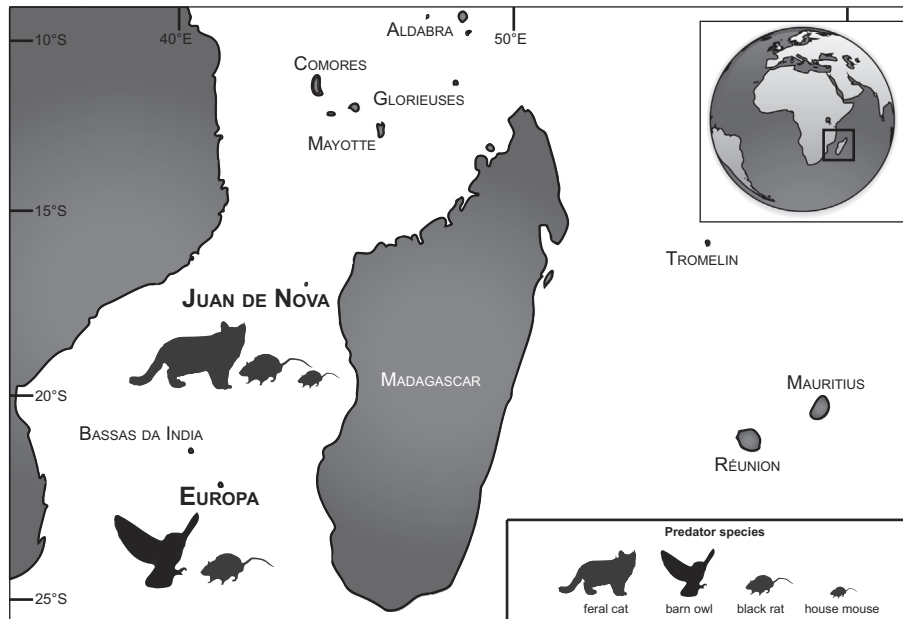


Fig. 2. Map of studied sites and associated communities of predators.

Table 1
Seabird population sizes on Europa and Juan de Nova (number of breeding pairs).

Species	Europa	Juan de Nova	Year	Source
Red-tailed Tropicbird (<i>Phaethon rubricauda</i>)	2000		2012	Pinet and Rubio unpub. data
Tropical Shearwater (<i>Puffinus lherminieri</i>)	<50		1997	Le Corre and Jaquemet (2005)
White-tailed Tropicbird (<i>Phaethon lepturus europae</i>)	1000		2012	Pinet and Rubio unpub. data
Great Frigatebird (<i>Fregata minor</i>)	1100		1997	Le Corre and Jaquemet (2005)
Lesser Frigatebird (<i>Fregata ariel</i>)	1200		1997	Le Corre and Jaquemet (2005)
Sooty Tern (<i>Onychoprion fuscatus</i>)		450,000	2013	Orlowski and Amouroux (2014)
Sooty Tern (<i>Onychoprion fuscatus</i>)	760,000		2003	Le Corre and Jaquemet (2005)
Crested Tern (<i>Sterna bergii</i>)		200	1997	Le Corre and Jaquemet (2005)
Red-footed Booby (<i>Sula sula</i>)	3000		1997	Le Corre and Jaquemet (2005)
Caspian Tern (<i>Hydroprogne caspia</i>)	10		1997	Le Corre and Jaquemet (2005)

tropicbirds (*Phaethon rubricauda* and *Phaethon lepturus europae*) were found outside tern colonies during summer trapping sessions on Europa. Stomach contents of 299 black rats ($n = 126$ for Juan de Nova and $n = 173$ for Europa) were analysed to determine their diet. The stomach content was considered a reflection of the last meal. The stomachs were emptied and the content was flushed into a Petri dish and then filtered through a sieve of 1 mm mesh. All fragments larger than the mesh were collected and fixed in 70% alcohol, and then observed under a microscope. Only stomachs containing more than 50 fragments were used for analysis, all others were considered empty (Pisanu, personal communication). Seabird feathers were identified using a reference collection of tropicbirds and sooty terns chicks' feathers. Results are expressed as frequency of occurrence by food item. The differences in food composition were tested between seasons (presence vs. absence of sooty terns), between islands and within island sites with parametric or nonparametric analyses of variance on the transformed frequencies of occurrence (arcsine of the square root), depending on the normality of the data.

2.3. Diet of apex predators

2.3.1. Cats

Diet of cats on Juan de Nova was analysed from the 323 fresh scats collected in summer (sooty tern breeding season) and winter

between 2008 and 2012. Degraded scats were not considered. Fresh samples picked from the ground reflect food consumption of cats at the time of collection as scats degrade quickly in the environment (Sanchez et al., 2004). In addition, scats can be considered a reflection of the daily consumption of food by a cat (Fitzgerald and Karl, 1979). Each sample was dipped in warm water for 12 h and then the contents were passed over a 1 mm mesh sieve. The fragments retained by the sieve were observed under a microscope. Each fragment was identified to family or species level. The relative conservation of the fragments in the scats allowed quantification of individuals of each prey species. Results of the food contents of cats are given in relative abundance of the total number of prey consumed. Seasonal differences (presence vs. absence of sooty terns) in relative abundances of prey were tested by ANOVA on normalized data (arcsine of the square root).

To estimate the contribution of different prey to the diet of cats at a longer time-scale, we collected on a single visit (2006) tissue samples (liver) from 16 individuals (5 females and 11 males) for stable isotope analysis on nitrogen and carbon. Carbon isotopes are particularly useful to determine sources of consumption and to distinguish marine prey from terrestrial prey (Peterson and Fry, 1987). The nitrogen isotopes are used to determine the trophic position of individuals, because nitrogen isotope values tend to increase in a predictable manner between successive levels of consumers in the food chain (Schoeninger et al., 1983). We modelled

the contribution of different preys with the Bayesian multi-source mixture model SIAR ('Stable Isotope Analysis in R') (Parnell et al., 2010). SIAR offers a number of advantages over other mixture models because it can integrate the known variability of sources and uncertainty of trophic enrichment factors (TEF) (Parnell et al., 2010). We included the mean and standard deviation of the isotopic composition of the main sources of prey. During the same visit (2006) we sampled seabirds (sooty terns), rats, mice and invertebrates (carnivores, scavengers and herbivores) as potential sources. TEF were taken from the literature, 3.4‰ for nitrogen and 1.5‰ for carbon, each with a deviation of $\pm 0.5‰$ to take account of the variability observed in the literature (Vander Zanden and Rasmussen, 2001). The results of the contribution of each source to the diet of cats are presented in the form of intervals corresponding to 50% and 95% of the probability density.

2.3.2. Barn owls

The diet of barn owls on Europa was analysed from pellets. The pellets were collected regularly during successive visits between 1994 and 2010. Collection of samples was carried out at nests and at diurnal roosting places. Each pellet was soaked in warm water for 12 h to separate the different fragments. The contents were then rinsed and sieved with 1 mm mesh. All the fragments retained by the sieve were then observed under a microscope. Type and number of distinct prey were identified for each pellet. Results of the food contents of barn owls are given in relative abundance of the total number of prey consumed. Seasonal differences (presence vs. absence of sooty terns) in relative abundances of prey were tested by ANOVA on normalized data (arcsine of the square root).

2.4. Seabird monitoring

On Juan de Nova, the predation rate by cats on sooty terns was measured at the arrival of birds on the island (i.e. birds on the ground at night) and during incubation and brooding (i.e. birds on the ground day and night). We conducted daily counts of carcasses on four sampling areas of 0.25 ha (50 m \times 50 m) randomly selected within tern colonies. The number of tern carcasses from three categories was recorded: (1) tern preyed upon by a cat and consumed at least in part, (2) tern preyed upon by a cat but not consumed and (3) carcass without evidence of predation. Values for the second category may be underestimated (and hence those of first category may be overestimated) due to the presence of scavengers on colonies (pied crows, *Corvus albus* and hermit crabs). The average mortality per hectare per day was also calculated from the sum of the number of carcasses of the first two categories. We extrapolated the number of terns preyed upon to the scale of the entire colony by multiplying the mortality rate estimated by colony size (Keitt et al., 2002; Peck et al., 2008).

On Europa, the breeding success of 5 seabird species nesting on the ground (*P. rubricauda*, *P. lepturus europae*) or in trees (*Fregata ariel*, *Fregata minor* and *Sula sula*) was measured. This parameter is defined as the ratio of the number of chicks that fledged compared to the number of eggs laid by breeding pairs. For red-tailed tropicbirds (*P. rubricauda*), breeding success was monitored on the main island (where rat density is very high) and on the islet where rats were controlled in 2008 but not in 2009. We also monitored red-tailed tropicbirds nests at night with autonomous video systems to assess the interactions between breeding birds and nocturnal predators (rats, owls, crabs) on the main island. Video devices were set around a total of 10 nests representing different breeding stages: incubation, brooding and when the chick is left alone at night. During 10 to 20 successive nights, every hour between 5 pm and 8 am the next morning, 30 min sequences were recorded.

3. Results

3.1. Trophic ecology of black rats

Analysis of 299 stomach contents revealed that plants and arthropods were the two main categories of food consumed by rats (Fig. 3). The frequency of occurrence of plants in the stomach contents was on average (\pm SD) $93.6 \pm 5.2\%$ and was constant among rat groups (island \times season \times habitat combinations, Kruskal–Wallis, $p > 0.05$) whereas the frequency of occurrence of arthropods varied significantly around an average of $80.1 \pm 17.5\%$ ($p < 0.05$). The frequency of occurrence of sooty terns remains in stomachs of rats trapped in tern colonies were respectively $44.0 \pm 21.0\%$ and $71.4 \pm 15.1\%$ on Juan de Nova and Europa. On Europa rats trapped in summer outside tern colonies showed no evidence of consumption of tropicbirds. The remains of sooty terns found in the stomachs of rats trapped in tern colonies were all chicks' natal down feathers.

On Europa, from over 147 h of red-tailed tropicbirds nest surveillance footage, only two types of potential nocturnal predators could be observed: rats and hermit crabs. Hermit crabs are very abundant in areas where nests were monitored. Although they were often observed, their presence in the nests seemed harmless (i.e. crabs crossing nests). No predation event was directly recorded but many visits of rats were recorded and attacks were observed on chicks left alone before predation (three chicks out of 10 nests were preyed upon during standby phases of the camera, between two successive recordings). Visits of rats in nests were very frequent with $0.34 \text{ visit h}^{-1} \text{ nest}^{-1}$. However, visit rates varied depending on the breeding status of the nest. Observations of rats were much more frequent when the chick was left alone ($1.11 \text{ visit h}^{-1} \text{ nest}^{-1}$) than when adults were incubating ($0.17 \text{ visit h}^{-1} \text{ nest}^{-1}$) or brooding ($0.43 \text{ visit h}^{-1} \text{ nest}^{-1}$).

The average (\pm SD) breeding success of seabirds measured on Europa was very low ($13.5 \pm 9.3\%$, all species and all seasons pooled) (Table 2). The breeding success of red-tailed tropicbirds on the main island was very low and constant around an average of $4.8\% (\pm 3.1\%)$. When rats were controlled in 2008 on the islet, breeding success of red-tailed tropicbirds reached 32%, which is 4 times more than on the main island that same year (8.2%) (Table 2). The following year (2009), the breeding success of red-tailed tropicbirds was once again closer to the main island (8.5% against 4.1%). Only two species had a breeding success over 10% on the main island (Table 2).

3.2. Trophic ecology of apex predators

3.2.1. Cats (Juan de Nova)

A total of 323 cat scats were collected on Juan de Nova over 7 different months between 2007 and 2010. The overall diet of cats is characterized by a high consumption of invasive rodents with relative abundances of 46.1% of rats and 19.3% of mice (Fig. 4a). We found an average of 0.53 ± 0.66 rat and 0.45 ± 0.94 mouse per scat. The diet of cats presented major seasonal variations between austral summer and winter ($p < 0.001$) (Fig. 4a). A sudden change in the relative abundance of preys occurred during the arrival of sooty terns for breeding (Fig. 4a). During sooty terns breeding season (September to April), rats were in lower proportions (22.3%) and cats consumed large numbers of terns (45.4%), representing an average of 0.70 ± 0.81 tern per cat and per day. We therefore estimated that during the breeding season of terns (~ 210 days), a single cat would eat about 150 terns (i.e. $0.7 \text{ tern per day} \times 210 \text{ days}$). Monitoring of tern colonies also showed that only 45% of carcasses had signs of consumption (category 1), which means that a cat could kill on average more than twice as many terns it consumed (i.e. about 330

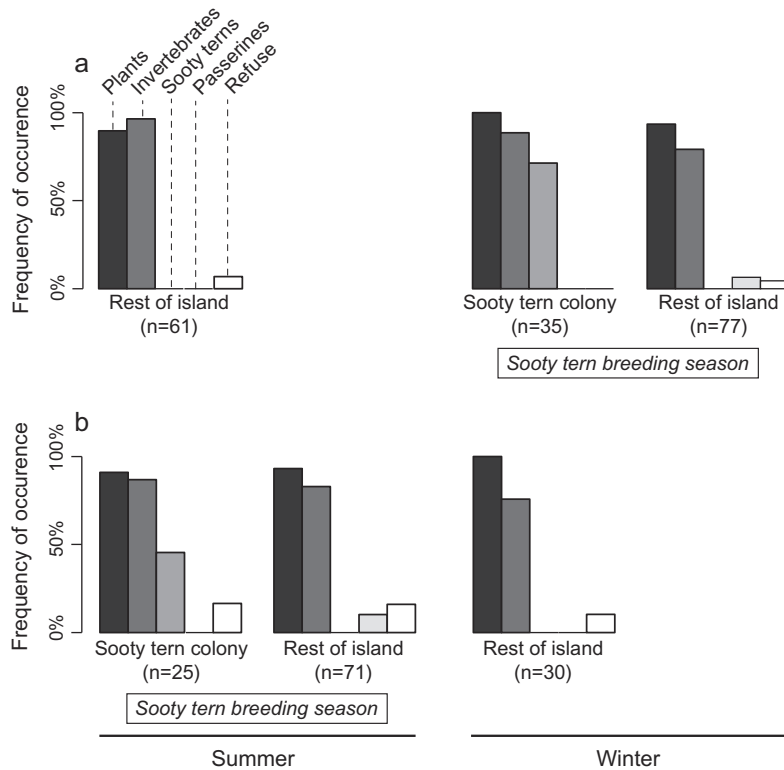


Fig. 3. Frequencies of occurrence of different food items in the food diet of cats on (a) Europa and (b) Juan de Nova, depending on season (winter vs. summer) and place of trapping (sooty terns colony vs. rest of island).

Table 2
Breeding success of seabirds of Europa on main island and islet. In brackets the number of nests monitored.

Species	Breeding season	Breeding success	Breeding success (islet)
<i>P. rubricauda</i>	2008–2009	8.2% (120)	32.0% (28)
	2009–2010	4.1% (147)	8.5% (24)
	2011–2012	2.0% (50)	
<i>P. lepturus europae</i>	2008–2009	6.9% (43)	
<i>F. ariel</i>	2008–2009	26.6% (124)	
<i>F. minor</i>	2008–2009	7.5% (106)	
<i>S. sula</i>	2008–2009	21.5% (79)	

terns). However, scavenging by pied crows was very common on tern colonies (D. Ringler pers. obs.) and is likely to have biased the observed proportion of terns consumed by cats (i.e. less than 45%) and therefore to underestimate the average number of terns killed per cat and per year (i.e. more than 330 terns). Cat predation of sooty terns averaged 5.5 ± 4.5 terns $\text{ha}^{-1} \text{day}^{-1}$ and increased between pre-nuptial and the incubation phase of terns with respectively 3.5 ± 3.3 terns $\text{ha}^{-1} \text{day}^{-1}$ in August (pre-laying phase) and 7.5 ± 4.2 terns $\text{ha}^{-1} \text{day}^{-1}$ in December (incubation and early chick rearing). Considering the colony size (51 ha), we estimated a total of 37,000–80,000 terns were killed during breeding season (i.e. respectively 3.5 terns $\text{ha}^{-1} \text{day}^{-1}$ and 7.5 terns $\text{ha}^{-1} \text{day}^{-1} \times 51$ hectares $\times 210$ days).

Stable isotope mixture models showed some diet variability between cats (Fig. 5). Three isotopically homogeneous groups of cats were distinguished by visually assessing graphs with individual isotopic ratio. The first group, containing exclusively females ($n = 5$) consumed mainly terns, mice and reptiles (Fig. 5a). The

second group, containing exclusively males ($n = 4$) consumed equally all potential sources of prey, including a significant proportion of terns (Fig. 5b). Finally for the last group also containing exclusively males ($n = 7$), the main sources of food were rats, passerines and arthropods. For this group, terns did not seem to contribute to the diet (Fig. 5c).

3.2.2. Barn owls (Europa)

Rats were the main source of food for barn owls on Europa (0.85 ± 0.73 rats pellet $^{-1}$) (Fig. 4b). Owls also ate seabird chicks, very rarely adults (<8% of adults, all sooty terns), and infrequently prey on arthropods, passerines or turtle hatchlings (Fig. 4b). We identified remains of sooty terns, frigatebirds and tropicbirds in the pellets. The diet of owls varied significantly depending on the presence of sooty terns on the island. In the absence of terns, the diet of barn owls was largely composed of rats. During the breeding season of sooty terns, and particularly after hatching (August to October), terns became the preferred prey of owls (0.62 ± 0.89 tern pellet $^{-1}$).

4. Discussion

4.1. Trophic position of black rats and direct impact on seabirds

Black rats on Juan de Nova and Europa have a broad opportunistic and omnivorous diet. They feed on plants, invertebrates, passerines and seabirds. The diet of rats showed some variation depending on the habitat and season. These changes have been typically attributed to changes in the availability of food (Caut et al., 2008), or an additional need for protein intake for juveniles (Cole et al., 2000) or breeding females (Clark, 1981). Here it is involving primarily a response to changes in prey availability, particularly the massive influx of sooty terns during summer on Juan

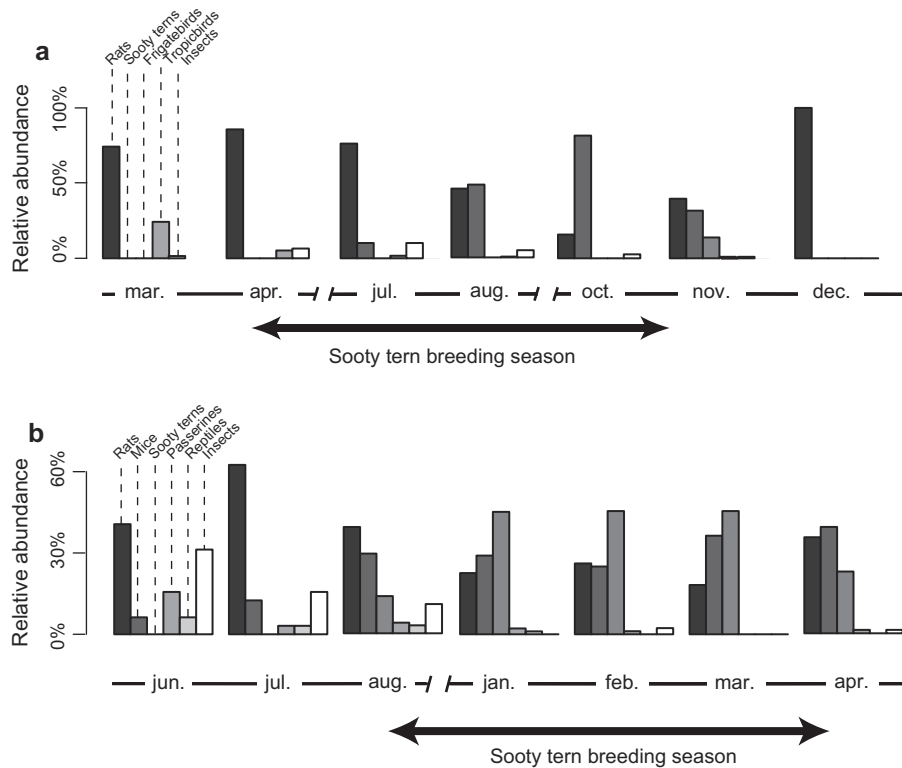


Fig. 4. Monthly relative abundances of prey found in (a) barn owl pellets from Europa, and (b) cat scats from Juan de Nova. The period of presence of sooty terns on the island is added for information.

de Nova and winter on Europa. On Juan de Nova and Europa, results suggest that rats present in or near the colony of sooty terns are significantly supplementing their diet with sooty terns chicks and possibly eggs. The analysis of stomach contents did not allow identifying the consumption of eggs, either because eggs are quickly digested or their size limits predation (Zarzoso-Lacoste et al., 2011). The direct impact of rats on sooty terns seems relatively low compared to the population sizes of the colonies (Table 1). Indeed, given their mean density on both islands (less than 10 rats ha^{-1} , see Russell et al., 2011a) we estimate that rats can consume 10,000–15,000 sooty tern chicks per island and per year (i.e. less than a 2% decrease in breeding success). It probably explains the persistence of this species on both islands in spite of the presence of rats for at least 150 years.

On Europa, monitoring of breeding success and video surveillance provided evidence of a severe direct impact of rats on red-tailed tropicbirds. In this context, i.e. a significant difference between predator and prey population sizes (2000 pairs of red-tailed tropicbirds vs. more than 100,000 rats), stomach content analysis cannot be considered as a suitable method. Video surveillance showed that rats often visited nests of red-tailed tropicbirds, more than reported elsewhere (Gula et al., 2010). These visits occurred especially when the chicks were left alone by their parents. Monitoring of nests every 3 days indicated that the peak failure of breeding birds occurs within 15 days after hatching, when the chicks are still small enough to be preyed upon by rats (Ringler, unpublished data). In this study, the experimental reduction of rat density on the islet caused a clear improvement of red-tailed tropicbirds breeding success. Le Corre (1998) also showed that local eradication of rats on the same islet increased breeding success to 79% (i.e. 15 times higher than on the main island). These findings provide strong evidence that rats contribute to the substantial decline in the red-tailed tropicbirds population (40% decrease of the population in less than 20 years, Le Corre, unpublished data).

The direct effect of rats on other species of seabirds on Europa is also apparently high. We found abnormally low breeding success rates (between 5% and 25%) for other species of seabirds regardless of the type of nesting. In particular, it is very likely that white-tailed tropicbirds (*P. lepturus* endemic subspecies, see Le Corre and Jouventin, 1997) are as impacted by rats as red-tailed tropicbirds since the two species have similar ecological traits. Given the small size of the declining population of white-tailed tropicbirds (~1000 pairs), the risk of extinction of this endemic subspecies is currently very high. Risk of local extinction is also very high for tropical shearwaters (*Puffinus lherminieri*) that were still breeding in very low numbers.

4.2. Interactions with apex predators: mesopredator or hyperpredation prey?

Our results suggest that rats play both the role of seabird predators and prey for apex predators. This will have consequences for native prey and conservation strategies to adopt, depending on the level of hyperpredation or potential for mesopredator release effect to arise in the case of eradication of apex predators.

For long-lived species such as seabirds, population growth is much more sensitive to changes in adult survival than to changes in breeding success (Dumont et al., 2010; Russell et al., 2009). Should cats be eradicated on Juan de Nova, it is unlikely that a decrease in seabird breeding success caused by rat predation on chicks would exceed the benefits accrued due to a significant increase in adult survival (Bonnaud et al., 2010). On Ascension Island (South Atlantic), the survival of adult sooty terns increased due to the eradication of cats, and although direct impact of rats on tern chicks slightly increased, the population of sooty terns maintained a positive growth rate (Hughes et al., 2008). Although mesopredator release effect is in theory possible on Europa, the density of barn owls, the apex predator, is so low that their

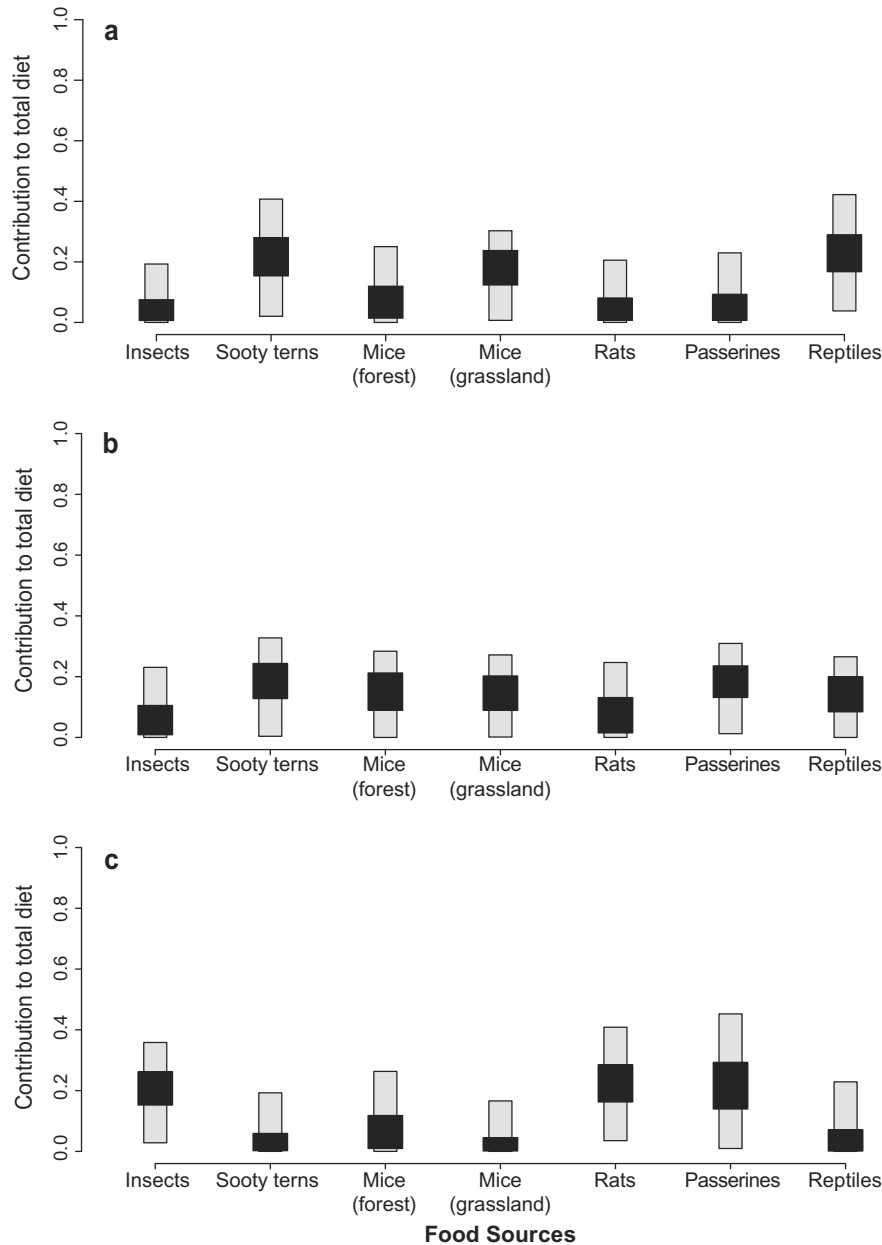


Fig. 5. Contributions of each food source in the diet of cats from Juan de Nova ($n = 16$) obtained from SIAR mixing models. The data are separated into three isotopically homogeneous groups with (a) all female cats ($n = 5$), and two distinct groups of males (with (b), $n = 4$ and (c), $n = 7$). The grey boxes represent intervals containing 95% of the probability density of the contribution of each source to the diet and the black boxes represent the interval containing 50% of the probability density.

removal could not lead to a release of rats. Besides, population dynamics of rats on Europa and Juan de Nova appear to be primarily driven by bottom-up structuring forces of resource availability and habitat complexity and not by apex predators (Russell et al., 2011a) (Fig. 6). In particular, rainfall controls seasonal variation in densities (i.e. cycles) including a severe decline during the dry season (Fig. 6). Eradication of apex predators on both islands is therefore unlikely to cause numerical release of rats. However, cats' predation pressure plays an additional top-down role regulating the morphology (decrease in body size) and movements of rats (decrease in home range size) on Juan de Nova (Ringler et al., 2014; Russell et al., 2011a) (Fig. 6). Thus changes in individual traits (i.e. an increase of home range size and body size) more than an increase in density are therefore likely to be observed after any removal of cats in Juan de Nova.

In the absence of alternative prey populations apex predators may collapse when their main prey are extinguished. The barn owls and cats clearly showed changes in diet in the absence of seabirds. Although we did not study demographic responses of apex predators to diet switching, it is very likely that rats maintain populations of apex predators on both islands. The likelihood that apex predators are supported by rodents all year round is particularly strong on tropical islands as rat densities are generally very high (Russell et al., 2011a), which poses a greater threat on tropical islands to native biodiversity (either migratory or resident) than non-tropical islands. On Juan de Nova, the impact of cats on sooty terns surpasses the direct effect of rats because, unlike rats, cats prey on both chicks and adults (Le Corre, 2008). Cats could cause each year the loss of the equivalent of 4% of the size of the sooty terns colony. The impact of cats is even higher since the majority

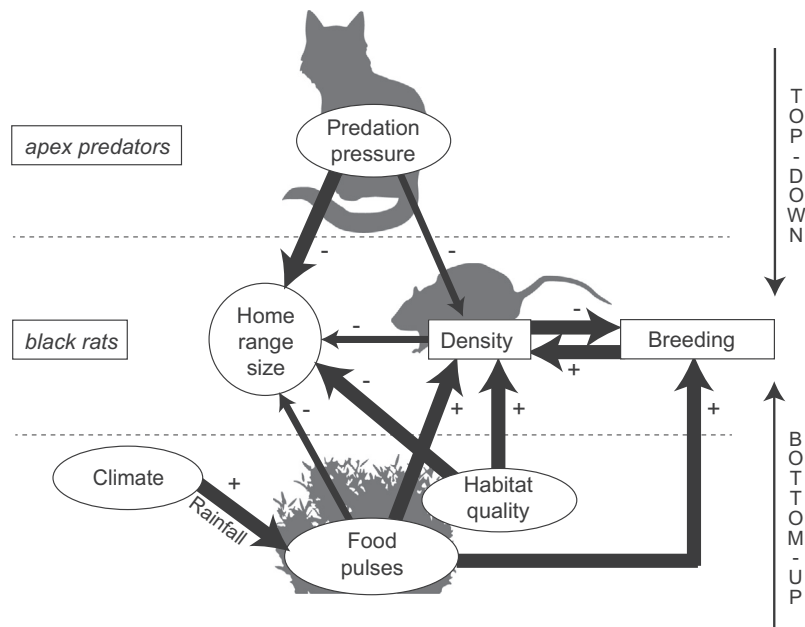


Fig. 6. Schematic representation of the main drivers of population (density, breeding) and behavioural traits (home range size) of black rats on Europa and Juan de Nova. Derived from Russell et al. (2011a) and Ringler et al. (2014). Width of arrows indicates strength of regulation.

of the birds killed are not consumed, due to the specific behaviour common to mammalian carnivores of ‘surplus killing’ (Kruuk, 1972). In this study we estimated that more than half of the terns were not killed consumed. Hence, the hyperpredation process involving cats, rats and seabirds, is likely to be a strong force on Juan de Nova. Recent counts suggest that the sooty terns population is undergoing a severe decline (from 2,000,000 pairs in 2003 to 450,000 pairs in 2013, see Orłowski and Amouroux, 2014). Native migratory species may be particularly susceptible to hyperpredation (Bate and Hilker, 2012). The introduction of cats to Raoul Island (New Zealand) in the early 19th century, and rats a few years later, led to the disappearance of a very large colony of sooty terns. While there were still 80,000 pairs in 1967, the species was declared locally extinct in 1997 (Veitch et al., 2004). The case of Raoul Island probably foretells the fate of the population of sooty terns on Juan de Nova. Our results also support the hypothesis that the hyperpredation process occurring on Juan de Nova may be buffered by intraspecific competition. Indeed stable isotope models show that only some cats were specialised in seabird predation. This is probably a response to territoriality among individuals. Female cats and some males occupy peripheral areas of the island near colonies of sooty terns (which is confirmed by the capture locations of individuals) probably leaving territories around the military camp (waste, high rodent densities) to dominant males. Strong territoriality could delay the risk of local extinction through hyperpredation since in this configuration only some cats cause an impact on native prey (Bate and Hilker, 2012).

On Europa, rats also subsidize owls, and without invasive rats they could probably not persist on the island. However, alternative factors seem to limit the density of owls to a very small number (less than 15 pairs). The density of owls is so low that they do not have a severe (indirect) effect on seabirds, in contrast to the Farallon Islands where mice subsidize burrowing owls preying upon ashy storm-petrels (Russell, 2011). Because rats and owls prey on the same seabird life-stages (eggs and chicks), the direct effect of abundant rats (up to 80 rats ha⁻¹) greatly outweighs any negative effect of owl predation. Thus, although an indirect hyperpredation process is possible, it does not occur here because

the direct impacts of each species on seabirds are stronger than any indirect effect.

4.3. Eradication opportunities

Responses to management interventions (i.e. species specific eradications) on Europa and Juan de Nova can be predicted based on functional relationships between rats, and other predators and prey in the system. It is typically recommended that all invasive predators be eradicated simultaneously, to avoid potential unwanted indirect effects subsequent to the eradication of a single predator (Dowding et al., 2009; Zavaleta et al., 2001). For technical or financial issues, simultaneous eradications may not be possible, despite conservation urgency. Targeting a single species offers several scenarios, some of which could result in adverse effects on native species.

4.3.1. Juan de Nova

Knowing the occurrence of rats in the diet of cats, eradication of rats by poisoning may greatly affect the population dynamics of cats through secondary poisoning (which could be a deliberate management decision, see Griffiths, 2011). However, keeping cats on islands, even in reduced numbers, remains a significant threat to the persistence of native prey (Vazquez-Dominguez et al., 2004). Because all cats on Juan de Nova are feral there are no calls for their conservation, in contrast to other inhabited islands where there are typically calls for domestic cats to remain following rat eradication (Nogales et al., 2004). Eradication of rats only on Juan de Nova is then not recommended. As rats compete with mice on Juan de Nova (Russell et al., 2011a), the mouse population might also increase rapidly after the elimination of rats (Caut et al., 2007). However, mice impacts on seabirds remain negligible compared to those of rats. Removal of brown rats (*R. norvegicus*) on Tromelin over 8 years ago has been beneficial to seabird populations and native vegetation despite higher densities of mice after rat eradication (Le Corre et al., 2015). While eradicating both rodents and cats is a desirable management goal, our data suggest that hyperpredation threatens remaining seabirds and

mesopredator release effect is unlikely. Thus until such time as simultaneous rat and mouse eradication is possible, cat eradication would have clear conservation value for seabirds.

4.3.2. Europa

Under rat eradication the risk of non-target impacts on barn owls is an issue. If further research demonstrates that the owl population is native, this should be to maintained by preventing secondary poisoning (e.g. captive holdings during the operation, see Merton et al., 2002; Howald et al., 2010). Alternatively, if owls have been introduced, their elimination can be seen as a conservation objective. Regardless the status of owls, rat eradication is the highest conservation priority for the island since their direct impact, especially on small seabird populations, may contribute in the near future to local extinctions of multiple seabird species.

Indirect interactions have become a major concern in the field of conservation biology. The case studies on tropical islands presented here show that the relationship between predators and prey are rarely simple. A minimal understanding of how species interact in an ecosystem before human intervention can prevent future 'surprise effects'. The likelihood of an indirect effect following a species introduction or eradication will depend on the nature of trophic relationships, which in turn depend on the identity of each species, and the composition of the community of the island.

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DR, JR and MLC designed research. DR and JR performed research and analysed data. DR, JR and MLC wrote the paper.

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