

Responses of seabirds to the rabbit eradication on Ile Verte, sub-Antarctic Kerguelen Archipelago

S. Brodier¹, B. Pisanu¹, A. Villers^{1,2,3}, E. Pettex¹, M. Lioret¹, J.-L. Chapuis¹ & V. Bretagnolle²

¹ Département Ecologie et gestion de la biodiversité, Muséum National d'Histoire Naturelle, UMR 7204 CERSP, Paris, France

² Centre d'Etudes Biologiques de Chizé-CNRS, Villiers-en-Bois, France

³ Section of Ecology, Department of Biology, University of Turku, Turku, Finland

Keywords

Oryctolagus cuniculus; invasive mammal; burrowing petrels; brown skua; conservation program; Sub-Antarctic island.

Correspondence

Jean-Louis Chapuis, Département Ecologie et gestion de la biodiversité, Muséum National d'Histoire Naturelle, UMR 7204 CERSP, 61 rue Buffon, 75231 Paris cedex 05, France. Tel: +33 1 40 79 32 63
Email: chapuis@mnhn.fr

Editor: Todd Katzner

Received 3 September 2010; accepted 10 February 2011

doi:10.1111/j.1469-1795.2011.00455.x

Abstract

Studies on the role of introduced rabbits, *Oryctolagus cuniculus*, on islands have mainly focused on their negative impacts on vegetation. However, little attention has been paid to their influence on vertebrate communities. On Ile Verte (148 ha) in the sub-Antarctic Kerguelen Archipelago, rabbits are the only mammal that have been introduced. The long-term consequences of their eradication in 1992 on both native, burrowing seabird prey populations and their predator, the brown skua *Catharacta skua*, were investigated between 1991 and 2005. Densities of breeding petrels were followed on site with three plant communities differing in their soil depth. In addition, the diet and breeding activities of skuas were evaluated on the entire island area. The density of breeding pairs of the most abundant petrel species, the blue petrel *Halobaena caerulea*, which only nested at the site with deep-soil, increased by approximately eightfold during the 6 years following the rabbit eradication. Of the other species nesting in deep soil, there was an approximately fourfold reduction in the Antarctic prion, *Pachyptila desolata*, but such a decrease in breeding pair densities was not observed in areas with shallow soils. The South-Georgian diving petrels, *Pelecanoides georgicus*, was the rarest species, nesting only on mineral soils, and for which breeding pairs did not vary through time. The total numbers of fledged chicks of skua on the island significantly increased during the study period, but not the total number of breeding pairs. Thus, brown skuas were not affected by the disappearance of rabbits and rather benefited from an increase of their preferred prey. Blue petrels recovered quickly to sites with deep-soil, benefiting from the rabbit eradication and the cessation of burrow disturbance. The decrease of Antarctic prions could have been the result of an exclusion process from nesting areas on the deep soil site by blue petrels.

Introduction

Introduced mammals represent a major threat for fauna and flora of oceanic islands causing declines and sometimes extinction of numerous native species that lack natural defenses against invaders (Atkinson, 1989, 2001; Williamson, 1996; Courchamp, Chapuis & Pascal, 2003). Introduced predators can also alter the structure and function of ecosystems (Croll *et al.*, 2005; Fukami *et al.*, 2006; Towns *et al.*, 2009; Wardle *et al.*, 2009). Sub-Antarctic islands are particularly sensitive to such introductions because they are characterized by simplified terrestrial ecosystems with few plant and animal species (Frenot *et al.*, 2005). Instead, they harbour the richest seabird communities in the world, with many species of ground-nesting petrels (Weimerskirch, Zotier & Jouventin, 1989). These species have been impacted by introduced mammals, especially domestic cats *Felis silvestris* and murid rodents (mainly *Rattus* spp. and *Mus*

musculus) (Moors & Atkinson, 1984; Dowding & Murphy, 2001; Wanless *et al.*, 2007; Jones *et al.*, 2008).

The negative impact of rabbits, *Oryctolagus cuniculus*, on seabird populations has received little attention, despite the introduction of this herbivore to a large number of islands around the world (Flux & Fullagar, 1992). However, on some islands, rabbits have already been eradicated for the purpose of seabird habitat conservation (Imber, Harrison & Harrison, 2000; Priddel, Carlile & Wheeler, 2000; Bried *et al.*, 2009) or rabbit eradication is being planned (Parks & Wildlife Service, 2007). Rabbits can alter seabird habitat by their direct effects on vegetation cover and by accelerating erosion processes (Chapuis, Barnaud & Boussès, 1994; Copson & Whinam, 1998; Priddel *et al.*, 2000). Moreover, rabbits also show direct behavioural interference as they compete with burrowing petrels for space in areas with deep soil (Brothers, 1984; Weimerskirch *et al.*, 1989; Imber *et al.*, 2000; Bried *et al.*, 2009). Additionally, rabbits are suspected

to have artificially increased the population of brown skuas *Catharacta skua* on Macquarie Island, thereby contributing to an increased predatory pressure upon burrowing petrel and prion populations (Jones & Skira, 1979).

In 1991, an initiative was planned to test the resilience of native ecosystems and provide information on food web manipulations for future restoration actions (Chapuis *et al.*, 1995). The consequences of rabbits' eradication on burrowing seabird species had previously remained largely untested (but see Bried *et al.*, 2009), and the study was carried on one island of the Kerguelen Archipelago, the Ile Verte, where rabbits were eradicated in July 1992 (Chapuis *et al.*, 2001). Long-term monitoring of seabird communities on this island, including breeding pair densities of burrowing petrels and prions along with breeding activity and diet of the brown skua, was established to test whether the rabbit eradication had a direct or an indirect influence on seabird populations.

This paper describes the responses of seabirds to rabbits' eradication on Ile Verte. Based on our observations and other studies, we expected that following rabbit's removal: (1) burrowing seabirds number should increase as a direct consequence of the cessation of disturbances for space use in burrows; (2) such process would indirectly benefit the brown skuas by increasing their preferred prey.

Methods

Study area

The Kerguelen Archipelago (48°25'–50°00'S; 68°27'–70°35'E) is formed by a main island (6700 km²) and less than a hundred smaller islands ranging from 0.01 to 200 km². The climate is characterized by a mean annual rainfall between 438 and 921 mm. The mean monthly air temperatures range from 1 to 4 °C in the coldest month (July) and from 7 to 9 °C in the warmest month (January) (records from Météo-France, Port-aux-Français, 1991–2005). These islands are characterized by the low diversity of terrestrial communities (Vernon, Vannier & Tréhen, 1998; Frenot *et al.*, 2001), no native terrestrial mammals (Chapuis *et al.*, 1994) and 33 breeding seabird species (Weimerskirch *et al.*, 1989). Since the 19th and early 20th centuries, the use of these islands by whalers and seal hunters resulted in the intentional or accidental introduction of seven species of terrestrial mammals (Chapuis *et al.*, 1994). Among these species, the rabbit was introduced in 1874 (Kidder, 1876) and is now widespread (Boussès, 1991).

As part of a restoration program initiated in this archipelago, rabbits were eradicated by poisoning from three similarly sized islands with low-diversified vegetation communities located in the Golfe du Morbihan (Chapuis *et al.*, 1995; 2001). On one of these islands, the Ile Verte (148 ha; 49°30'23"S; 70°02'40"E), the restoration program began in October 1991 and ended in February 2006, with the eradication taking place during the winter season 1992 (July).

Burrowing petrels

The distribution of breeding petrel species differs according to habitat characteristics (Hunter, Croxall & Prince, 1982; Schramm, 1986; Genevois & Buffard, 1994; Catry *et al.*, 2003; Barbraud & Delord, 2006). From 1991 to 2006, the density of breeding pairs of burrowing petrels was monitored on the three main plant communities differing in their soil depth (for full description, see Chapuis, Frenot & Lebouvier, 2004) present on Ile Verte. These were closed communities of *Acaena magellanica* (Rosaceae) on deep organic soil (depth: 48 ± 6 cm; *n* = 24) (Site 1), open communities of *A. magellanica* on thin organo-mineral soil (17 ± 1 cm; *n* = 21) (Site 2) and fellfield communities on mineral soil (19 ± 1 cm; *n* = 30) (Site 3). Plant communities were nearly monospecific with cover in *A. magellanica* > 75% for closed ones, ranging between 25 and 75% for open ones, and between 2 and 25% for fellfields (see Chapuis *et al.*, 2004). No erosion processes occurred between 1992 and 1998 after rabbits eradication (Chapuis *et al.*, 2004).

On each of these three plant communities, a site was chosen and marked burrows were monitored monthly from October to February (on average 48 ± 1 burrows), corresponding to the breeding phase of these birds (see Moncorps *et al.*, 1998). We used acoustic playbacks for two consecutive nights per month to assess burrow occupancy (Bretagnolle, 1989; Bretagnolle & Lequette, 1990). Playbacks included calls of each of the main species present at the study plots. A burrow was noted as 'occupied' whenever a male or a female responded to the recorded calls. The monthly maximal count of occupied burrows was selected for analysis. As years progressed, some burrows disappeared. In such cases, new burrows were marked to keep the total number of burrows approximately constant. Additionally, all burrows were counted every year within an area selected from each site (supporting information Table S1). Burrow densities were calculated as the number of burrows per 100 m². A density index of breeding pairs per 100 m² was obtained by multiplying the percentage of occupied burrows by the density of burrows from each site. No data could be collected during the breeding season 1993–1994.

Brown skuas

Each year from 1991 to 2006, the total number of territorial pairs of skuas and fledged chicks per pair were recorded between October and January over the entire area of Ile Verte. Breeding territories were searched for by walking throughout the island (Moncorps *et al.*, 1998; Mougeot, Genevois & Bretagnolle, 1998). The diet of skuas was investigated in January or early February, which is the period immediately before chicks fledge (Moncorps *et al.*, 1998). Skua diet was examined by identifying prey remains in the nesting areas of breeding pairs, with the exception of 1995 (when no identifications were made) and 2000 (when identifications were made in mid-February after the chick-rearing period). Species identification was based on wing

length and morphology. Results are expressed in relative abundance of each prey as a percentage (Moncorps *et al.*, 1998).

Data analysis

We used linear regression analyses to investigate the variation in breeding pair densities of burrowing petrels, and breeding pairs and fledging chicks of brown skuas. Because of the longitudinal nature of the data collection, we controlled for bias in temporal autocorrelation in variance analyses (Crawley, 2007). We ran linear models with generalized least squares and a corAR1 matrix. We then fit a simple linear model without the autocorrelation structure and compared the two models using Akaike information criterion (AIC) (Venables & Ripley, 2002). The model including the temporal autocorrelation having a difference in AICs between the two models was <3.0 . Normality in residual distribution was checked using quantile–quantile plots. Normality in variance homogeneity was checked using a fitted versus residual plot (Zuur *et al.*, 2009). All variables were rank encoded to meet normality in the residual distribution. All statistics were performed using R 2.11.1 (R Development Core Team, 2010; <http://www.R-project.org>). In this paper, the mean is always followed by its SE.

Results

Burrowing petrel densities

The blue petrel, *Halobaena caerulea*, was mainly found in burrows at Site 1, with a breeding pair density index of 7 ± 1 pairs per 100 m^2 . There was an average of approximately two breeding pairs per 100 m^2 of the Antarctic prion, *Pachyptila desolata*. Few petrels were found at Site 2, with both the South-Georgian diving petrel, *Pelecanoides georgicus*, and Antarctic prions breeding at a density of approximately one pair per 100 m^2 , and no breeding blue petrels, that is, at a density of <0.1 breeding pairs per 100 m^2 (supporting information Table S1). The South-Georgian diving petrel was the only petrel species nesting at Site 3, with an average nesting density of 0.4 ± 0.1 pair per 100 m^2 .

At Site 1, the density of breeding pairs of blue petrels increased from one pair per 100 m^2 in 1991–1992 before rabbits eradication to eight pairs per 100 m^2 in 1997–1998, that is, 6 years after rabbits removal, then remained more or less stable with an average of around 7 pairs per 100 m^2 (Fig. 1). This trend was not significant over the study period ($P = 0.08$; Table 1). In contrast, the breeding density of Antarctic prions significantly decreased over the study period from three pairs per 100 m^2 in 1991 down to zero in 2006 ($P < 0.01$; Table 1; Fig. 1).

At Site 2, densities of breeding pairs of Antarctic prions and South-Georgian diving petrels remained almost stable over the study period, ranging between one and two pairs

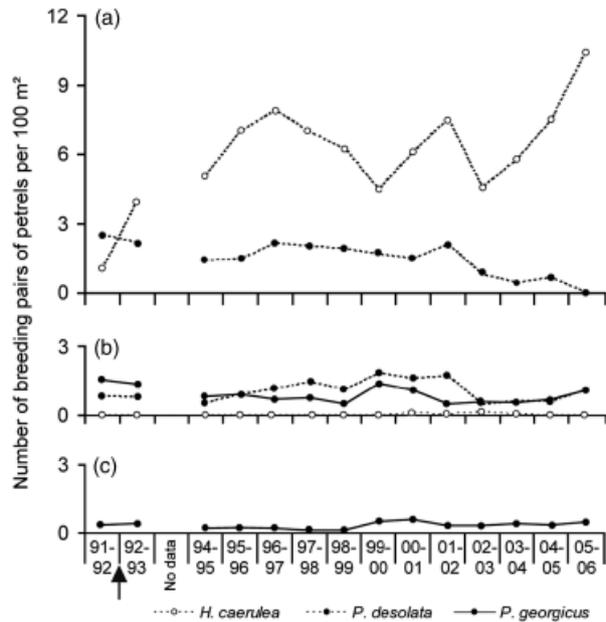


Figure 1 Variation in density of breeding pairs of seabirds at (a) a closed community of *Acaena magellanica*, (b) an open community of *A. magellanica* and (c) a fell-field sites. The arrow indicates rabbit eradication.

per 100 m^2 (both species combined), and were not related to time (Antarctic prions: $P = 0.89$; South-Georgian diving petrels: $P = 0.13$; Table 1; Fig. 1). Blue petrels were rarely encountered in the open community of *A. magellanica* (Fig. 1).

Finally, the South-Georgian diving petrels at Site 3 remained at a very low density, with less than one breeding pair per 100 m^2 . There was no temporal trend in their breeding density ($P = 0.16$; Table 1; Fig. 1).

Brown skuas

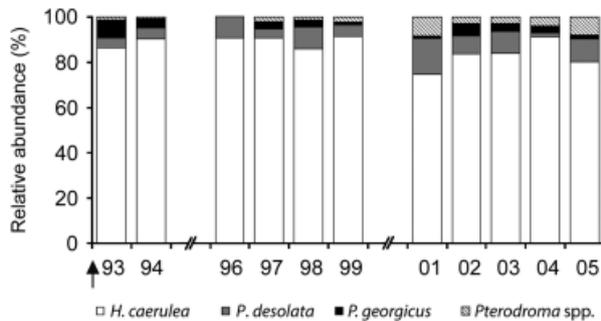
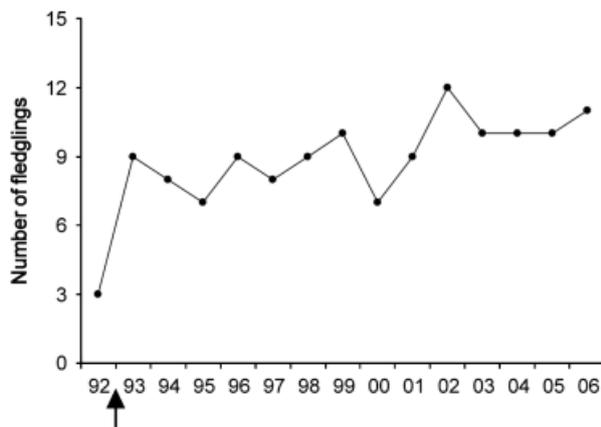
Over the study period, the yearly mean number of identified prey items per breeding pair of skuas ranged between 54 ± 27 (in 2001, when three breeding areas were present and sampled) and 167 ± 10 (in 2002, with seven sampled areas). Blue petrel dominated the skua diet (range: 80 ± 2 – $91 \pm 2\%$) and was constant over time (Fig. 2). Antarctic prions, South-Georgian diving petrels, and large-bodied petrels (*Pterodroma* spp.), were small proportions of the diet.

The mean number of breeding pairs of skuas was 6 ± 1 (range: 3–8), and the mean overall number of chicks was 9 ± 1 (range: 3–12). Breeding pairs did not significantly increase with time ($P = 0.26$; Table 1) and did not vary with density of breeding pairs of blue petrels ($P = 0.60$; Table 1). Instead, the number of fledging chicks significantly increased with time ($P < 0.01$; Table 1; Fig. 3), but was not related to the density of breeding blue petrels ($P = 0.22$; Table 1).

Table 1 Results of model selection, temporal autocorrelation Φ and regression coefficients, from the linear fits exploring the relationships between time and density of breeding pairs of petrels at the three plant communities, and breeding pairs and number of chicks of brown skuas *Catharacta skua* in the total area of Ile Verte between 1992 and 2005

Dependent variable	Sources of variation	δ_{AICs}	Φ	Coefficient \pm SE	P
Breeding pairs density					
Site 1					
Blue Petrel	Year	2.2	–	0.48 ± 0.25	0.08
Antarctic Prion	Year	0.8	–	-0.74 ± 0.20	<0.01
Site 2					
Antarctic Prion	Year	3.5	0.631	0.08 ± 0.52	0.89
Diving Petrel	Year	1.7	–	-0.43 ± 0.26	0.13
Site 3					
Diving Petrel	Year	0.1	–	0.40 ± 0.26	0.16
Brown Skua					
Pairs	Year	0.5	–	0.35 ± 0.29	0.26
	Blue petrel			0.16 ± 0.29	0.60
Chicks	Year	1.7	–	0.84 ± 0.21	<0.01
	Blue petrel			-0.28 ± 0.21	0.22

All variables were rank-encoded to meet normality in residuals distribution.

**Figure 2** Variation in the diet of the brown skua *Catharacta skua*. The arrow indicates rabbit eradication.**Figure 3** Variation in the number of fledged chicks of brown skuas *Catharacta skua*. The arrow indicates rabbit eradication.

Discussion

Our results highlight that rabbits eradication was (1) directly beneficial to blue petrels breeding in deep soil habitats; (2)

may have been indirectly beneficial to the rearing of skua's chicks by increasing their preferred prey; (3) may have had an indirect negative effect on breeding pairs of Antarctic prions through increased exclusion from nesting sites by increasing number of pairs of breeding blue petrels.

On closed communities of *A. magellanica*, burrow occupancy of blue petrels increased by eightfold over 6 years once the rabbits were eradicated. Although, we lacked a control island (e.g. island with rabbits and no eradication), there is evidence that the increase in blue petrels is a result of rabbit eradication because there was no observation of an increase of blue petrels of this magnitude at other study sites of this archipelago. For instance, long-term monitoring of blue petrels on Ile Mayes (a nearby 450 ha island not inhabited by rabbits) indicated stability of the blue petrel population size between 1990 and 1996 (with a decrease in recruitment rate), and then a decrease in population size between 1997 and 2000, which could be linked to increased winter mortality-related climatic changes at sea (Barbraud & Weimerskirch, 2003). Because blue petrels increased in density on Ile Verte, rabbits must have exerted a direct disturbance effect on petrel breeding activities, originating from interactions between rabbits and birds for the occupation of burrows in deep soils. Furthermore, it is likely that the burrows left empty after rabbits' extirpation may have offered favourable nesting opportunities for blue petrels.

On Kerguelen, brown skuas mainly feed on blue petrels and, to a lesser extent, on Antarctic prions (Moncorps *et al.*, 1998; Mougeot *et al.*, 1998; Mougeot & Bretagnolle, 2000; this study). On Ile du Cimetièrre, which is close to Ile Verte and where rabbits were present, blue petrels accounted for between 78 and 90% of the diet of skuas from 1987 to 1994, while rabbits accounted for <10% (Moncorps *et al.*, 1998). Therefore, rabbits are only an occasional prey item for skuas on Kerguelen, probably resulting from either predation on young or weakened rabbits, or from scavenging. Following rabbits' eradication on Ile Verte, we found

that the number of fledging chicks of skuas increased. Such a pattern may have been related to the increased availability of its preferred prey, the blue petrel, although we found no significant relationship between the number of breeding pairs or of fledged chicks and their major food item.

In contrast, Antarctic prions and South-Georgian diving petrels did not show such strong responses to rabbits' eradication, presumably because these two species can nest on thin organo-mineral soil and mineral soil, which were not used by rabbits for digging burrows. Moreover, we found no evidence of significant predation pressure by brown skuas on this prion species. The decrease in breeding Antarctic prions on closed communities of *A. magellanica* along with the increase in blue petrels may indicate a competition for space between these two species. This hypothesis is also supported by the stability of breeding pair densities of Antarctic prions on Site 2 with thinner soil layer investigated in this study. Such displacement from breeding areas on deep soil habitat, which should be further investigated, has already been shown on Ile Mayes between the blue petrel and the thin-billed petrel, *Pachyptila belcheri* (Genevois & Buffard, 1994), a closely related species.

Conclusion

The eradication of rabbits was rapidly beneficial to breeding pairs of blue petrels, by increasing the availability of undisturbed suitable burrowing areas. Such direct relationship between rabbits and a species of burrowing petrels was not detected before our study. Indeed, rabbit eradication or control operations were usually conducted on islands where food webs were more complex, that is, including other introduced mammals such as cats, rats and ungulates (e.g. Imber *et al.*, 2000; Priddel *et al.*, 2000; Copson & Whinam, 2001; Torr, 2002; Bergstrom *et al.*, 2009). Our results do not support the Jones & Skira (1979) hypothesis where rabbits as an alternative prey play an indirect role in increasing predatory pressure on burrowing petrels by sustaining brown skuas populations. Rather, our study indicates that both breeding predators and their preferred prey benefited from rabbits eradication. Antarctic prions, however, seemed to suffer from the increase in number of breeding pairs of blue petrels, but only on deep soil areas where blue petrels are usually dominant.

Acknowledgements

This research was supported by the Institut Polaire Français (IPEV, Programme 136), the CNRS (Zone atelier antarctique) and the Ministère de l'Aménagement du Territoire et de l'Environnement (Programme 'Recréer la nature'). We thank two anonymous referees for their constructive comments on the paper and B. Planade for the English. We also wish to thank J. Asseline, M. Charavin, D. Haubreux, A. Hédél, J. Le Cuziat, L. Lefèvre, A. Le Roch, V. Le Roux, A. Lucas, V. Magnet, V. Marsaudon, R. Périn and D. Rolland, for their dedicated work in the field.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1. Details of yearly areas prospected for each plant community by counting the total number of burrows

(N), the number of marked burrows (n), and months where the maximum number of occupied burrows by breeding pairs of the Blue Petrel, *Halobaena caerulea*, Antarctic Prion, *Pachyptila desolata*, and South Georgian Diving Petrel, *Pelecanoides georgicus*, were observed.

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