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INVASIVE RODENTS ON ISLANDS

Avoiding surprise effects on Surprise Island: alien species control in a multitrophic level perspective

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Abstract Eradications of invasive alien species have generally benefited biodiversity. However, without sufficient planning, successful eradications can have unexpected and unwanted consequences for native species and ecosystems. In particular, the "surprise effect" is the rapid increase of hitherto unnoticed species following the sudden removal of an invasive alien that was exerting an ecological force on those species (predation, competition or herbivory, for example). The only way to prevent these undesired outcomes is to adapt the control programme following the characterization of the trophic relationships between the invasive alien species and the invaded communities, that is, to view the control with a holistic perspective. Here, we illustrate this point with the study of the role of the ship rat (*Rattus rattus*), which invaded a tropical pacific atoll, Surprise Island, New Caledonia. We assessed the risk of surprise effects during a pre-eradication phase of several years, and then adapted our eradication strategy accordingly.

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Introduction

The invasion of ecosystems by alien species is currently viewed as one of the most important causes of native biodiversity loss (Vitousek et al. 1997). Island populations are especially vulnerable to this threat because their dispersal opportunities are limited and because most of them have evolved in the absence of strong competition, herbivory, parasitism or predation. Invasive alien species are responsible for a very large fraction of documented island vertebrate extinctions (Dulloo et al. 2002; Courchamp et al. 2003; Towns et al. 2006), and the same is probably true for less studied organisms such as terrestrial invertebrates.

In the past decades, much effort has been devoted to the design and implementation of new methods and strategies to contain, control or eradicate a wide range of alien mammals on invaded islands (e.g., Krajick 2005). Tremendous progress has been made using physical (trapping, shooting), chemical (poisoning), and biological (lethal pathogens, engineered immunocontraception) methods. With respect to poisoning methods, delivery designs continue to improve with the development of exclusive bait stations, attractive baits (for the target species only), and the use of global positioning system (GPS) for bait delivery by helicopter (Morrison et al. 2007).

As a result, eradications are successful on increasingly large or difficult islands and eradication efforts are thus encouraged, triggering a desirable dynamic in biological conservation (Myers et al. 2000; Nogales et al. 2004; Campbell and Donlan 2005; Martins et al. 2006; Howald et al. 2007). In many cases, the elimination of the alien invasive species is followed by rapid and often spectacular recovery of impacted local populations of a wide variety of taxa. However, practically the only metric used to measure the success of eradication programmes is absence/presence of the target species at the end of the control period. However, eradication success cannot be reduced to effective alien removal, because eradication of alien invasive species should be viewed as a necessary, but not single, step towards ecological restoration (Atkinson 2001). This is essential if biodiversity managers wish to switch from conservation to restoration projects (Young 2000). The real measure of success, in addition to the absence of the target alien species, should be the restoration of communities, or at least the recovery of some target populations of local plants or animals. There are many reasons why restoration may not occur naturally following the removal of an alien species; for example, native species may have been extirpated or the habitat may have been too deeply modified. Counterintuitively, the control of invading alien species per se can also have adverse consequences on the ecosystem.

The most studied of these undesired effects includes primary poisoning of nontarget species (e.g., native rodents and granivorous birds) and secondary poisoning of nontarget predators and scavengers (e.g., raptors, insectivorous birds, and bats) during rat eradication campaigns using poison baits (Merton 1987; Eason and Spurr 1995; Howald et al. 1999; Jackson and van Aarde 2003). Other unwelcome byproducts of alien control or eradication may result from trophic relationships between the alien and the native species; for example, rabbits have been introduced to many islands but their management can be controversial: they are undesired because of their overgrazing of many native and endangered species, but may also be welcome as prey for endangered native predators (Gangoso et al. 2006).

Also, some alien invasive species may dramatically increase following the release of an ecological force (herbivory, predation, competition) formerly exerted by the now eradicated target alien species. There is a great variety of interactions among alien species, both direct and indirect, many of which have a potential effect at the population level (Simberloff and Von Holle 1999). The control of dominant alien species may facilitate the colonization/invasion of other alien species (Cabin et al. 2000; Zavaleta et al. 2001). In many cases, an alien species eradication that has been successful in terms of actual population removal has turned out to be disastrous because said removal has triggered chain reactions that were neither expected nor contained (Courchamp et al. 2003). Because of these interactions, any alteration to the species composition can have cascading effects throughout the ecosystem (Chapin et al. 2000).

These unexpected and undesired effects based on chain reactions have been termed “surprise effects” or “Sisyphus effects” (Mack and Lonsdale 2002). They have been discussed in many different situations, and potentially concern all trophic levels. They are generally more likely to occur when ecosystems contain more than one invasive species (i.e., the great majority of islands), and/or when invasive species have eliminated native species and replaced them functionally (Zavaleta et al. 2001); for example, several eradications of exotic herbivores have been linked to dramatic increases in exotic plant populations. A typical illustration of this is the population explosion of the exotic vine *Operculina ventricosa* on Sarigan Island, following the removal of feral pigs and goats which until then had held them at very low density (Kessler 2001). Surprise effects can also involve predatory or competitive relationships; the sudden removal of a top predator, or of a superior competitor, can release a prey, a mesopredator or a lower competitor from strong ecological pressure and generate a population explosion (Courchamp et al. 1999; Caut et al. 2007). As it is difficult to predict the global outcome of the removal of key species, invasive alien species eradication should not be attempted without a careful pre-eradication study of the relationships of the target species within the community and of the likely consequence of its sudden eradication. Adapted eradication designs may then be crucial for the restoration of multiply invaded ecosystems.

Despite the potentially detrimental consequences for biodiversity management, the concept of the surprise effect has so far been considered in theoretical rather than practical cases (see Courchamp and Caut 2005 for a review). The aim of those theoretical studies was to trigger new empirical studies taking into account the potentially disastrous surprise effects in alien species eradication programs. The present study aimed to follow these conceptual guidelines while conducting the eradication of an alien mammal from an insular ecosystem, taking into account the trophic relationships between the invasive target species and the key species in the invaded ecosystem. We report on the eradication of the black rat *Rattus rattus* from Surprise Island (New Caledonia). In this paper, we demonstrate the importance of the pre-eradication study, which allowed us to characterize the ecosystem, to study the trophic relationships of the rat and other species on the island, and to prevent possible surprise effects. We explain how each of these results is progressively taken into account to define our final strategy of eradication. We explain how the eradication was performed and report its success both in terms of rodent eradication and absence of surprise effects, at least in the short term.

Materials and methods

Island choice

The experiment was conducted on Surprise Island (18°28′55″S/163°05′12″E), one of the four islands of the D'Entrecasteaux Reefs, 230 km north of New Caledonia (Fig. 1a). The climate is tropical, tempered by trade winds. Mean temperature is 25.8°C with a minimum in August and a maximum in February. Average annual rainfall is 750 mm (at Koumac city), with a minimum in September and a maximum in March. Temperature and rainfall define four seasons: one hot and humid season from December to March when cyclones can occur, and a cool and dry season from July to October, separated by intermediate seasons (CTRDP 1987). This island is an uninhabited coral atoll of 24 ha (400 × 800 m^2) raised 2 m above sea level. Surprise Island was colonized around 1890 for guano mining, which continued until 1930. This activity was reported to result in the invasion of black rats (Laboute 1989; Beugnet et al. 1993). Surprise Island is a refuge for breeding marine vertebrates including sea turtles and seabirds. Both groups are very sensitive to human disturbance, and rats were reported to prey on seabirds on Surprise Island (Robinet et al. 1997). In 2002, we decided to study the relevance and feasibility of an eradication programme, based on a solid pre-eradication study of the ecosystem.

The remoteness of the island and the difficult sea conditions during a large part of the year (i.e., cyclones) restricts the number of ships available for transportation, and thus the number of possible visits. We conducted one survey per year from 2002, each time at a similar period to allow interannual comparisons. We chose the month of November so that most breeding bird species would be present (Robinet et al. 1997). However, we also conducted one additional survey at a different time of year to assess the seasonal variability of the rat impact. We chose February (2005), a period when breeding seabirds are absent from the island but another potential resource is abundantly present: newly hatched sea turtles (see Caut et al. 2008 for more details). During all these surveys, we assessed the characteristics and short-term change of the plant and animal communities on the island.

Pre-eradication studies

Characterization of plant communities

As no map was previously available for this island, we used a Thales GPS 6502sk/mk to carry out precise cartography of the island, focusing on the surface of the main vegetation units (about 25,000 GPS points). The GPS also provided georeferenced points of all the protocols for year-by-year comparisons. In addition, we characterized the main vegetation units more precisely using: (1) five plant plots in each habitat unit: species identification in 20 × 20 m^2 to assess the cover of each species present; (2) seven point-scale transects of 20 m to assess the cover of each species at different heights (Mueller-Dombois and Ellenberg 1974); (3) georeferenced annual photos for visual comparison of the plant communities (Fig. 1b). In addition, all plant species were collected and kept in 70% alcohol for later identification in the laboratory.

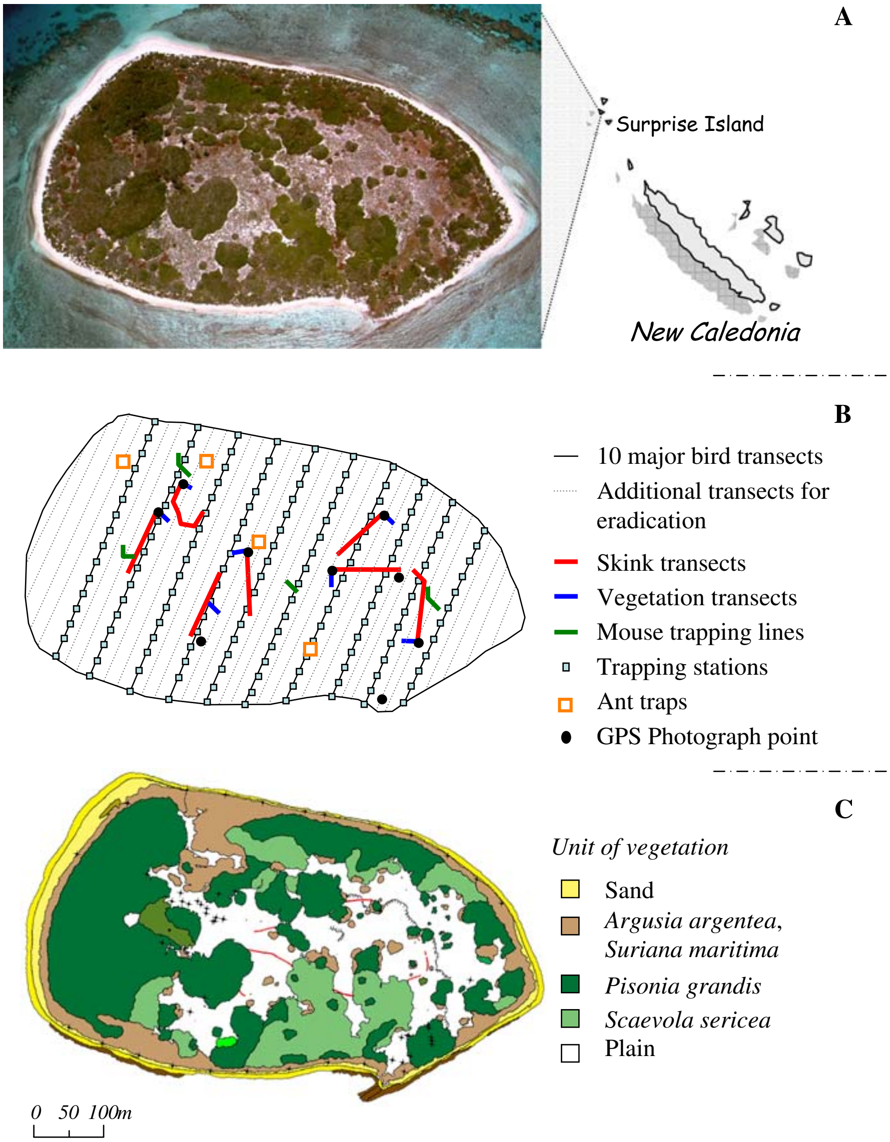

Fig. 1 **a** Aerial photo (by J.-B. Duaux) of Surprise Island, d'Entrecasteaux Reefs, New Caledonia. **b** Spatial representation of the sampling design used to characterize plant and animal communities. *Blue squares* represent general trapping stations, each comprising a rat trap, an insect pitfall, and an insect attraction bowl. **c** The four major distinct habitats delimited using submetric GPS

Characterization of animal communities

We established ten major line transects across the island, spaced 50 m apart to maintain independence between them (e.g., to keep from counting the same birds several times) (Fig. 1b). The direction was maintained using a compass. Together, the transects covered a total of about 3,000 m. These transects were chosen to cover the maximum surface of the island and were used for most of our surveys in order to reduce our impact on the island.

Tropical seabird species are known to breed asynchronously over long periods, resulting in many species breeding simultaneously on tropical islands. To assess population sizes of seabirds we used the line transect technique, which is efficient in terms of data gathering per unit effort (Bibby et al. 1992). Line transects also allowed comparisons with previous estimates made on the island (Robinet et al. 1997). We walked the ten line transects at low speed (0.5–1 km/h), and counted birds within a fixed 10-m-wide band (5 m at each side of the line). The 5-m distance was estimated by sight (by the same observer each year). For each transect, we noted the habitat types and the number and status of birds present (adult, juvenile, downy chick, naked chick, egg, empty nest) every 10 m (see Robinet et al. 1997). Birds found dead were used for sample collection.

Pitfall traps were used to sample ground arthropods (10 cm diameter × 15 cm height partially filled with soapy water) and attractive yellow traps were used for flying arthropods (20 × 20 × 10 cm^3 partially filled with soapy water). Arthropod traps were deployed over 2 days along every other major transect (yellow traps every 75 m and pitfall traps every 50 m, Fig. 1b) and the material was stored in 70% alcohol until identification in the laboratory.

Ant communities were sampled in all main vegetation units within 30 × 30 m^2 areas, in each of which we deployed (1) 24 pitfall traps for 24 h to sample the presence and abundance of ant species and (2) 18 bait stations (baited with honey or peanut butter) monitored hourly from sunrise to sunset to assess species-specific foraging activity (Fig. 1b). The ground surface temperature near the baits was measured every 15 min with HOBO Dataloggers to relate it to the interspecific competition in foraging activity.

Terrestrial reptiles were sampled on seven 100-m transects defined in the main habitat units (Lorvelec et al. 2004). We counted the number of skinks at specified distances from the transect line over a 15-min period to calculate an index of density (Bibby et al. 1992; Thomas et al. 2002). Marine reptiles were monitored each morning around the seashore by counting tracks from marine turtle females that came to nest in the night and went back to the sea in the early morning. This counting allowed us to estimate approximately the peak of the nesting season, thus to deduce the peak of the hatching period, and therefore to organize a field trip aiming at assessing the potential impact of rats on sea turtles hatchlings.

Impact of rats

An understanding of the population ecology and feeding behavior of *R. rattus* is necessary to help decide upon eradication necessity and, if eradication is needed, provide a framework upon which baiting programs can be more effective.

We estimated the population size using INRA rat traps (34 × 13 × 13 cm^3) baited with peanut butter. Trap stations were set each year every 25 m along the ten line transects (constituting a trapping grid of 25 m × 50 m all over the island). For logistic reasons, we could only use 30 traps which we moved between transects. Traps were set for one or two consecutive nights for each line transect: November 2002, 200 trap-nights; November 2003, 143 trap-nights; November 2004, 120 trap-nights; February 2005, 62 trap-nights; November 2005, 131 trap-nights before eradication. Traps were opened in the late afternoon and checked and closed each morning.

We collected general information for each trap: whether or not it was sprung, the presence of bait, and captures of rats and nontarget species. We calculated an index of abundance (IA) taking into account the number of corrected trap-nights (Nelson and Clark 1973): $\mathrm{IA} = 100 \times \mathrm{captures}/(\mathrm{TU} - S/2)$; $\mathrm{TU} = P \times N$, where P is the number of trapping nights, N is the number of traps, S is the total of traps sprung by any causes, TU is the number of trap nights, and $\mathrm{TU} - S/2$ is the number of corrected trap nights.

In order to assess the impact of the *R. rattus* population we focused on its diet. We chose to adopt the widest possible perspective and went beyond a species-centered study to encompass as many important resource items as possible. Captured individuals were killed to collect tissue samples for diet analysis. We recorded the sex, general health status, and sexual maturity of killed rats, together with various biometric parameters (length of body, tail, right foot and right ear, total weight, and weight without viscera).

The stomach and faeces of rats were removed and washed and the contents were examined in the laboratory. The relative contributions of plant items and animal prey were estimated for each stomach and faecal sample under binocular lenses and a microscope. We developed an extensive microphotographic collection of the epidermal tissues of the Surprise Island plant species (120 different items) and animal prey items as a reference for identifying fragments. Samples from livers of captured rats and samples from potential rat food items were collected for stable isotope analysis. We used the isosource model (Phillips and Gregg 2003), which calculates the range of all possible source contributions for systems where the number of potential sources is greater than $n + 1$, n being the number of isotopes. Isotopic models typically use the mean δ^{13}C and δ^{15}N values for each type of diet, corrected for the discrimination factor of the consumer (Caut et al. 2008).

To quantify the impact of rats on seabirds through egg predation, we counted the number of all nests with eggs or chicks for nesting species on the seashore and on the plain (Fig. 1c) for all surveys.

It is now established that control attempts may affect nontarget species through trophic interactions, but little is known concerning their consequences on competitive relationships; for example, the eradication of rats from an island could trigger a demographic explosion of a competing mouse population (Caut et al. 2007).

Because a mouse had been reported on the island before, we set INRA traps for mice. Three trap lines were established in different habitats across the island (Fig. 1b). Mouse traps were set along each trap line (60 m) every 3 m. Traps were set for several consecutive nights for each line transect depending on the year: November 2002, 74 trap-nights; November 2003, 280 trap-nights; November 2004, 140 trap-nights; February 2005, 40 trap-nights; November 2005, 400 trap-nights before eradication. We collected the same general information for each trap and calculated the same IA as for rats. Captured mice were killed to collect tissue samples for stable isotope analysis, and biometric parameters were recorded (length of body, tail, right foot and right ear, weight), as well as sex and sexual maturity.

Eradication

The February 2005 eradication was timed to minimize physical disturbance of nesting seabirds and marine turtles. We used rodenticide bait blocks ($3 \times 3 \times 1$ cm^3, 25 g) containing 0.005% bromadiolone (second-generation anticoagulant toxicant). Bait blocks were covered with paraffin wax to prolong their durability in a wet climate. We hand-distributed the baits across the total surface of the island on a grid of 5 m × 5 m. First, we cut 38 transects (one every 15 m) across the island (15 km of transects in the vegetation, Fig. 1b). On each of these 38 transects and every 5 m, we dropped one bait block and tossed one at 5 m to the left and another to the right. Every morning, we registered whether the cubes were intact, chewed or missing. We conducted four sessions of baiting (days 0, 6, 11, and 18). About 950 kg ($\sim$40 kg/ha) of rodenticide baits were used in total (250 kg/session, $\sim$11 kg/ha). In addition to baiting, traps were used to monitor rats just prior to, during, and after the eradication campaign (131 night-traps before the first baiting session and 300 night-traps after the first session).

Post-eradication

In November 2006 we returned to the island to confirm the eradication of rodents and to begin the post-eradication survey. We estimated the population size of rats and mice with the same protocol (149 trap-nights for rats and 200 trap-nights for mice) and we calculated the IA for each species. The post-eradication survey consisted of repeating the same protocols for all the ecosystem units (plants and animals) as in the pre-eradication phase.

Results

Pre-eradication studies

Characterization of plant communities

Plant identification and GPS mapping revealed four contrasting vegetation units: (1) a ring of shrubs around the island with two dominant species, *Argusia argentea* and *Suriana maritima* of 1–3 m in height, (2) a monospecific arboreal stratum of 3- to 10-m-high *Pisonia grandis*, (3) scattered, dense patches of *Scaevola sericea* of 1–3 m in height, and (4) a central plain with more than a dozen main herbaceous species (Fig. 1c). An illustration of the spatial covering of the plant species present in each main vegetation unit (obtained from the plant plots and in agreement with the point-scale transects) is presented in Fig. 2. Overall, 103 coconut trees (*Cocos nucifera*) were counted around the island. No coconut sapling was found prior to rodent eradication. The 36 most common plant species are listed in Table 1. A limited stand of *Cassytha filiformis*, a potentially invasive plant native to Florida, was present on the island.

Characterization of animal communities

A total of 15 marine bird species were observed on Surprise Island (Table 1), with nine breeding (Table 1). Robinet et al. (1997) recorded two more breeding species in 1996: the bridled tern *Sterna anaethetus*, which we saw breeding (unsuccessfully)

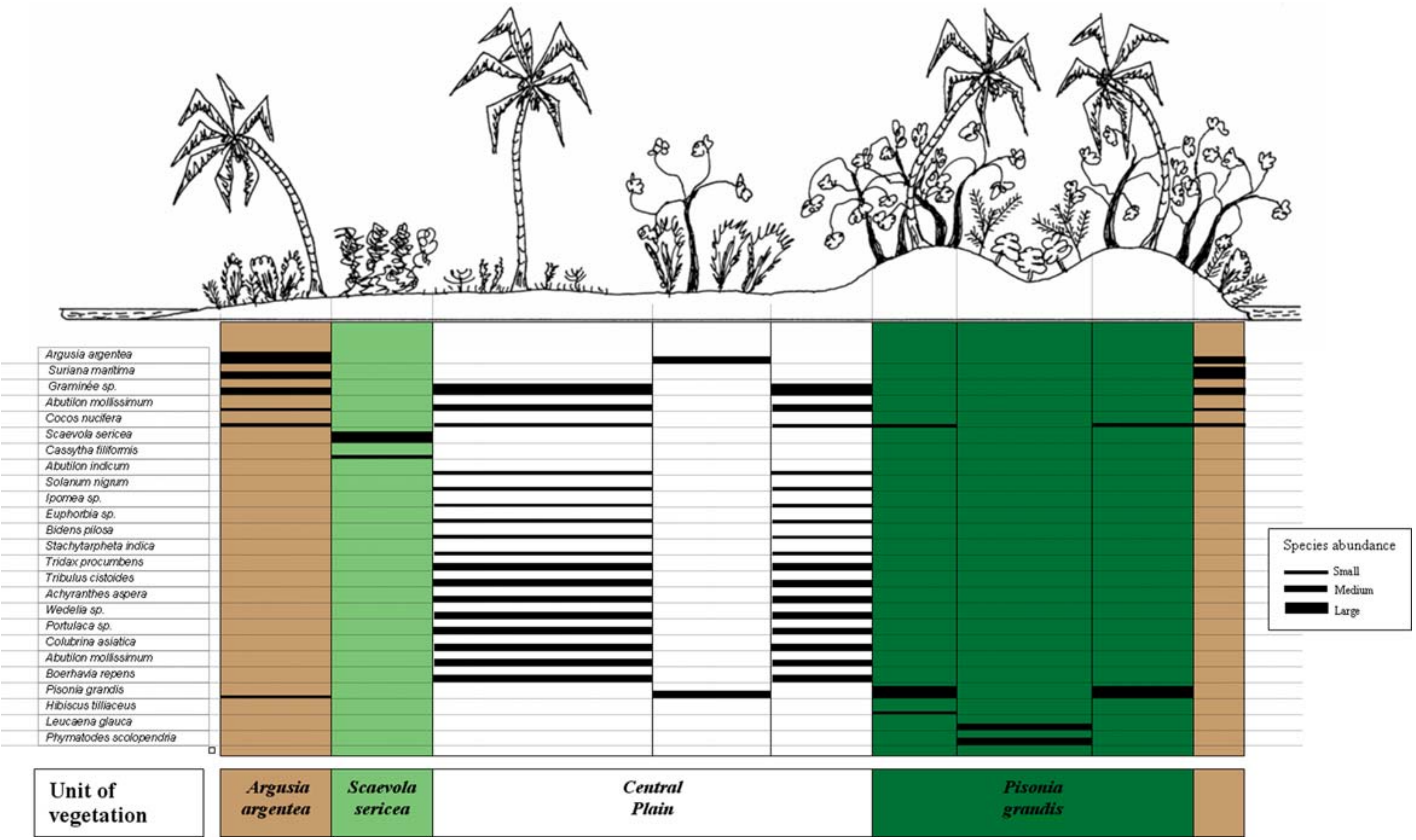

Fig. 2 Characterization of the main vegetation units. The species names and cover are given for eight 20 × 20 m^2 areas, which were measured across one of the ten major line transects. The drawing above represents the vegetation type of each square. The color codes are the same as in Fig. 1c. Species abundance was categorized into three levels corresponding to 0–25% cover (*low*), 25–75% (*medium*), and 75–100% (*high*)

Table 1 Species or families present on Surprise Island

Taxa					
Plants	***Stenatophrum micrathum***	***Portulaca* sp.**	***Achyranthes aspera***	*Stachytarpheta indica*	*Lantana camara*
	Lepturus repens	*Ipomea* sp.	*Solanum nigrum*	*Vigna lutea*	*Mariscus pennatus*
	Cenchrus calyculatus	***Scaevola sericea***	***Tridax procumbens***	***Abutilon indicum***	*Triumfetta procumbens*
	Cynodon daxtylon	***Hibiscus tiliaceus***	*Leucaena glauca*	*Wedelia aristata*	***Microsorum scolopendrium***
	Pisonia grandis	*Cassytha filiformis*	*Wedelia uniflora*	***Colubrina asiatica***	
	Tribulus cistoides	*Euphorbia* sp.	***Cocos nucifera***	*Brassica* sp.	
	Argusia argentea	***Abutilon mollissimum***	*Bidens pilosa*	*Caesalpinia bonduc*	
	Suriana maritima	***Boerhavia repens***	*Thuarea involuta*	*Canavalia* sp.	
Mammals	*Rattus rattus*	*Mus musculus*			
Marine reptiles	***Chĕlonia mydas***				
Terrestrial reptiles	*Lepidodactylus lugubris*	*Caledoniscincus haplorhinus*			
Sea birds	*Sula sula rubripes**	***Anous minutus****	*Sterna sumatrana*	*Fregata ariel**	***Puffinus pacificus****
	Sula dactylatra personata*	***Anous stolidus****	*Sterna bergii*	*Fregata minor**	*Phaeton rubricauda**
	Sula leucogaster plotus*	*Sterna anaethetus*	*Sterna fuscata*	*Arenaria interpes*	*Pluvialis dominica fulva*
Marine arthropods	*Oxypode quadrata*	*Grapsus* sp.			

	Coleoptera	Diptera	Hemiptera	Hymenoptera	Other
Terrestrial arthropods	**Buprestidae**	**Anthomyiidae**	Anthocoridae	Argidae	Blaberidae
	Cerambycidae	Cecidomyidae	Aphididae	Bethylidae	**Blattidae**
	Chrysomelidae	**Drosophilidae**	Cicadellidae	Braconidae	Sminthuridae
	Coccinellidae	Empididae	Delphacidae	Formicidae	Forficulidae
	Curculionidae	**Otitidae**	**Eurymelidae**	Dolichoderinae	Oligomatidae
	Melandryidae	Phoridae	Miridae	Myrmicinae	Geometridae
	Nitidulidae	Pyrgotidae	Ochteridae	Platygastridae	Heliozelidae
	Ptilidae	**Stratiomyidae**	**Oxycarenidae**	Orussidae	Tortricidae
	Rhizophagidae	Tachinidae		Scelionidae	**Acrididae**
	Silphidae	Tanyderidae		Siricidae	**Gryllidae**
	Tenebrionidae	Tephritidae			*Pagurus* sp.

Items found in rat diets are marked in bold. * Breeding birds species

only in the year 2002, and the buff-banded rail *Gallirallus philippensis*, which we did not observe during the entire study period and may now be extinct.

Two species of terrestrial reptiles are present on Surprise Island: the skink *Caledoniscincus haplorhinus*, endemic to New Caledonia, and the gecko *Lepidodactylus lugubris*. Both are probably allochthonous. Surprise Island is an important nesting beach for the green turtle *Chelonia mydas* (Table 1). The four main vegetation units supported species of at least ten orders of terrestrial arthropods. Hermit crabs were abundant over the whole island and two species of marine crab were found on the beach (Table 1). Ant surveys revealed the presence of seven introduced

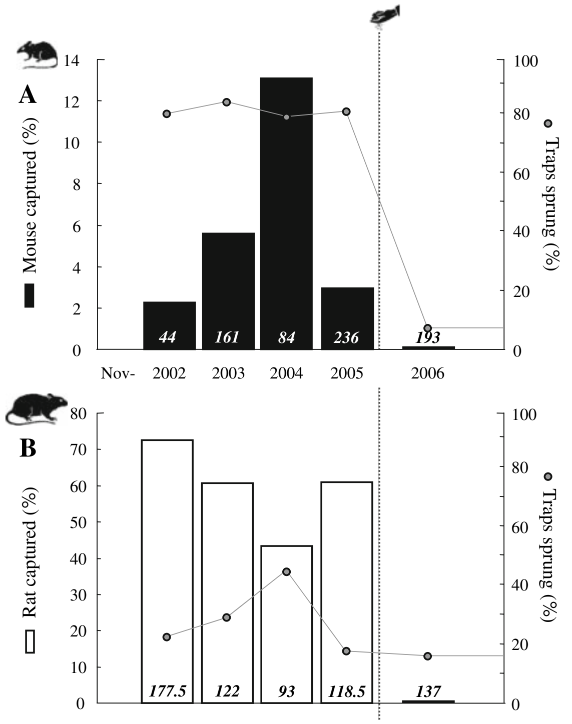

Fig. 3 Captures of mice (**a**) and rats (**b**) during the study. *Bars* represent the percentage of corrected trap-nights containing at least one rat or mouse. The number of corrected trap-nights is marked in italics inside each bar (see text for correction factor). The *hand icon* represents the eradication campaign separating pre- and post-eradication phases. *Grey circles* represent the percentage of traps sprung

species (*Tetramorium simillimum*, *Tetramorium bicarinatum*, *Tapinoma melanocephalum*, *Monomorium floricola*, *Cardiocondyla emeryi*, *Paratrechina longicornis*, and *Brachymyrmex obscurior*) and of *Pheidole oceanica*, the only species that can be considered native on Surprise Island. Each habitat had a dominant ant species; the native one was dominant in *Scaevola* patches (Cerdá et al., unpublished results).

A small population of mice, *Mus musculus*, was localized in the plain of Surprise Island. Mean IA during the pre-eradication phase was 5.98% (Fig. 3a). The average of traps sprung was very high (82.01%). Rats were observed triggering mouse traps, and thus were in all probability the main cause of this high percentage.

Impact of rats

Trapping confirmed the presence of rats all across the island. Mean IA during the pre-eradication phase was 59.40% (Fig. 3b). Even if capture rates were corrected, this is probably an underestimate of abundance. In fact, other species regularly closed the traps (mostly hermit crabs attracted by the baits, but also seabirds). Overall, an average of 28.64% of the traps were sprung (Fig. 3b).

As opportunistic predators, rats are notorious for their impact on a variety of animal (bird, reptile, insect) and plant (root, flower, seed) species. Our diet analyses of stomach contents suggest that many plant and animal species were food items for the rats (species in bold in Table 1); for example, plants were found in the guts and faeces of 100% ($n = 16$) of the rats collected in November and 67% ($n = 6$) of the rats collected in February (Caut et al. 2008). *C. filiformis*, a potentially invasive plant, was found in the gut of one rat and thus could potentially be problematic following rat removal: removed from this consumption, *Cassytha* could invade the island. Several categories of insects (Orthoptera, Coleoptera, and Lepidoptera) and skinks were observed in large proportions in the gut and faeces of trapped rats.

Conventional diet analyses and observations allowed the selection of different prey as inputs for isotopic models (isosource). Results from stable isotopic models depicted proportions of food in the diet of rats that were concordant with information derived from conventional diet analysis. Heavy impact is likely on seabirds, which could constitute as much as 24% of rat diet (see details in Caut et al. 2008). In the absence of birds, rats compensated marginally by preying more heavily on other components of their diet, but mostly shifted their diet by preying heavily upon another endangered species, the hatchlings of sea turtles, which could constitute as much as 45% of rat diet in those periods.

Our studies on the island also highlighted a partial overlap of the diet of the two rodents and a general shortage of available water that would make the two rodent species competitors for watery plants. A mathematical model showed that the control of the superior competitor (the rat) would lead to an increase in the inferior competitor (the mice), as pressure from competition was lifted. We called this process the competitor release effect (Caut et al. 2007). This increase may be sudden and dramatic if the superior competitor was eradicated and could also occur in conditions where the two competitors are controlled simultaneously. In that case, the inferior

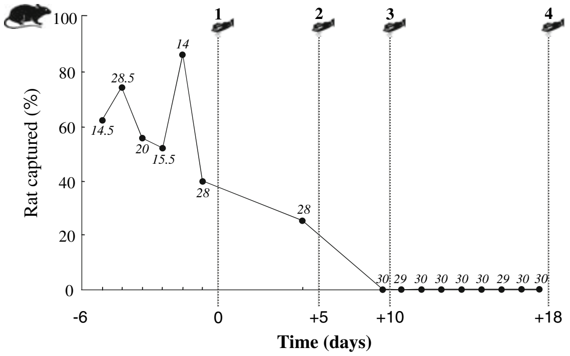

Fig. 4 Monitoring rat captures during the eradication campaign. Rats captured are measured as corrected trap-nights containing at least one rat. Time 0 represents the first eradication session on October 11, 2005. The hand icon numbers each baiting session. The number of corrected trap-nights is marked near each point

competitor increased despite being controlled. This occurred as soon as the inferior competitor benefited from the differential effect of the simultaneous control of both competitors, that is, when the indirect positive effect of control (the removal of their competitors) exceeded its direct negative effect (their own removal).

Eradication

As rats and mice were trapped throughout the eradication, it was possible to adapt the number of poisoning sessions to the declining number of trapped rats and mice. Bait cubes were often found partially eaten and frequently bore the marks of two broad rat-like incisors and dead rats were found throughout the island. The effectiveness of poison at reducing rat densities was high, and no rat sign was found after the second poisoning session (Fig. 4). However, two additional poisoning sessions were carried out as the mouse numbers remained uncertain. In particular, the small size of the mouse population and the high percentage of mouse traps sprung by rats in the earlier sessions (Fig. 3a) made it difficult to assess the effectiveness of poisoning on the mouse population. However, we observed dead mice throughout the baited grids 5 days after baiting commenced, and mice had full access to the baits from the second session onwards. The stand of *C. filiformis* was removed to prevent post-eradication spread. Ant communities were left untouched as the local species was found to be dominant over the seven alien ant species and none would be affected by the baits.

Post-eradication

In November 2006, trapping confirmed the absence of rats on Surprise Island (Fig. 3b). Despite uncertainty during eradication we were also able to confirm the absence of mice in 2006 (Fig. 3a). The same trapping effort was carried out as in the previous years but this time the percentage of mouse traps sprung decreased to 7% (ten times less than in the pre-eradication phase, Fig. 3a). This suggests that rats were the main cause of the high percentage of mouse traps sprung during the pre-eradication phase and the remaining 7% were probably due to wind, hermit crab, and seabirds. Another survey in 2007 confirmed rodent absence.

Data from one observation 1 year post-eradication is insufficient to draw any conclusion on the recovery of the plant and animal communities. However, the post-eradication surveys allowed us to confirm the absence of rat sign; for example, many coconuts (a readily available water resource on the island) were found uneaten and many coconut seedlings emerged (which was rarely observed during the pre-eradication phase). Mice have not been found on the island, but we did not detect any upsurge of plants or invertebrates.

Discussion

We have considered the eradication of an invasive alien species from a multitrophic level perspective. During a 4-year study, we assessed the place of the ship rat within the invaded plant and animal communities, in order both to evaluate the need for its eradication and to anticipate the likely outcomes of its sudden removal. Our study combined a large number of approaches, including vertebrate surveys, monitoring of plant cover, trapping of invertebrates, classical diet analyses, stable isotope analyses, and population dynamics modeling. Our results indicate that rats were having an important impact on some species on the island and that their removal was needed. We also showed the presence of other introduced species which could be involved in potentially strong relationships with the rats. In order to avoid chain reactions following the removal of rats, we redesigned our eradication strategies. No rodent was found, nor any surprise effect detected, 2 years after eradication.

Eradication strategy

The main aim of the chosen approach for this ecosystem restoration was to predict and avoid any possible surprise effect following the rat removal by assessing the alien's place in the trophic web. This approach has led to an adapted eradication strategy that aimed at being successful on both fronts: total rat removal and absence of chain reactions. Many authors have given rather precise guidelines based on their experience, and much relevant information can be found in published studies (e.g. Myers et al. 2000). The strategy of rat eradication on Surprise Island is based on our results from the pre-eradication phase, each point being taken into account progressively to define the final strategy of eradication:

1. *The need to start eradication*. We showed an important impact of rats on the whole ecosystem, in particular on seabirds and sea turtles (Caut et al. 2008). As the populations of several bird were declining on the island, it was feared that some could share the fate of the buff-banded rail, which went extinct on the island just prior to our study. It was necessary to start eradication.
2. *The presence of mice*. Rats compete with mice, so following the removal of rats, mouse numbers can increase greatly (Innes et al. 1995; Murphy et al. 1999). Due to the existence of a small population of mice on Surprise Island, we decided to assess the potential risks of a surprise effect if rats were eradicated without controlling mice. To this end, we postponed the eradication campaign for 1 year. A mathematical model was developed to assess the risks of mouse population increase following different rat control regimes. This work showed that removing the rats while leaving the mice on the island was not an option, and that both rodents had to be eradicated simultaneously (Caut et al. 2007).
3. *The absence of other problematic alien species*. Four years of research prior to the eradication campaign convinced us that mice were the only potential problem of surprise effect on the island. Alien ant species were dominated by the local ant species (Cerdá et al. unpublished results) and the only small patch of a potentially invasive plant, *C. filiformis*, could be (and effectively was) easily removed during the campaign.
4. *The selected eradication method*. Despite recently improved efficiency, especially concerning the eradication of rodents from larger islands, trapping methods remain logistically difficult, and are costly in material, manpower, and time. Poisoning can have a high cost efficiency on large and/or poorly accessible islands; its rapid effect is also advantageous. The need to distribute the lethal devices by hand and on foot over the whole island also influenced our choice towards poison baits over traps, as disturbance of birds would have been significant with the latter. Because the same poison baits were used and distributed on the same grid for both rodent species, the poisoning could be carried out in a single operation. As a result, a single team dispatched on the island would be sufficient to distribute the baits and check the traps, which would considerably reduce cost, effort, and time compared with two separate control programmes for rats and mice.
5. *The spacing of baits*. In consideration of the need to remove mice, we redesigned our rat control protocol on Surprise Island, basing it on a more intense level of control in order to remove the populations of the two species simultaneously. The common spacing between baits to eradicate ship rats from islands is around 25 m, based on their typical home range size (e.g., Taylor and Thomas 1993). However, the distance between bait stations varies with the target species and the area of operation (Moro 2001) and mice, having much smaller home ranges, could be missed by such a baiting grid. We thus reduced this spacing to 5 m for simultaneous eradication of mice and rat.
6. *The choice of the type of poison*. Despite its advantages over trapping, poison often reaches nontarget species. Numerous birds have been killed by either primary or secondary poisoning during field use of the poison in New Zealand (Williams et al. 1986; Eason and Spurr 1995; Jackson and van Aarde 2003). An ecosystem approach to eradication must provide a balance

between efficacy and the risks to nontarget species in the choice of poison (Zavaleta et al. 2001). Our pre-eradication study suggested that no local species would be affected by primary or secondary poisoning. Bromadiolone is lethal to both rats and mice (Mathur 1997; Brown and Singleton 1998). The choice of 25-g poison cubes of bromadiolone involved minimal risk to other species because it is known to be less toxic to invertebrates and reptiles and is unattractive to marine birds. Once the eradication began, the only nontarget animals regularly seen in contact with baits were hermit crabs; as far as we know the island's birds and reptiles did not attempt to eat baits. Two years after the eradication, no poison effect has been seen on populations of nontarget species.

7. *Poisoning sessions*. Toxic effects of bromadiolone do not start until around 3 days after ingestion, allowing initially neophobic consumers a few days to acquire an attraction for the cubes and accumulate a lethal dose of toxins before any aversion to the cubes can be developed (Brown and Singleton 1998). As it was assumed that not all rodents would be killed by the first distribution of baits, poisoning sessions were spaced at least 4 days apart. In addition, competition between rats and mice for food may prevent mice from accessing the baits (Harris and Macdonald 2007). The amount, density, and duration of poisoning should give rats enough time to be eradicated so that mice can have full access to the baits and disappear in turn. We performed a session of poisoning every 4 days for four sessions (Fig. 4) and laid a total of 950 kg of baits (one 25-g bait every 5 m).

Success

The success of an eradication programme can basically be measured in two ways. The first way, often the only one considered in practice, is the verification that the target species is no longer present. Generally accepted guidelines use a period of 2 years before official declaration of successful rat eradication. This point can now be considered effectively met, as neither rodents nor their sign were observed in November 2006 and in November 2007. According to this first criterion, rat eradication from Surprise Island is a success.

The second measure of eradication success is an assessment of achievement of the effects desired through eradication: restoration of the ecosystem in general, and recovery of some focal species (Young 2000; Atkinson 2001). This measure of eradication success is more rarely used, often because it requires in-depth pre- and post-eradication ecological studies. In many cases, either the financial support is lacking, or the management and the study of the ecosystem are carried out by distinct entities with complementary but distinct goals and biodiversity management is not systematically followed by applied research on the ecosystem. The need to integrate research and management has been highlighted before, together with the importance of post-eradication monitoring (Blossey 1999; Donlan et al. 2003). Although long-term monitoring can be deemed an unnecessarily heavy and costly effort if the target alien species is known to have been successfully removed, it is essential for at least two reasons. The first is that study of the recovery of an invaded ecosystem may provide crucial data to deepen our knowledge of biological invasions (Walker 1998; Myers et al. 2000; Sakai et al. 2001; Sax et al. 2007). The second is that, even if the target alien species is removed, restoration is not guaranteed, for example, because of surprise effects. In our case, such chain reactions have not been observed 2 years after rat eradication, thus providing us with a second measure of success.

Post-eradication monitoring

In addition, long-term monitoring of the post-eradication ecosystem is crucial to prevent reinvasion. It is crucial to be able to ascertain that the population has actually been eradicated, down to the very last individual (Morrison et al. 2007). Long-term monitoring would ideally benefit from comparison with nearby ecosystems in which the target alien species has never been present, in order to unambiguously associate the observed changes of the restored ecosystem to the removal of the aliens. This protocol has been called the before-after-control-impact (BACI) design, and is very demanding to put into practice but scientifically justified (Manly 2000). This design is easier to implement in archipelagos, where some adjacent islands are free of the focal introduced species and can be compared in the long term with the focal island. Because such nearby islands are often very similar in most biotic and abiotic aspects, parallel studies allow the estimation of the effect of alien species removal (as well as the estimation of their impact prior to eradication). The d'Entrecasteaux Reef consists of four islands, only one of which was invaded by rodents. During the Surprise Island rodent eradication programme, we visited the three other islands in order to be able in the future to assess the differences and similarities compared with the ecosystem of Surprise Island. In particular, we observed the bird communities, with the objective of relating future changes on Surprise Island either to rat removal or to shared bioclimatic causes. A post-eradication study will be conducted in the long term and its preliminary results published in a few years.

Importance of eradication studies

Control programmes of invading alien species, including the eradication of mammals from islands, have been increasing in numbers in the last few decades (Myers et al. 2000; Courchamp et al. 2003; Nogales et al. 2004; Campbell and Donlan 2005; Martins et al. 2006; Howald et al. 2007). In parallel, it has become more evident to both managers and researchers that eradication programmes are powerful conservation tools (Donlan et al. 2003). However, eradication studies, especially those discussing conservation strategies toward the management of exotic species, evaluating the conservation benefits of their control or reporting research on eradication techniques, are still greatly underrepresented in the literature (Donlan et al. 2003; Lavoie et al. 2007; Simberloff 2001). Probably as a result, eradication programmes remain peripheral to the biodiversity management community while not yet being fully supported in ecological research (Simberloff 2001; Donlan et al. 2003). More coordination between science and management has been advocated before, and studies based on eradication strategies or programmes incorporating research should be a high priority (Donlan et al. 2003). This study, integrating both research and management, is an attempt to contribute to this objective.

Trading-off research and management

Because it was primarily a research-based programme, our study of the ecosystem has covered both a large spectrum of species and a relatively large time span. Obviously, not all eradication programmes can afford to spend years on pre-eradication studies, especially if they are management based. Our approach, although globally very beneficial, requires a heavy commitment both from the researchers and from the financiers. From a purely research perspective, one can also make the point that the pre-eradication study was neither sufficiently long, nor wide enough, in terms of species covered or details acquired. A more thorough assessment of rat impact would have been interesting, but it would have required a logistically (and financially) more constraining study, which would also have to have been carried out for longer. Although there is a clear need to formally define the impact of alien species on invaded communities (Parker et al. 1999), this is balanced by a delicate trade-off between the necessity to better understand the focal ecosystem and an obligation to act fast (Simberloff 2003). In our case, the trade-off imposed by the dramatic decline of some bird species likely to be rat prey (Robinet et al. 1997) and the recently observed predation on sea turtle hatchlings (Caut et al. 2008) limited us to a 4-year study before we eradicated the rats. Although this trade-off will almost always be present, it is important to keep in mind that a minimal study of the trophic relationship of the focal invasive alien species with the invaded ecosystem is crucial in order to design the most suitable control strategy, avoid possible surprise effects, and ensure conservation success on all fronts.

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