INTRODUCED MAMMAL IMPACTS ON SEABIRDS IN THE ÎLES ÉPARSES, WESTERN INDIAN OCEAN

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SUMMARY

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Invasive mammals have devastated endemic island communities throughout the world, and seabirds have proven particularly vulnerable, with many species extinctions. Introduced predators have had the greatest effect through direct predation, but this effect can now be mitigated by modern eradication techniques. However, the removal of a species from a community can generate different indirect effects depending on the trophic levels that are interacting. Conservation managers eradicating introduced mammals must consider ecosystem-wide effects and view island management within a "whole ecosystem" context. It is important to consider unexpected indirect effects from eradications. However, eradication of introduced mammals should not be delayed, especially when direct effects such as predation are a known cause of terminal decline for a threatened species. We use the French Îles Éparses of the Western Indian Ocean, with their various combinations of six introduced mammals, to demonstrate the direct and indirect effects that introduced mammals may have, and how those effects might affect the regionally important seabirds with breeding colonies on the islands. We conclude by making recommendations for the future management of the islands.

RÉSUMÉ

Les mammifères introduits ont détruit les communautés endémique des iles partout dans le monde, et les oiseaux marins ont été très vulnérable, avec plus d'extinctions d'espèces. Les prédateurs introduits ont eu un plus grand impacts par le prédation direct, mais ces causes peuvent être apaise maintenant par les techniques moderne d'éradication. Cependant, la suppression d'une espèce dans une communauté peut créer des effets différents et indirect dépendre de quels niveaux trophiques sont en interaction. Les directeurs de conservation qui font l'éradications des mammifères introduits doivent considérer les effets dans l'écosystème total et prendre des décisions de gestion des îles dans un contexte écologique global. Il ne faut pas perdre de vue les effets inattendus et indirects de ces éradications. Cependant, les mesures de lutte contre les prédateurs introduits sont a mettre en place sans délai, en particulier quand les effets directs tels que prédation sont une cause connu du déclin définitif pour une espèce menacé. Nous utilisons les Îles Éparses françaises de la zone Océan Indien Occidental, avec leur nombre de combinaisons des six mammifères introduits, démontrer les effets directs et indirects que les mammifères introduits peuvent avoir, et comment ces effets affectent les colonies des oiseaux marins importante dans le région et qui se reproduisent sur ces îles. Nous conclurons en faisant des recommandations pour la direction futur des îles.

Key words: Community, conservation, ecosystem, hyperpredation, indirect, invasive, mesopredator release

INTRODUCTION

Introduced species remain the greatest threat to biodiversity on islands (Vitousek *et al.* 1997), and introduced mammals have had a particularly disproportionate impact on insular species (Ebenhard 1988, Clout & Russell 2008). The impacts of introduced mammals can be both direct and indirect. Direct impacts are readily demonstrated through predation and herbivory, but consistent indirect impacts have proven more difficult to demonstrate across systems and often involve unpredictable interactions.

Eradication methods have provided a powerful conservation tool to restore island ecosystems by permanently removing introduced mammals, now possible on islands greater than 10 000 ha (Clout & Russell 2006). This permanent removal immediately mitigates the direct impacts of introduced mammals. However, invasive mammals have usually been present on islands for a substantial period of time and are well embedded within ecosystem functioning (Ebenhard 1988). Their permanent removal can generate unexpected outcomes by indirect pathways, which may hamper conservation and restoration efforts (Courchamp *et al.* 2003). However, these removals do provide opportunities for testing the strength and relationships of interactions within a community ecology framework (Blackburn 2008, Towns 2009).

Seabirds spend parts of their lives in marine and terrestrial environments alike, utilising the marine environment for food resources and the terrestrial environment to breed. They are well adapted to long periods of flight in the marine environment, but are less well adapted to movement on land, particularly during breeding. This leaves them vulnerable to disturbances in the terrestrial environment, as a result of poor escape mechanisms

and nest-guarding behaviour. Thus, introduced predators generally reduce reproductive success and adult survival in seabirds (Moors & Atkinson 1984). Adult and subadult survival can also be influenced by the marine environment, particularly through fisheries by-catch and prey depletion (Tasker *et al.* 2000). Islands in particular are the terrestrial environment utilised by most of the world's seabirds (Schreiber & Burger 2001), and thus their protection forms a major part of seabird conservation (Wilcox & Donlan 2007)

In this paper, we review the distribution and effects of introduced mammals on islands in the Western Indian Ocean French territories, collectively known as the Îles Éparses ("scattered islands"). We consider the relationships between introduced mammals and seabirds, and we describe both the direct and indirect impacts that introduced mammals could have within these islands. We conclude by making recommendations for future conservation effort on these islands, accounting for the complex relationships between multiple introduced mammals.

ÎLES ÉPARSES

The Îles Éparses are a collection of French overseas island territories in the Western Indian Ocean (Fig. 1) managed by the Terres Australes et Antarctiques Françaises (TAAF) since February 2007 and composed of Île Europa, Île Juan de Nova and the Îles Glorieuses (Grand Glorieuse, Roches Vertes and Ile du Lys) in the Mozambique Channel, and Île Tromelin north of Réunion. The barely emerged coral reef Bassas da India is also included within the Îles Éparses. The islands are managed from Réunion, which is part of France and hence the European Union. All the islands except Juan de Nova were classified as nature reserves in 1975. Weather stations have been present on all four islands since the middle of the 20th century, providing important data on the trajectories of tropical cyclones. Since 1973, French military have been regularly stationed on Europa, Juan de Nova and Grand Glorieuse.

Six of the most widespread and devastating invasive mammals have been introduced to the Îles Éparses (Table 1): goats *Capra hircus,* cats *Felis catus,* rabbits *Oryctolagus cuniculus,* Brown Rats *Rattus norvegicus,* Black Rats *R. rattus* (Fig. 2) and mice *Mus musculus.* Previous records of Brown Rats on the Iles Glorieuses have been a misinterpretation of early colloquial descriptions of "brown" rats for the brown-colour morph of Black Rats present. In addition, the Etruscan Shrew *Suncus etruscus* has been introduced to Grand Glorieuse [although its exact taxonomy and origin remain unresolved (Probst & Tézier 2000)], and donkeys *Equus asinus,* briefly to Europa.

The Îles Éparses are breeding grounds for a large number of seabird species and include regionally important breeding sites for Great *Fregata minor* and Lesser Frigatebirds *F. ariel,* Red- *Phaethon rubricauda* and White-tailed Tropicbirds *P. lepturus,* Red-footed *Sula sula* and Masked Boobies *S. dactylatra* and Sooty Terns *Sterna fuscata* (Table 2).

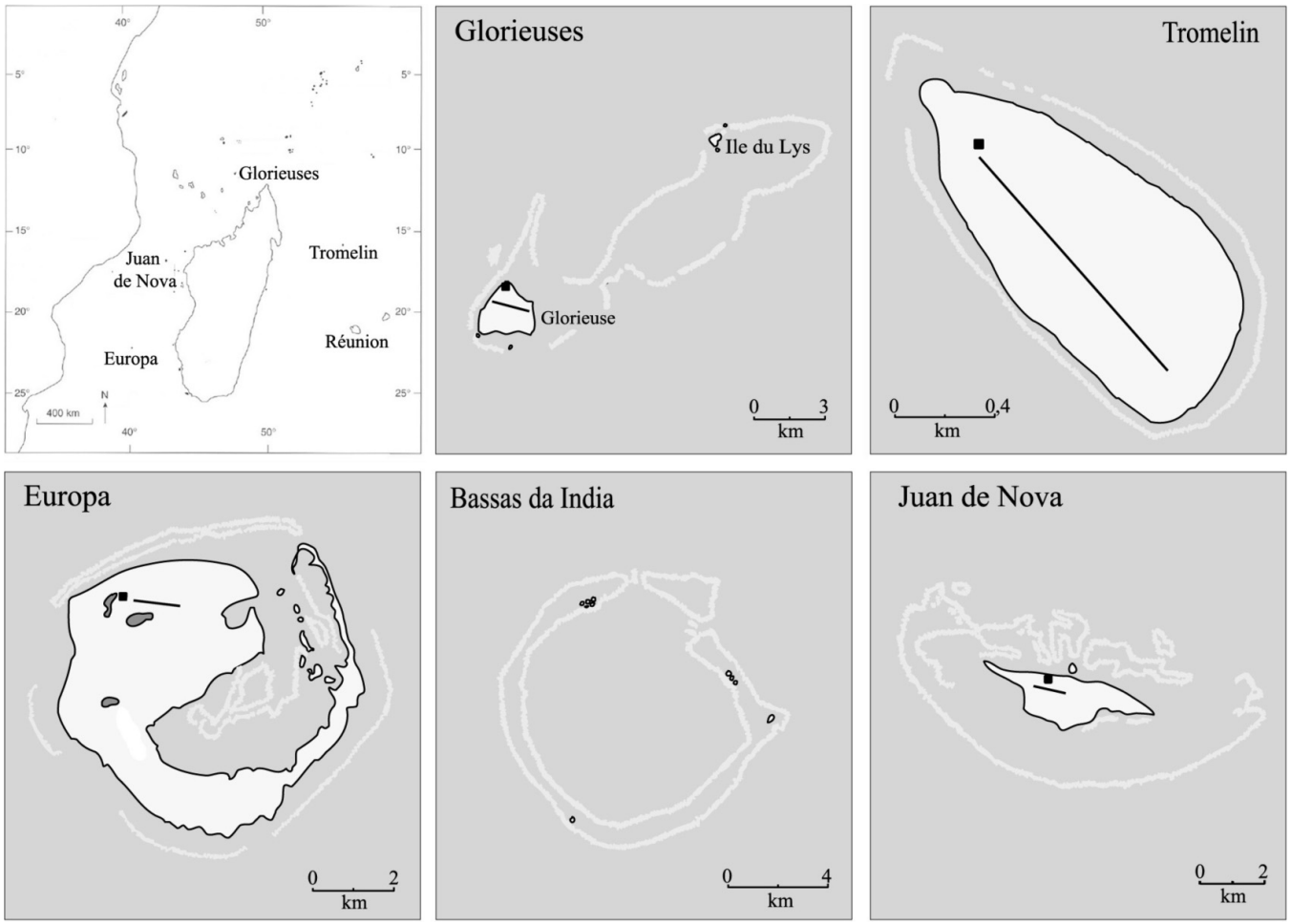

Fig. 1. The Îles Éparses, Western Indian Ocean. (Source: Gargominy 2003)

In addition to mammal introduction, various other anthropogenic disturbances have occurred on the islands. On Europa, settlement was attempted in 1860 and again in 1910, including a 96 ha sisal plantation at the northern tip, which is now spreading naturally. On Juan de Nova, guano mining occurred intermittently from 1897–1967. On Grand Glorieuse, settlers cleared most of the native vegetation and cultivated coconut and maize from 1880 to 1958, resulting in the extirpation of all breeding seabird species. Ile du Lys was also formerly mined for guano. Tromelin has remained relatively undisturbed, although in 1761, 90 Madagascan slaves

TABLE 1
Introduction date and status of mammals introduced to the Îles Éparses

Island	Size	Species	Introduction	Current status
Europa	2223 ha[a]	Donkeys	1948	Naturally died out <1974
		Goats	1860	~200–300
		Cats	1948	Removed 1948
		Rabbits	1860	Naturally died out 1959–1964
		Black Rats	<1860	Abundant
Juan de Nova	561 ha	Cats	<1980s	~50–60 (eradication commenced 2006)
		Black Rats	<1980s	Abundant
		Mice	<1980s	Abundant
Grand Glorieuse	462 ha	Cats	<1893	~30
		Black Rats	<1882	Abundant
		Shrews	<2000	Rare
Île du Lys	12 ha	Goats	1906–1921	Naturally died out <1971
		Black Rats	<1882	Eradicated 2003
Tromelin	97 ha	Rabbits	1954–1968	Naturally died out 1986
		Brown Rats	1857–1953	Eradicated 2005
		Mice	<1856 (1761?)	Abundant

[a] Excluding 836 ha mangrove.

TABLE 2
Seabird population sizes (number of breeding pairs) in the Îles Éparses[a]

Species	Scientific name	Island[b]					
		Europa	Juan de Nova	Grand Glorieuse	Roches Vertes	Île du Lys	Tromelin
Audubon's Shearwater	*Puffinus lherminieri*	50	—	—	—	—	—
White-tailed Tropicbird	*Phaethon rubricauda*	1 000	—	e	—	—	—
Red-tailed Tropicbird	*Phaethon lepturus*	3 500	—	e	—	—	—
Great Frigatebird	*Fregata minor*	1 100	—	e	—	e	e
Lesser Frigatebird	*Fregata ariel*	1 200	—	—	—	—	e
Red-footed Booby	*Sula sula*	3 000	e	e	—	—	500
Masked Booby	*Sula dactylatra*	—	—	—	—	e	300
Brown Booby	*Sula leucogaster*	—	—	—	e	—	—
Abbott's Booby	*Sula abbotti*	—	—	e	—	—	—
Sooty Tern	*Sterna fuscata*	760 000	2 000 000	—	??	270 000	e
Crested Tern	*Sterna bergii*	—	250	e	—	—	—
Caspian Tern	*Hydroprogne caspia*	10	—	—	—	—	—
Brown Noddy	*Anous stolidus*	—	—	—	e	300	e

[a] From Le Corre 1996 and Le Corre & Jaquemet 2005. Good historical records exist for all islands except Juan de Nova.
[b] An "e" indicates recorded extirpation since human discovery.

were abandoned on the island for 15 years, after which only seven female survivors were rescued.

Direct impacts

The direct effects of introduced mammals on island ecosystems have been well documented both at the species and the community scale (e.g. Blackburn *et al.* 2004, Jones *et al.* 2008). Predation by introduced predators is the only direct impact of introduced mammals on seabirds. Seabirds have evolved responses to avian predation by sight, but they have no strategy for coping with mammalian predation by scent, leaving them particularly vulnerable to direct predation by many introduced mammals [e.g. dogs, cats, rats, mongooses (Le Corre 2008)]. Cats are able to prey upon all but the largest seabirds at most life stages (Nogales *et al.* 2004). Introduced rats have had devastating direct impacts on vulnerable seabirds at all life stages (Jones *et al.* 2008) and on many other species and taxa (Towns *et al.* 2006) through omnivorous predation. Mice have received less attention, but can prey upon a wide range of insects and seeds (Angel *et al.* 2009) and recently have been observed preying upon large seabirds, though in such a manner that it is almost akin to "parasitizing" (Wanless *et al.* 2007).

In the Îles Éparses, direct impacts of cats on seabirds have been found for Sooty Terns on Juan de Nova (Peck *et al.* 2008). A number of other ground-nesting seabirds, such as tropicbirds and shearwaters, are conspicuously absent from the island—a likely consequence of historical cat predation and forest clearance. Direct impacts of Black Rats have been found for Red-tailed Tropicbirds on Europa (Le Corre 1998) through a local eradication experiment in March 1995 using 10 kg/ha of bromadiolone on the small northern lagoon islet (2.65 ha). Following rat removal, reproductive success of Red-tailed Tropicbirds increased from 31% (n = 39) to 79% (n = 43) (Appendix 2 in Le Corre 1998). Before they were eradicated in May 2003, Black Rats were observed killing nesting Brown (Common) Noddies *Anous stolidus* at night on Île du Lys (van der Elst & Prys-Jones 1987). The impact of Brown Rats on Tromelin was never quantified before their eradication in December 2005 by means of bromadiolone. No direct impacts of mice on seabirds have been found on Juan de Nova or Tromelin (before or after rat eradication). Since the clearing of the native vegetation for plantation and the introduction of multiple mammal species, no seabirds currently breed on Grand Glorieuse.

Fig. 2. Introduced Black Rat *Rattus rattus* on Europa Island.

TABLE 3
Indirect impacts of introduced mammalian predators on seabird islands

Indirect impact	Trophic levels	Introduced mammals
Trophic cascade	superpredator–mesopredator–prey	cats–rats–birds, rats–mice–birds
Apparent competition	predator–(prey–prey)	cats–(rats–mice), cats–(mice–birds)
Interspecific competition	(predator–predator)–prey	(cats–rats)–birds

Goats do not directly affect seabirds, but on Europa, they browse seedlings and branches of *Euphorbia* trees, the main species of the native dry forest used as breeding habitat by all tree-nesting seabirds (frigatebirds and boobies). Thus goats probably reduce or slow the natural regeneration of the forest.

Indirect impacts

Indirect impacts are most readily considered as those changes that occur between species and that are not a result of direct physical interactions (Wootton 1994). The indirect pathway can involve either biotic (e.g. changes in other fauna or flora) or abiotic (e.g. changes in the physical or chemical environment) factors (Strauss 1991). For simple systems, indirect impacts can be broadly classified into three categories depending on the nature of the interaction, following Wootton (1994, Table 3). Indirect impacts on species can take the form of changes in abundance, behaviour, morphology or other characteristics (Strauss 1991).

Courchamp and colleagues theoretically developed many of the indirect interactions with conservation impacts that may result from the presence of multiple introduced species on islands. These include mesopredator release as a trophic cascade in which asymmetrical intraguild predation occurs (Courchamp *et al.* 1999a), hyperpredation as apparent competition (Courchamp *et al.* 1999b, 2000) and competitor release as interspecific competition (Caut *et al.* 2007). Given the global distribution of multiple introduced mammal species on islands, it is likely that some of these indirect impacts are manifest; however, their strength and ubiquity are more difficult to demonstrate, although researchers often hasten to caution about indirect secondary effects as a result of single-species removals (e.g. Zavaleta *et al.* 2001).

Where a super (top) and meso (middle) predator exist, the prey of the mesopredator may be affected by removal of the top predator (Fig. 3) after the release of the mesopredator from predation, a process known as "mesopredator release" (Soulé *et al.* 1988). Furthermore,

Fig. 3. Mesopredator release effect—for example, on Juan de Nova. Arrows indicate direction and nature of interactions.

when the super- and mesopredator both share the same prey (asymmetrical intraguild predation), removal of one predator will change the direct predation dynamics of the entire system, through a change in abundance or behaviour of the remaining predator (Courchamp *et al.* 1999a). Asymmetrical intraguild predation is, in fact, the simultaneous expression of apparent and interspecific competition, in which the mesopredator is both predator and prey (Polis *et al.* 1989). Generally, for mesopredator release to occur, strong top-down (predation) control within a system is required (Russell *et al.* 2009). Mesopredator release may possibly occur on Juan de Nova following the eradication of cats currently underway; however, evidence of mesopredator release on islands is equivocal (e.g. Rodríguez *et al.* 2006, Rayner *et al.* 2007, discussion in Le Corre 2008).

Alternatively, if a predator shares two prey species, an increase in one prey may increase the predator, causing a decline in the alternative prey (Fig. 4). This effect may mistakenly be attributed to direct competition if only the two prey species are monitored and is hence termed "apparent competition" (Holt & Lawton 1994). This dynamic requires a strongly bottom-up (resource)–controlled system, in which an increase in prey causes an increase in predators. On islands where one prey is a native and the other introduced, the introduced prey can subsidise the predator during periods of low resources (e.g. winter), increasing the overall impact on the native prey in a process known as "hyperpredation" (Courchamp *et al.* 1999b, 2000). In contrast to mesopredator release, hyperpredation has been demonstrated on many islands, such as Whale Island in New Zealand (Imber *et al.* 2000), Macquarie Island in Australia (Taylor 1979) and Kerguelen Island in the sub-Antarctic (Gaucel & Pontier 2005). Hyperpredation may possibly occur on Europa, where the diet of predatory Barn Owls *Tyto alba* consists almost exclusively of introduced rats, allowing the persistence of a small population of owls that also prey upon Sooty Terns during their breeding season, as similarly occurs in the nearby Seychelles (Ebenhard 1988, p. 36). The status of owls on Europa is uncertain with respect to time or method of introduction.

Introduced goats do not directly affect seabirds, but they play a major role regulating plant population dynamics through intense herbivory. Conditions are thus created for interspecific competition between goats and introduced rodents, the latter of which utilise dense vegetation as habitat (Fig. 5). Goats can now be readily eradicated from islands (Campbell & Donlan 2005), and a release of vegetation usually follows (Bullock *et al.* 2002, Kessler 2002). Introduced herbivore eradication could thus indirectly benefit rats through a process we term "habitat release effect." The impact of herbivore eradication is further complicated if invasive weeds are released from browsing (Bullock *et al.* 2002, Kessler 2002), which may directly alter seabird breeding habitat in either positive or negative ways (Vidal *et al.* 2000). In a similar situation on sub-Antarctic Campbell Island in New Zealand, the removal of cattle and sheep increased native vegetation cover (Meurk 1982). Not long after cats naturally died out, quite possibly as a result of the negative effect of increased damp vegetation on their survival and hunting of introduced Brown Rats.

Where two rodent species coexist, indirect impacts may occur through shared bottom-up (resource) or top-down (predator) controls (Fig. 6), as interspecific and apparent competition respectively. Removal of only one rodent species (e.g. Brown Rats on Tromelin) may have either positive or negative effects on the other, depending on the form of control. The theoretical dynamics of a bottom-up moderated system have been studied by Caut *et al.* (2007). This dynamic assumes that, via a shared resource, interspecific competition is a strong regulator of rodent population size (i.e. negative covariance of the two population sizes). Instead, independent resources may independently drive population size of the two rodent species and a change in resource conditions may be reflected by increases in both populations (i.e. positive covariance of the two population sizes) leading to increased direct impacts upon prey species (Houlahan *et al.* 2007). Nonetheless the eradication of rats, but not mice, from many islands around the world has been followed by an increase in at least mouse conspicuousness if not

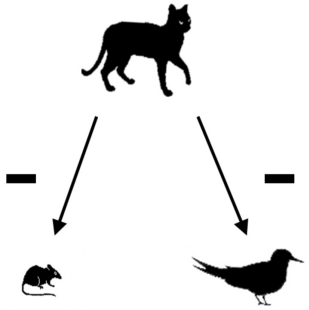

Fig. 4. Hyperpredation—for example, on Juan de Nova. Arrows indicate direction and nature of interactions.

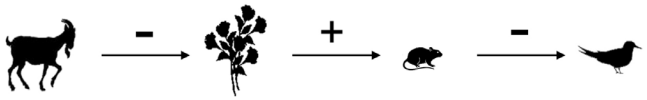

Fig. 5. Habitat release effect—for example, on Europa. Arrows indicate direction and nature of interactions.

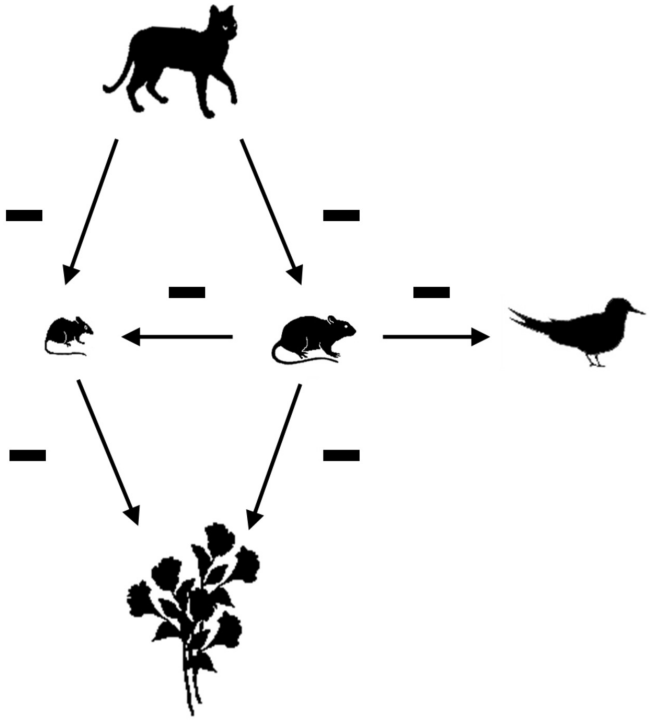

Fig. 6. Interference (direct) and exploitative (indirect) competition for a shared resource and apparent competition (indirect) by a shared predator for two rodent species. Arrows indicate direction and nature of interactions.

density (Caut *et al.* 2007). On Tromelin, in the absence of predators, mice appear to have remained at similar abundance despite Brown Rat eradication, although the mice may still be recovering from the effects of an attempted eradication campaign contemporaneously with Brown Rats.

Alternatively, when an introduced predator (e.g. the cat) is present, the system dynamic is characterised by hyperpredation. Apparent competition occurs, and the behavioural and dietary differences between the rodents may lead to differential impacts on different seabird species (Jones *et al.* 2008).

Confirming which indirect impacts may play important roles in community regulation can be difficult and requires data on trophic niches and abundance (Caut *et al.* 2009) and an understanding of community regulation. On Juan de Nova, the direct diet of cats indicates the species that play a role in community dynamics, and hence might be involved in indirect relationships after the cat eradication currently underway (2006 onward). However, it must be remembered that diet primarily reflects prey density and not the strength of indirect relationships. Cat diet is dominated by Sooty Terns, followed by rats and mice in order of decreasing importance (Peck *et al.* 2008). The Sooty Terns are seasonal breeders most affected by direct cat predation, and rodents would provide an off-season resource for cats. Stable isotope work suggests that rats do not prey upon mice; instead, the isotopic signature reveals that rats may be subsidised by vegetation, while mice depend more heavily on insects. Furthermore, rodent trapping on Juan de Nova reveals that mice are relatively more abundant in grasslands, and Black Rats are more abundant in forest, suggesting some level of resource and habitat partitioning. Therefore, depending on the impact of rodents on seabirds, the system could resemble either mesopredation when rodents also prey upon seabirds or hyperpredation by cats when rodents merely supplement the cat diet with a comparatively negligible effect on seabirds.

The presence of multiple introduced mammals on an island can lead to negative interactions between the species such as we have described here. Indirect impacts on species of conservation concern arise from the removal of one introduced species. Indirect impacts can also arise from positive interactions between introduced species resulting from the addition (i.e. invasion) of a new species. A positive feedback process that has been termed "invasional meltdown" (Simberloff & Von Holle 1999, Simberloff 2006) might be initiated. Such a process has been documented on Christmas Island, where Crazy Ants *Anoplolepis gracilipes* kill Red Land Crabs *Gecarcoidea natalis,* releasing seedling recruitment, which enhances scale insects that Crazy Ants can harvest to form supercolonies (O'Dowd *et al.* 2003).

Conservation priorities

The importance of indirect effects and their consideration in conservation management, especially species deletions through eradication, will ultimately depend on their strength relative to direct impacts (i.e. predation). Direct effects of introduced predators tend to be stronger and more regulatory than are indirect effects (Schoener & Spiller 1999). The direct impacts on seabirds of introduced predators, including cats, rats and mice, are readily observed and immediate, and have played a significant role in the extinction of seabirds and other species (Courchamp *et al.* 2003, Towns *et al.* 2006). Along with habitat destruction, this role was clear on Juan de Nova and Grand Glorieuse. The most powerful conservation tool to prevent these direct predatory impacts is species eradication (Howald *et al.* 2007). Unless there is compelling evidence of strong indirect interactions between species, which may generate surprise effects (Caut *et al.* 2009), then, when a species of conservation concern (i.e. Threatened) is in decline, the eradication of the introduced species producing the direct impact should be considered a priority.

Within the framework discussed earlier, we suggest that hyperpredation and competitor release, both bottom-up-driven processes, play an important role in indirect island community dynamics. Strong herbivory will also head to a habitat release effect. Although mesopredator release has been theoretically hypothesised, we suggest that it might only affect special community cases, in which the indirect impact of an increase in rats far outweighs the impact of cats and suppressed rats together. Whether such a case occurs will also depend on the differential predation of seabird age classes by cats and rats, and on the level of top-down regulation. Given the strength of the direct predatory impact of cats on most insular species, particularly seabirds, we suggest that mesopredator release is not a widespread phenomenon and should certainly not be used as evidence to postpone cat eradication campaigns. Perhaps only for small seabird species surviving in refugia inaccessible to cats, but where the more agile rat can reach (e.g. cliff nesters), might mesopredator release remain a valid concern.

The eradication of all six introduced mammal species present in the Îles Éparses is now possible on reasonably large islands [except for mice (MacKay *et al.* 2007)], and given the direct devastation by these species on other islands throughout the world, eradication should be a priority. Goats could be eradicated from Europa, allowing the important regeneration of endemic forest; however, goat eradication may cause a habitat release and an increase in rats as the forest regenerates. However, Black Rat eradication from Europa could be undertaken before the indirect effect of increased vegetation occurs. Additionally, invasive plants may be released from goat browsing and become more widespread. Cat eradication on Juan de Nova is a priority and has been underway since 2006 (see Peck *et al.* 2008), but mesopredator release is unlikely, given that remote islands and rodent populations are generally driven by resource-limited bottom-up dynamics (Krebs 1999, Sanchez-Pinero & Polis 2000). Although islands can host large populations of seabirds, the resources subsidising these populations are derived from the ocean and are thus not directly available to introduced mammals. The eradication of Black Rats and mice is feasible on Juan de Nova within the near future. Most successful eradication campaigns of introduced rodents on tropical islands have been ground-based operations (see Thomas & Taylor 2002 for a history of such campaigns in New Zealand). Although there are no seabird populations present on Grand Glorieuse to be affected by introduced mammals, the reptile community is threatened by the presence of cats. Eradication of introduced mammals would be straightforward and would provide an opportunity to study the recolonization (either naturally or intentionally) by seabird species. Black Rats have already been eradicated from smaller Île du Lys. The failed eradication of mice from Tromelin is not a major concern given the paucity of direct impacts of mice on seabirds, but it does provide an opportunity to study the biology of mice on tropical islands.

Although the Îles Éparses are oceanic and isolated in origin, reinvasion is always possible (Clout & Russell 2008), and biosecurity

controls (e.g. Russell *et al.* 2008a, b) will therefore be necessary to maintain pest-free status following eradication. Such controls will be particularly important if any islands become ecotourism sites, substantially increasing traffic to the islands. Island biosecurity monitoring and quarantine controls must be implemented on all of the Îles Éparses for all air and sea traffic.

The eradication of introduced mammals from the Îles Éparses will have widespread benefits not just for seabirds, but for entire communities; however, other introduced species such as ants and weeds must also be considered in wider island-based management plans. The eradications would not only benefit the native biodiversity, but also provide other benefits such as ecotourism and the well-being of humans stationed on the islands.

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REFERENCES

ANGEL, A., WANLESS, R.M. & COOPER, J. 2009. Review of impacts of the introduced house mouse on islands in the Southern Ocean: are mice equivalent to rats? *Biological Invasions* 11: 1743–1754.

BLACKBURN, T.M. 2008. Using aliens to explore how our planet works. *Proceedings of the National Academy of Sciences, USA* 105: 9–10.

BLACKBURN, T.M., CASSEY, P., DUNCAN, R.P., EVANS, K.L. & GASTON, K.J. 2004. Avian extinction and mammalian introductions on oceanic islands. *Science* 305: 1955–1958.

BULLOCK, D.J., NORTH, S.G., DULLOO, M.E. & THORSEN, M. 2002. The impact of rabbit and goat eradication on the ecology of Round Island, Mauritius. In: Veitch, C.R. & Clout, M.N. (Eds). Turning the tide: the eradication of invasive species. Gland, Switzerland and Cambridge, UK: IUCN SSC Invasive Species Specialist Group. pp. 53–63.

CAMPBELL, K. & DONLAN, C.J. 2005. Feral goat eradications on islands. *Conservation Biology* 19: 1362–1374.

CAUT, S., CASANOVAS, J.G., VIRGOS, E., LOZANO, J., WITMER, G.W. & COURCHAMP, F. 2007. Rats dying for mice: modelling the competitor release effect. *Austral Ecology* 32: 858–868.

CAUT, S., ANGULA, E. & COURCHAMP, F. 2009. Avoiding surprise effects on Surprise Island: alien species control in a multitrophic level perspective. *Biological Invasions* 11: 1689-1703.

CLOUT, M.N. & RUSSELL, J.C. 2006. The eradication of mammals from New Zealand islands. In: Koike, F., Clout, M.N., Kawamichi, M., De Poorter, M. & Iwatsuki, K. (Eds). Assessment and control of biological invasion risks. Gland, Switzerland and Cambridge, UK: IUCN. pp. 127–141.

CLOUT, M.N. & RUSSELL, J.C. 2008. The invasion ecology of mammals: a global perspective. *Wildlife Research* 35: 180–184.

COURCHAMP, F., LANGLAIS, M. & SUGIHARA, G. 1999a. Cats protecting birds: modelling the mesopredator release effect. *Journal of Animal Ecology* 68: 282–292.

COURCHAMP, F., LANGLAIS, M. & SUGIHARA, G. 1999b. Control of rabbits to protect island birds from cat predation. *Biological Conservation* 89: 219–225.

COURCHAMP, F., LANGLAIS, M. & SUGIHARA, G. 2000. Rabbits killing birds: modelling the hyperpredation process. *Journal of Animal Ecology* 69: 154–164.

COURCHAMP, F., CHAPUIS, J.L. & PASCAL, M. 2003. Mammal invaders on islands: impact, control and control impact. *Biological Reviews* 78: 347–383.

EBENHARD, T. 1988. Introduced birds and mammals and their ecological effects: Swedish Wildlife Research. Stockholm: Svenska Jaegarefoerbundet. 106 pp.

GARGOMINY, O. (Ed). 2003. Biodiversité et conservation dans les collectivités françaises d'outre-mer. Collection Planète Nature. Paris: Comité français pour l'UICN. 246 pp.

GAUCEL, S. & PONTIER, D. 2005. How predator food preference can change the destiny of native prey in predator–prey systems. *Biological Invasions* 7: 795–806.

HOLT, R.D. & LAWTON, J.H. 1994. The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics* 25: 495–520.

HOULAHAN, J.E., CURRIE, D.J., COTTENIE, K., CUMMING, G.S., ERNEST, S.K.M., FINDLAY, C.S., FUHLENDORF, S.D., GAEDKE, U., LEGENDRE, P., MAGNUSON, J.J., MCARDLE, B.H., MULDAVIN, E.H., NOBLE, D., RUSSELL, R., STEVENS, R.D., WILLIS, T.J., WOIWOD, I.P. & WONDZELL, S.M. 2007. Compensatory dynamics are rare in natural ecological communities. *Proceedings of the National Academy of Science, USA* 104: 3273–3277.

HOWALD, G.R., DONLAN, C.J., GALVAN, J.P., RUSSELL, J.C., PARKES, J., SAMANIEGO, A., WANG, Y. , VEITCH, D., GENOVESI, P., PASCAL, M., SAUNDERS, A. & TERSHY, B. 2007. Invasive rodent eradication on islands. *Conservation Biology* 21: 1258–1268.

IMBER, M.J., HARRISON, M. & HARRISON, J. 2000. Interactions between petrels, rats and rabbits on Whale Island, and effects of rat and rabbit eradication. *New Zealand Journal of Ecology* 24: 153–160.

JONES, H.P., TERSHY, B.R., ZAVALETA, E.S., CROLL, D.A., KEITT, B.S., FINKELSTEIN, M.E. & HOWALD, G.R. 2008. Severity of the effects of invasive rats on seabirds: a global review. *Conservation Biology* 22: 16–26.

KESSLER, C.C. 2002. Eradication of feral goats and pigs and consequences for other biota on Sarigan Island, Commonwealth of the Northern Mariana Islands. In: Veitch, C.R. & Clout, M.N. (Eds). Turning the tide: the eradication of invasive species. Gland, Switzerland and Cambridge, UK: IUCN SSC Invasive Species Specialist Group. pp. 132–140.

KREBS, C.J. 1999. Current paradigms of rodent population dynamics - what are we missing? In: Singleton, G.R., Hinds, L.A., Leirs, H. & Zhang Z. (Eds). Ecologically-based rodent management. Monograph No. 59. Canberra: ACIAR. pp. 33–48.

LE CORRE, M. 1996. The breeding seabirds of Tromelin Island (western Indian Ocean): population sizes, trends and breeding phenology. *Ostrich* 67: 155–159.

LE CORRE, M. 1998. Relations entre les oiseaux marins pelagiques tropicaux et l'environnement oceanique: le cas de l'Ile Europa (Canal du Mozambique) [these de doctorat]. Paris, France: l'Universite Paris 6. 104 pp.

LE CORRE, M. 2008. Cats, rats and seabirds. *Nature* 451: 134–135.

LE CORRE, M. & JAQUEMET, S. 2005. Assessment of the seabird community of the Mozambique Channel and its potential use as an indicator of tuna abundance. *Estuarine, Coastal and Shelf Science* 63: 421–428.

MACKAY, J.W.B., RUSSELL, J.C. & MURPHY, E.C. 2007. Eradicating house mice from islands: successes, failures and the way forward. In: Witmer, G.W., Pitt, W.C. & Fagerstone, K.A. (Eds). Managing vertebrate invasive species: proceedings of an international symposium. Fort Collins, Colorado: USDA/APHIS/WS, National Wildlife Research Center. pp. 294–204.

MEURK, C.D. 1982. Regeneration of subantarctic plants on Campbell Island following exclusion of sheep. *New Zealand Journal of Ecology* 5: 67–75.

MOORS, P.J. & ATKINSON, I.A.E. 1984. Predation on seabirds by introduced animals, and factors affecting its severity. In: Croxall, J.P., Evans, P.G.H. & Schreiber, R.W. (Eds). Status and conservation of the world's seabirds. Technical publication no. 2. Cambridge, UK: International Council for Bird Preservation. pp. 667–690.

NOGALES, M., MARTIN, A., TERSHY, B.R., DONLAN, C.J., VEITCH, C.R., PUERTA, N., WOOD, B. & ALONSO, J. 2004. A review of feral cat eradication on islands. *Conservation Biology* 18: 310–319.

O'DOWD, D.J., GREEN, P.T. & LAKE, P.S. 2003. Invasional 'meltdown' on an oceanic island. *Ecology Letters* 6: 812–817.

PECK, D.R., FAULQUIER, L., PINET, P., JAQUEMET, S. & LE CORRE, M. 2008. Feral cat diet and impact on Sooty Terns at Juan de Nova Island, Mozambique Channel. *Animal Conservation* 11: 65–74.

POLIS, G.A., MYERS, C.A. & HOLT, R.D. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20: 297–330.

PROBST, J.M. & TÉZIER, R. 2000. Première mention du Pachyure étrusque *Suncus etruscus* aux Glorieuses. *Bulletin Phaethon* 11: 53.

RAYNER, M.J., HAUBER, M.E., IMBER, M.J., STAMP, R.K. & CLOUT, M.N. 2007. Spatial heterogeneity of mesopredator release within an oceanic island system. *Proceedings of the National Academy of Sciences, USA* 104: 20862–20865.

RODRÍGUEZ, C., TORRES, R. & DRUMMOND, H. 2006. Eradicating introduced mammals from a forested tropical island. *Biological Conservation* 130: 98–105.

RUSSELL, J.C., BEAVEN, B.M., MACKAY, J.W.B., TOWNS, D.R. & CLOUT, M.N. 2008a. Testing island biosecurity systems for invasive rats. Wildlife Research 35: 215–221.

RUSSELL, J.C., TOWNS, D.R. & CLOUT, M.N. 2008b. Review of rat invasion biology: implications for island biosecurity. *Science for Conservation* 286. Wellington: Department of Conservation. 53 pp.

RUSSELL, J.C., LECOMTE, V., DUMONT, Y. & LE CORRE, M. 2009. Intraguild predation and mesopredator release effect on long-lived prey. Ecological Modelling 220: 1098–1104.

SANCHEZ-PINERO, F. & POLIS G.A. 2000. Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. *Ecology* 81: 3117–3132.

SCHOENER, T.W. & SPILLER, D.A. 1999. Indirect effects in an experimentally staged invasion by a major predator. *American Naturalist* 153: 347–358.

SCHREIBER, E.A. & BURGER, J. (Eds). 2001. Biology of marine birds. Boca Raton: CRC Press. 722 pp.

SIMBERLOFF, D. 2006. Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecology Letters* 9: 912–919.

SIMBERLOFF, D. & VON HOLLE, B.V. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1: 21–32.

SOULÉ, M.E., BOLGER, D.T., ALBERTS, A.C., WRIGHT, J., SORICE, M. & HILL, S. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* 2: 75–92.

STRAUSS, S.Y. 1991. Indirect effects in community ecology: their definition, study and importance. *Trends in Ecology and Evolution* 6: 206–210.

TASKER, M.L., CAMPHUYSEN, C.J., COOPER, J., GARTHE, S., MONTEVECCHI, W.A. & BLABER, S.J.M. 2000. The impacts of fishing on marine birds. *ICES Journal of Marine Science* 57: 531–547.

TAYLOR, R.H. 1979. How the Macquarie Island Parakeet became extinct. *New Zealand Journal of Ecology* 2: 42–45.

THOMAS, B.W. & TAYLOR, R.H. 2002. A history of ground-based rodent eradication techniques developed in New Zealand, 1959–1993. In: Veitch, C.R. & Clout, M.N. (Eds). Turning the tide: the eradication of invasive species. Gland, Switzerland and Cambridge, UK: IUCN SSC Invasive Species Specialist Group. pp. 301–310.

TOWNS, D.R., ATKINSON, I.A.E. & DAUGHERTY, C.H. 2006. Have the harmful effects of introduced rats on islands been exaggerated? *Biological Invasions* 8: 863–891.

TOWNS, D.R. 2009. Eradications as reverse invasions: lessons from Pacific rat (*Rattus exulans*) removals on New Zealand islands. *Biological Invasions* 11: 1719-1733.

VAN DER ELST, R. & PRYS-JONES, R.P. 1987. Mass killing by rats of roosting Common Noddies. *Oryx* 21: 219–222.

VIDAL, E., MEDAIL, F., TATONI, T. & BONNET, V. 2000. Seabirds drive plant species turnover on small Mediterranean islands at the expense of native taxa. *Oecologia* 122: 427–434.

VITOUSEK, P.M., MOONEY, H.A., LUBCHENCO, J. & MELILLO, J.M. 1997. Human domination of earth's ecosystems. *Science* 277: 494–499.

WANLESS, R.M., ANGEL, A., CUTHBERT, R.J., HILTON, G.M. & RYAN, P.G. 2007. Can predation by invasive mice drive seabird extinctions? *Biology Letters* 3: 241–244.

WILCOX, C. & DONLAN, C.J. 2007. Resolving economic inefficiencies: compensatory mitigation as a solution to fisheries bycatch–biodiversity conservation conflicts. *Frontiers in Ecology and Environment* 5: 325–331.

WOOTTON, J.T. 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* 25: 443–466.

ZAVALETA, E.S., HOBBS, R.J. & MOONEY, H.A. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution* 16: 454–459.