

Seabird population changes following mammal eradication at oceanic Saint-Paul Island, Indian Ocean

Christophe Barbraud^{a,*}, Karine Delord^a, Fabrice Le Bouard^b, Roald Harivel^b,
Jérémy Demay^{a,c}, Adrien Chaigne^b, Thierry Micol^{b,d}

^a Centre d'Etudes Biologiques de Chizé, CNRS UMR7372, 79360 Villiers en Bois, France

^b Réserve Naturelle Nationale des Terres Australes Françaises, TAAF, rue Gabriel Dejean, 97458 Saint-Pierre, France

^c Conservatoire d'espaces naturels de Languedoc-Roussillon, Salines de Villeneuve, chemin des salins, 34750 Villeneuve-lès-Maguelone, France

^d Ligue pour la Protection des Oiseaux, Fonderies Royales, 8 rue du Docteur Pujos, 17300 Rochefort, France

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ABSTRACT

The eradication of invasive mammals on islands is important for protecting seabird populations and insular ecosystems. However, the impacts of such eradications are insufficiently known because monitoring of potentially beneficiary species is often sporadic and limited. We performed a survey of all seabird species on Saint-Paul Island, southern Indian Ocean, 20 years after successful eradication of invasive black rat (*Rattus rattus*) and European rabbit (*Oryctolagus cuniculus*). Using complementary sampling designs including adaptive cluster sampling, stratified random sampling and entire sampling, we estimated population changes and colonization by new seabird species. A total of 13 seabird species were found breeding on Saint-Paul post-eradication compared to six before the eradication. Among the seven species that colonized the island, five (MacGillivray's prion *Pachyptila macgillivrayi*, fairy prion *P. turtur*, white-bellied storm petrel *Fregetta grallaria*, Antarctic tern *Sterna vittata*, sooty tern *Onychoprion fuscatus*) had relictual populations breeding on a nearby islet, and one (brown skua *Catharacta antarctica*) was a new breeding species. We also found breeding subantarctic little shearwaters *Puffinus elegans*. For species that were breeding on the Saint Paul pre-eradication, the mean annual population growth rate was 1.030 ± 0.093 (SE). Species known to be vulnerable to rat predation (prions, great-winged petrel *Pterodroma macroptera*, flesh-footed shearwater *Puffinus carneipes*, subantarctic little shearwater, white-bellied storm petrel, Antarctic tern) had the highest population growth rates. Two decades after the eradication of invasive mammals on a remote oceanic island, seabird populations were high beneficiaries. These findings further highlight the importance of invasive mammal eradication on islands as a conservation tool. Results are encouraging for the planned eradication of invasive mammals from nearby Amsterdam Island, and suggest this will mainly benefit terns and small burrowing petrels.

1. Introduction

Insular ecosystems, those that are small and naturally fragmented, warrant a high priority in biodiversity conservation as they host more than 15% of terrestrial species, and 61% of all recently extinct species and 37% of all critically endangered species are endemic to islands (Kier et al., 2009; Tershy et al., 2015). High levels of endemism richness and high extinction rates have motivated increasing conservation efforts on islands, such as the eradication of invasive mammals which was successfully undertaken on >850 islands worldwide (DIISE, 2018). Indeed, invasive nonnative mammals are the main cause of animal extinction on

islands and one of the most important threats to insular biodiversity (Clavero & García-Berthou, 2005; Szabo et al., 2012). However, the impacts of eradication of invasive mammals on islands are insufficiently known because monitoring of eradication outcomes, such as recolonization or population growth of potentially beneficiary species, is often sporadic and limited (Jones et al., 2016; Lavers et al., 2010; Towns, 2018). These deficiencies with outcome monitoring are particularly acute for seabirds (Brooke et al., 2018). For example, in their review Brooke et al. (2018) were able to estimate seabird population growth rate post-eradication for only 61 islands. This is partly due to several factors (Towns, 2018). First, due to the slow life-histories and long

* Corresponding author.

E-mail address: barbraud@cebc.cnrs.fr (C. Barbraud).

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generation time of seabirds, there is a delay in population growth following eradication of invasive mammals. Monitoring for at least 10 years, and preferably longer, after eradication is needed to identify population changes for seabirds due to their long generation time, slow life-histories, and low immigration rates (Brooke et al., 2018). Such long timescales are often beyond the remit of funding agencies and are incompatible with projects funded from short-term calls. Second, there are also logistical challenges (and associated costs) of reaching remote locations for undertaking surveys, and repeatable monitoring designs allowing to quantify population growth are not undertaken systematically. Third, assumptions are often made that positive outcomes at one locality will repeat on those nearby, even when communities differ. Other impediments to reporting eradication outcomes are unmeasurable claims of potential response by target species, and the unavailability of economical ways to measure the speed and scale of changes at the ecosystem level.

After the first successful eradication of rats from a large island [Breaksea Island, New Zealand, (Taylor & Thomas, 1993)] and the first use of aerial dropping to remove rats and rabbits from Enderby Island (Torr, 2002), the Administration of the French Southern Territories (TAAF) decided to undertake the eradication of rats from Saint-Paul Island where the endemic Macgillivray's prion had been removed by rats but with a remaining small breeding population (150 pairs) in a nearby islet (La Quille).

Black rats (*Rattus rattus*) and European rabbits (*Oryctolagus cuniculus*), but not house mouse (*Mus musculus*), were successfully eradicated from Saint-Paul Island, Indian Ocean, in the late 1990's (from 1997 to 1999; Micol & Jouventin, 2002). Absence of sightings or rat signs since then confirmed that the island is still rat free, and a maintenance program of bait stations disposed near landings points ensured that it remains rat free. Rats and mice were introduced between 1792 and 1874, and rabbits probably during the early 19th century (Segonzac, 1972). Despite encouraging recolonization signs by seabirds early after eradication (Micol & Jouventin, 2002), no systematic survey has been undertaken since eradication of rats and rabbits was confirmed. However, Saint-Paul was predicted as a site with highly threatened beneficiary species from invasive mammal eradication (Jones et al., 2016), with three potentially beneficiary endangered seabird species (northern rockhopper penguin *Eudyptes moseleyi*, sooty albatross *Phoebastria fusca* and Indian yellow-nosed albatross *Thalassarche carteri*).

The aim of our study was therefore to perform a comprehensive survey of all seabird species on Saint-Paul nearly 20 years after successful invasive rat and rabbit eradication, and to estimate population changes and colonization by new seabird species. Based on results obtained by Jones et al. (2016), who found that invasive mammal eradication benefited terrestrial insular fauna on 181 islands, and by Brooke et al. (2018), who examined what factors influence rates of population recovery for 181 seabird populations of 69 species following successful eradication projects, we made the following predictions. First, we expected positive population growth for seabird species that were reported to breed on Saint-Paul and a nearby islet and were known to be vulnerable to rats. Second, we predicted positive growth for seabird species that were not able to breed due to predation. For Saint-Paul this concerned small to medium size burrowing petrels such as MacGillivray's prion *Pachyptila macgillivrayi*, fairy prion *P. turtur*, great-winged petrel *Pterodroma macroptera*, flesh-footed shearwater *Puffinus carneipes*, little shearwater *P. assimilis*, and white-bellied storm petrel *Fregatta gallaria*, as well as the surface nesting Antarctic tern *Sterna vittata*, all known to breed on Saint-Paul and on an islet situated nearby (Tollu, 1984). Third, we expected faster growth rates for terns, as identified by Brooke et al. (2018) in a comparative study. Fourth, we predicted faster population growth if large source populations were nearby. La Quille is a mammal free predator islet situated 150 m offshore Saint-Paul. Until the eradication of invasive mammals on Saint-Paul it constituted the only refuge for breeding seabirds that formerly bred on Saint-Paul (Tollu, 1984). Before eradication the most abundant species breeding on La

Quille were Antarctic terns (≈ 200 breeding pairs, Segonzac, 1972), MacGillivray's prion (≈ 150 breeding pairs, Tollu, 1984) and great-winged petrels ($\approx 40\text{--}60$ breeding pairs, Micol & Jouventin, 2002). Four other species were breeding on La Quille but in very low numbers (Tollu, 1984). We thus predicted higher population growth rates for the three most abundant species on La Quille (Antarctic terns, MacGillivray's prion and great-winged petrels). Finally, Brooke et al. (2018) identified immigration as an important factor for colony growth. Because new species were previously observed as nonbreeding at Saint-Paul following eradication (Thiebot et al., 2010), thus constituting potential immigrants, and given that new species have been recorded as breeding on islands following rodent eradication (Croll et al., 2016), we expected new breeding species for Saint-Paul.

2. Methods

2.1. Study site

Saint-Paul Island ($38^{\circ}42'30''\text{S}$, $77^{\circ}32'30''\text{E}$) lies 90 km south of Amsterdam Island in the southern Indian Ocean, approximately 3400 km west of Australia and 4300 km east of South Africa. The total area of the island is 820 ha and the highest point is at 268 m. Three islets are situated along the northern coast of Saint-Paul: Ilôt Nord (90 m offshore), Rocher du Milieu and La Quille both 150 m offshore, the latter (0.7 ha; highest point 85 m) being the only islet vegetated and hosting breeding seabirds. Saint-Paul consists of the eroded top of a conic volcano of which part of the eastern side has disappeared (Fig. 1). This side of the island is characterized by a caldera invaded by the sea and surrounded by steep cliffs more than 200 m high. The western and southern slopes of the island are less steep, ending in 30 m vertical sea cliffs (see Supplementary material for further details).

Before the eradication, rats, mice and rabbits were the only remaining exotic mammals on Saint-Paul Island as cats, pigs and goats had disappeared decades ago. To evaluate the impact of the rat eradication on Saint-Paul seabird populations we conducted a variety of surveys in March/April 2005, 2006, 2012 and 2013 to coincide with breeding activities of winter breeding seabirds, and in December 2018 to coincide with breeding activities of summer breeding seabirds. Different survey types combining various sampling designs and enumeration methods were utilized to provide an abundance estimate of seabirds that occur on the island and to detect presence of rare species. Survey types were selected according to species-specific breeding habits, densities and site accessibility to fieldworkers, but the same methods were used in different years for consistency. Table 1 describes the sampling designs and enumeration methods used for each species. Burrows were assigned to species or groups of species according to identification of individuals captured in burrows and to burrow dimensions indicated in Table S1 (see Supplementary material).

2.2. Adaptive cluster sampling

Because we anticipated low densities of breeding burrowing petrels on the island, and since burrowing petrels often breed in clusters, we used systematic adaptive cluster sampling to estimate abundance of burrowing petrels (Thompson & Seber, 1996; Thompson, 1992). The systematic adaptive cluster sampling consisted of two steps. In the first step systematic sampling was applied, yielding an initial set of U sampling units (primary plots). Primary plots were positioned on transects with 100 m between each plot and 300 m between each transect (Fig. 1). Because from breeding ecology of the species, we expected higher colonization of coastal areas, a complementary coastal transect was established with 100 m between each primary plot. Each sampling primary plot consisted in a 10 m radius circle. In each plot, the presence of petrel burrows was determined by two experienced observers searching meticulously within the plot. If no burrow was present, the next primary plot was searched for. If at least one burrow was present, the second step

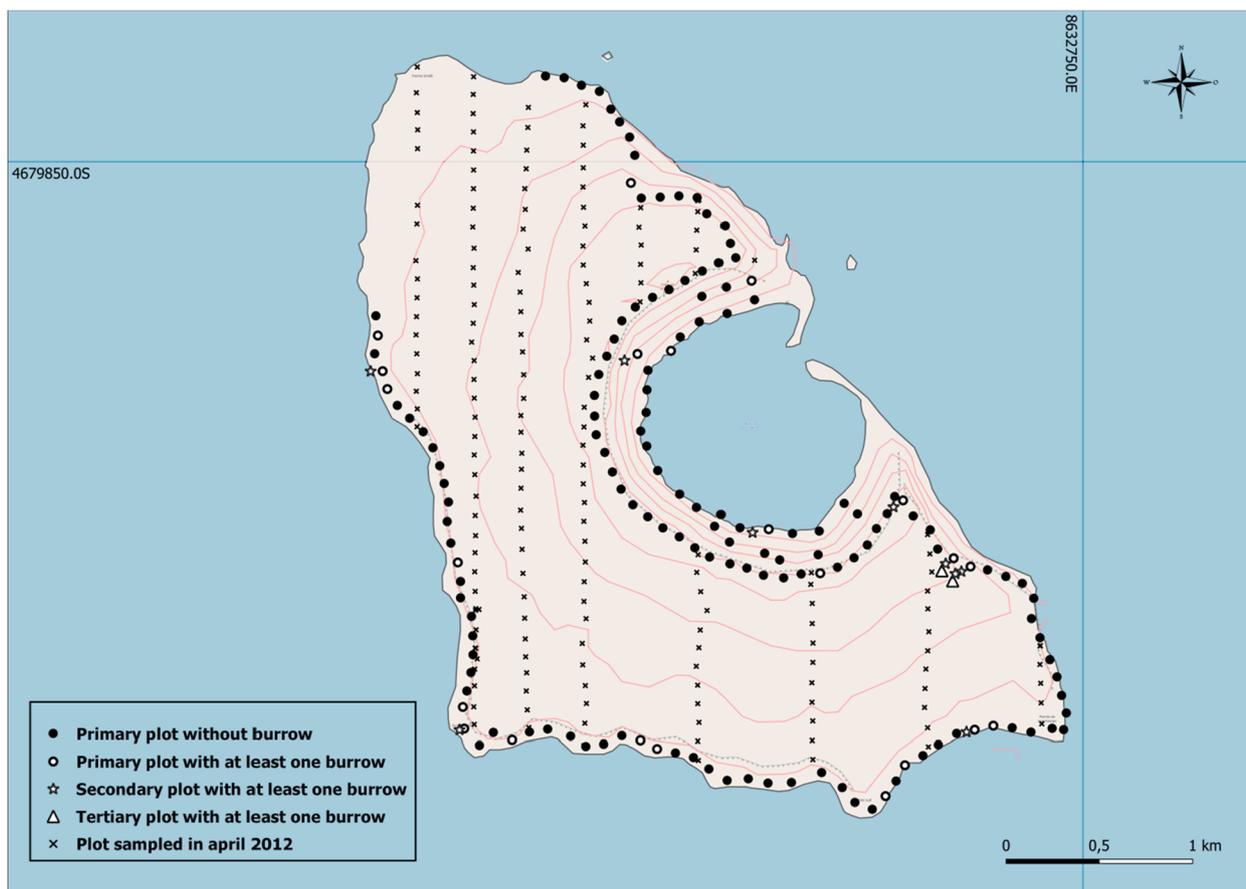


Fig. 1. Map showing Saint Paul Island and the sampling points from the adaptive cluster sampling.

Table 1

Sampling design and enumeration methods used to survey seabirds on Saint-Paul Island.

Sampling design		Enumeration method		Target situation	Species
Pre-eradication	Post-eradication	Pre-eradication	Post-eradication		
Systematic sampling	Adaptive cluster sampling	Complete counts	Complete counts	Elusive, low density	Burrowing petrels
Systematic sampling	Random sampling	Complete counts	Complete counts	Elusive, high density	Prions
		Capture-recapture	Capture-recapture	Elusive, high density	Prions
Entire sampling	Entire sampling	Complete counts	Incomplete counts	Elusive, high density	Flesh-footed shearwater
Entire sampling	Entire sampling	Complete counts	Complete counts	Conspicuous, surface-nesting	Northern rockhopper penguin, albatrosses, brown skua, sooty tern, Australasian gannet
Systematic sampling	Systematic sampling	Complete counts	Complete counts	Conspicuous, surface-nesting	Antarctic tern

adds neighboring circular plots (secondary plots) to this primary plot (and thus to the sample). The presence of at least one burrow in each one of these secondary plots was determined. If positive, further neighboring plots were added (tertiary plots). Plots were added repeatedly until no additional plots contained a burrow anymore. This procedure for selection in adaptive designs depends upon population numbers observed in the field (see [Supplementary material](#)).

2.3. Stratified random sampling

During successive visits and qualitative searches for petrel burrows on the island, two relatively small areas of high density of MacGillivray's and fairy prions were found (thereafter named colony 1 and colony 2). To avoid over-sampling these areas using the adaptive cluster sampling

approach (which could occur when the final sample size is many multiples of the initial sample size), we used stratified random sampling in high-density areas for MacGillivray's and fairy prions (see [Supplementary material](#)).

2.4. Entire sampling

Previous surveys showed that flesh-footed shearwaters breed in a colony situated on the northwest coastal area of Saint-Paul where nest densities are high (Roux, 1985; Segonzac, 1972). To avoid over-sampling this area using the adaptive cluster sampling approach, and since the flesh-footed shearwater colony is settled in a well-defined narrow coastal band northwest of Saint-Paul, we performed a true survey of the entire colony (i.e. the entire sampling frame was covered, see

Supplementary material).

Entire sampling was also used for conspicuous surface nesting species: northern rockhopper penguin, Indian yellow-nosed albatross, sooty albatross, brown skua (*Catharacta antarctica*), sooty tern (*Onychoprion fuscatus*), Antarctic terns, and Australasian gannet (*Morus serrator*). At the time of our last survey (December 2018), rockhopper penguins were ending their breeding cycle and chicks were preparing for departure at sea. We thus counted the number of chicks by direct counts. Indian yellow-nosed albatrosses, sooty albatrosses and Australasian gannets were incubating, so we counted the number of adults occupying a nest site. For brown skuas our visit corresponded to the chick rearing period, so we counted the number of nests with chicks and the number of pairs defending a territory. For terns, which breed in coastal cliffs (Segonzac, 1972), we counted territorial pairs when moving between plots situated on the coastal transect of the adaptive cluster sampling.

2.5. Mist-netting

As part of a companion study aiming at recapturing MacGillivray's prions previously equipped with geolocators, mist nets were set at night in one of the high density colony of MacGillivray's prions (colony 2). We thus used capture-recapture data from mist-netting sessions to estimate MacGillivray's prion abundance (see Supplementary material). We did not use lure calls during mist-netting sessions.

2.6. Incidental observations

Opportunistic observations of seabird species not monitored using standard survey methodologies described above were recorded in December 2018 and during previous visits on Saint-Paul since 1972.

2.7. Estimating population growth rates

Following Brooke et al. (2018) we estimated an annual rate of

Table 2

Numbers of breeding pairs or burrows with signs of occupation before or at the time of the eradication program (N_{init}) and during the 2018 survey (N_{2018}) of seabirds breeding on Saint-Paul Island (excluding La Quille islet). λ is the annual population growth rate estimated from N_{init} and N_{2018} (see Methods). $N_{LaQuille}$ indicates the estimated number of breeding pairs on La Quille nearby Saint-Paul.

Species	Counted unit	N_{init} (year)	Source for N_{init}	N_{2018}	λ	$N_{LaQuille}$
Northern rockhopper penguin	Chicks	2526 ^a (1993)	Guinard et al., 1998	3942 ^a	/	0
Indian yellow-nosed albatross	Breeding pairs	5 (1997)	C Barbraud pers. obs.	1	0.93	0
Sooty albatross	Breeding pairs	20 (1971)	Segonzac, 1972	20	1.00	0
Prions	Burrows	0 (1997)	Micol & Jouventin, 2002	1132 (573–1690) ^b	>1 ^h	160 ¹
Great-winged petrel	Burrows	3 (1997)	C Barbraud pers. obs.	91 (53–128) ^c	1.18	40–60 ²
Flesh-footed shearwater	Burrows	629 (1985)	Roux, 1985	2002 (1733–2271) ^d	1.04	0
Subantarctic little shearwater	Burrows	0 (1997)	C Barbraud pers. obs.	29 (27–30) ^e	>1	Few ¹
White-bellied storm petrel	Burrows	0 (1997)	C Barbraud pers. obs.	8 (4–11)	>1	Few ¹
Brown skua	Breeding pairs	0 (1997)	C Barbraud pers. obs.	8 ^f	>1	0
Antarctic tern	Breeding pairs	0 (1997)	C Barbraud pers. obs.	531 (355–683) ^g	>1	200 ³
Sooty tern	Breeding pairs	0 (1997)	C Barbraud pers. obs.	2	>1	1 ¹
Australasian gannet	Breeding pairs	2 (1993)	Lequette et al., 1995	2	1.00	0

^a Estimates are numbers of chicks counted before fledging. N_{init} was estimated from Guinard et al. (1998) based on a breeding success of 28% and a number of breeding pairs of 9023.

^b Estimated from a total number of burrows of prions with signs of occupation obtained from adaptive cluster sampling (i.e. 21) and stratified random sampling (i.e. 1112).

^c Estimated from a total number of burrows with signs of occupation obtained from adaptive cluster sampling and assuming burrows of medium-size petrels belonged to great-winged petrels.

^d Estimated from a total number of burrows with signs of occupation obtained from adaptive cluster sampling (i.e. 74) and entire sampling (i.e. 1928). Note that the N_{init} estimate does not account for burrow detection probability. λ estimated using the observed number of burrows in 2018 (1484, i.e. without correction for detection probability) was 1.03.

^e Estimated from a total number of burrows with signs of occupation obtained from adaptive cluster sampling and random sampling.

^f Includes all territorial pairs (breeding and nonbreeding).

^g Estimated from the extrapolated numbers obtained from the coastal transects (i.e. 526) and numbers estimated in the caldera (i.e. 5).

^h Indicates positive growth rate that could not be explicitly calculated since $N_{init} = 0$.

¹ Tollu (1984).

² Micol and Jouventin (2002).

³ Segonzac (1972).

population change (λ) for each species for which populations were different from zero at the time of eradication. λ was not estimated for northern rockhopper penguins since only chicks counts were available in 2018. We used the most recent population estimate (N_{init}) before or at the time of the eradication program and our population estimate obtained from the 2018 survey (N_{2018}). Then, λ was calculated as $\left(\frac{N_{2018}}{N_{init}}\right)^{(1/T)}$, T being the number of years separating the two estimates. $\lambda < 1$ represents a population decline, $\lambda > 1$ a population increase, and $\lambda = 1$ a stable population. Survey methods pre- and post-eradication were similar which makes us confident in the validity of the comparisons pre- and post-eradication (see Supplementary material).

3. Results

A total of 13 seabird species were found breeding on Saint-Paul Island compared to six before the eradication program (Table 2; Figs. 2 and 3). Among the seven species that colonized the island, five (MacGillivray's prion, fairy prion, white-bellied storm petrel, Antarctic tern, sooty tern) were previously breeding on La Quille, and one (the brown skua) is a new breeding species for Saint Paul. We also found breeding subantarctic little shearwater *Puffinus elegans* on Saint-Paul Island. Two additional species were observed on the island as non-breeding, black-bellied storm petrel *Fregetta tropica* and red-tailed tropicbird *Phaethon rubricauda*. For species that were breeding on the island before the eradication program, the annual population growth rate varied between 0.93 and 1.18 and the mean λ was 1.030 ± 0.093 (SE).

3.1. Adaptive cluster sampling

In April 2012, a total of 30 burrows were detected on the costal transect, none within the caldera, and only two burrows were detected on the land transects. Out of 154 primary plots on the coastal transect,

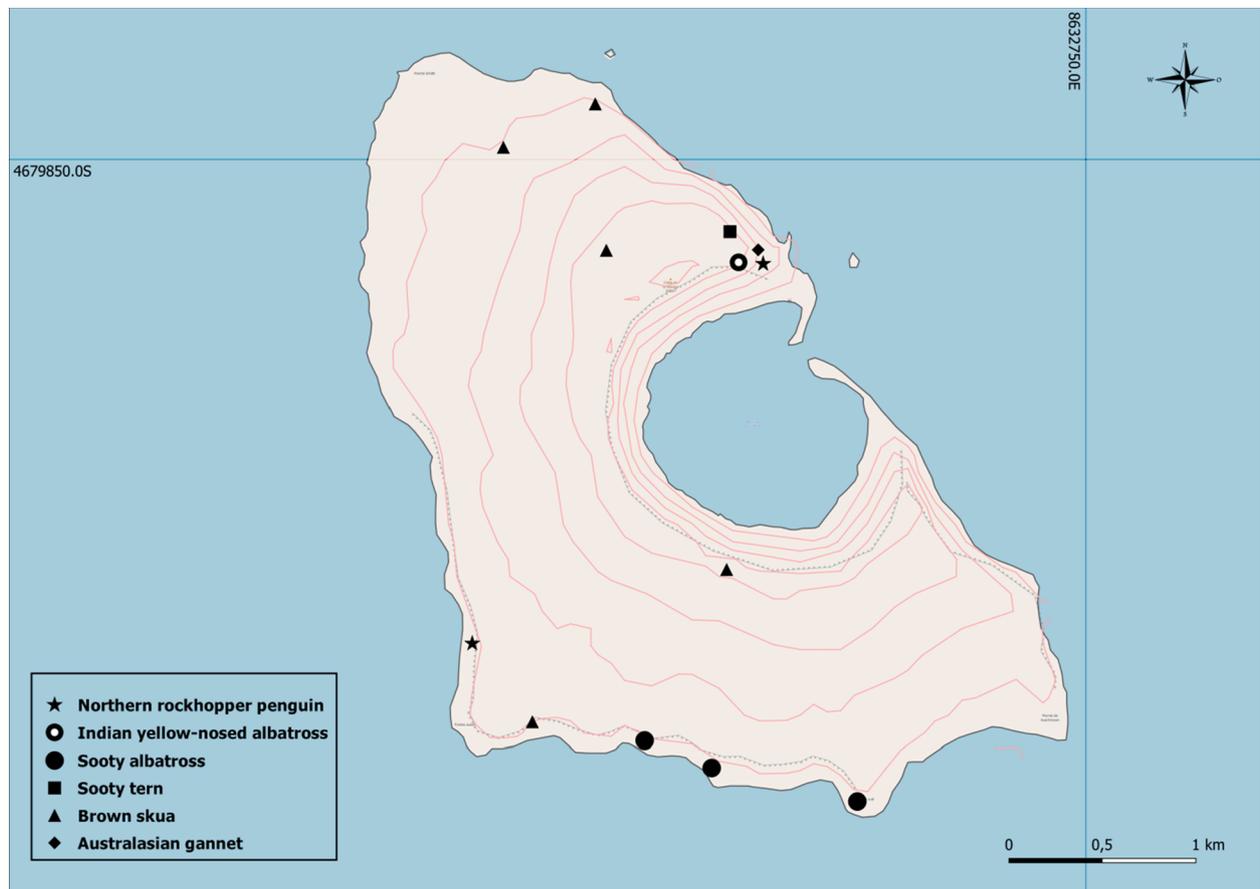


Fig. 2. Map showing the localization of breeding penguins, albatrosses, terns, skuas, and gannets on Saint Paul Island in 2018.

nine had at least one burrow with signs of occupation. The number of secondary, tertiary and quaternary plots with at least one burrow showing signs of occupation was five, one and one, respectively. The average number of burrows per plot (all plots confounded) was 1.9 ± 0.8 (SD).

In December 2018, a total of 48 burrows were detected on the coastal transect, including seven within the caldera. Out of 154 primary plots on the coastal transect, 11 had at least one burrow with signs of occupation. The number of secondary and tertiary plots with at least one burrow showing signs of occupation was eight and one, respectively. The average number of burrows per plot was 1.5 ± 0.8 . Among these 48 burrows, five (10.4%) were assigned to prions, one (2.1%) to subantarctic little shearwaters, 22 (45.8%) to medium sized petrels (i.e. such as great-winged petrels), 18 (37.5%) to flesh-footed shearwaters, and two (4.2%) to storm petrels.

Estimates of abundance from coastal transects were 126 ± 37 (SD) burrows (95% confidence interval estimated assuming a normal distribution: 52–200) and 198 ± 41 burrows (95% CI: 116–280) in 2012 and 2018, respectively. Assuming burrow assignment was correct and representative, and given the species-specific proportions above, there were 21 burrows of prions, four burrows of subantarctic little shearwaters, 91 burrows of medium size petrels, 74 burrows of flesh-footed shearwaters, and eight burrows of storm petrels in 2018.

3.2. Stratified random sampling

We found a total of 49 burrows of MacGillivray's or fairy prion in random sampling points. Mean densities of burrows of prions were 0.230 ± 0.025 (SD) burrow.m⁻² and 0.424 ± 0.177 burrow.m⁻² in colony 1 and colony 2, respectively (surface area of colonies: 1432 m² and 2079 m², respectively). Mean densities of burrows that showed signs

of occupations or were occupied were 0.177 ± 0.035 burrow.m⁻² and 0.413 ± 0.112 burrow.m⁻² in colony 1 and colony 2, respectively. This yielded a total number of prion (both MacGillivray's and fairy) burrows of 1212 (95% CI estimated assuming a normal distribution: 746–1678) and a total number of burrows with signs of occupation of 1112 (95% CI: 554–1669; 253 for colony 1 and 858 for colony 2). The proportion of burrows that showed signs of occupations or were occupied was 91.7%.

One burrow of subantarctic little shearwater was found in the two random sampling points in one colony (colony 1), corresponding to a density of 0.018 burrows per m² and a number of burrows of 25.

3.3. Mist-netting

Four species were captured in mist-nets: MacGillivray's prion, fairy prion, white-bellied storm petrel and black-bellied storm petrel (see Table S2 for measurements in [Supplementary material](#)). Very few capture-mark-recapture data were available for storm petrels so we only used capture-mark-recapture models for estimating population sizes of prions. The proportions of prion species caught in mist-nets were 77.2% for MacGillivray's prion and 22.8% for fairy prion.

For MacGillivray's prions, model selection criteria in program CAPTURE selected model Mtb as the best model. This model assumes a behavioral response to capture and temporal variation in both initial capture and recapture probabilities. The model estimated a total of 737 individuals in colony 2, albeit with high uncertainty (95% CI estimated from CAPTURE: 64–7651). Closure test suggested that the closure assumption was not fulfilled (closure test: $\chi^2 = 28.2$, $df = 11$, $P = 0.003$). However, this lack of fit was mainly due to one capture occasion during which a high number of new individuals were captured. The closure assumption was fulfilled when excluding this capture occasion ($\chi^2 = 17.1$, $df = 10$, $P = 0.072$).

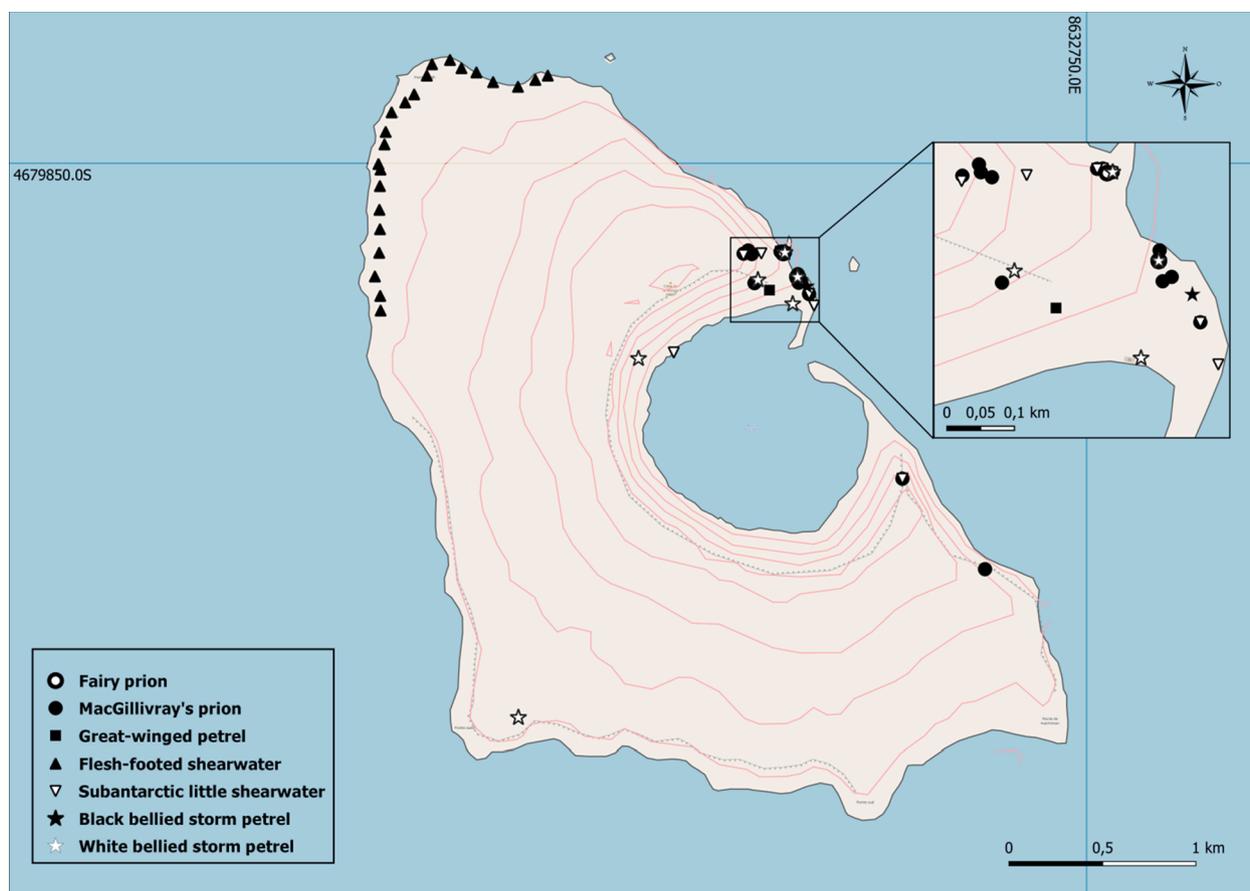


Fig. 3. Map showing the localization of breeding burrowing petrels, shearwaters and storm petrels on Saint Paul Island in 2018.

For fairy prions, model selection criteria selected model Mo and model Mh as the best models. These models assume constant capture probabilities and heterogeneity in capture probabilities, respectively. Model Mo and Mh estimated a total of 84 (95% CI: 36–280) and 91 (95% CI: 36–331) individuals in colony 2, respectively. Closure test suggested that the closure assumption was fulfilled (closure test: $\chi^2 = 3.6$, $df = 5$, $P = 0.61$).

3.4. Entire sampling

In 2018, for flesh-footed shearwaters a total of 1003 and 481 burrows were counted in rush and denuded habitats in the coastal colony, respectively. Burrow detection probability differed between rush and denuded habitats and was 0.640 ± 0.065 (SD) and 0.905 ± 0.047 , respectively. Thus, the total number of burrows was 2098 (95% CI assuming a normal distribution: 1782–2415). The proportion of burrows with signs of occupation was 0.919 ± 0.024 . Therefore, the total number of burrows with signs of occupation in the colony was 1928 (95% CI: 1659–2197).

Northern rockhopper penguins were breeding in two colonies (Fig. 2, $38^\circ 43' 52.30''S - 77^\circ 30' 40.45''E$ and $38^\circ 42' 44.51''S - 77^\circ 31' 44.48''E$), one in the caldera and one south of the Terrasse des Pingouins with 3942 and 260 chicks, respectively.

One breeding pair of Indian yellow-nosed albatross with an egg (5th December) was later seen with a chick on the 20th of December.

A total of 20 nests occupied by an adult sooty albatross were counted in the cliffs of the south coast.

Brown skuas were breeding on the western and southern slopes of the island with five breeding pairs with chicks and an additional three territorial pairs but without chicks.

Four sooty terns with territorial behaviors were observed in coastal

cliffs facing La Quille, but breeding status could not be confirmed since sites were inaccessible.

The average number of breeding pairs of Antarctic tern counted between plots of the adaptive cluster sampling outside the caldera was 4.215 ± 0.687 (SD) pairs per 100 m. When extrapolated to the entire coastal cliffs length, this yielded 526 pairs (95% CI assuming a normal distribution: 350–678). Very few (5) breeding pairs were counted within the caldera.

Two pairs of Australasian gannet were breeding on slopes facing La Quille, and three additional non breeding individuals were observed.

3.5. Incidental observations

During incidental observations and surveys, 11 seabird species were recorded pre-eradication and 20 post-eradication (Table 3). Six breeding seabird species were recorded pre-eradication in Saint-Paul Island and 11 (14 if adding species that were likely breeding) post-eradication (Table 3). New species recorded as breeding or likely breeding post-eradication on Saint-Paul were MacGillivray's prion, fairy prion, subantarctic little shearwater, white-bellied storm petrel and sooty tern. Three new species were recorded as nonbreeding during post-eradication: black-winged petrel, soft-plumaged petrel and red-tailed tropicbird.

4. Discussion

Our results clearly show that 20 years after the eradication of invasive mammals on Saint-Paul seabird populations were high beneficiaries. Most seabird populations grew following eradication, and all predictions were generally confirmed. First, all seabird populations had positive growth rates, except for Indian yellow-nosed albatrosses, sooty

Table 3

Seabird species observed on land at Saint-Paul Island (excluding La Quille) during surveys or as incidental observations. B: confirmed breeder, i.e. seen with an egg or a chick; NB: nonbreeder; B*: probable breeder, i.e. seen in a burrow but without an egg or chick or defending a territory.

Common name	Scientific name	Presence pre-eradication	Breeding status	Presence post-eradication	Breeding status
Northern rockhopper penguin	<i>Eudyptes moseleyi</i>	x	B	x	B
Amsterdam albatross	<i>Diomedea amsterdamensis</i>	x	NB	x	NB
Indian yellow-nosed albatross	<i>Thalassarche carteri</i>	x	B	x	B
Sooty albatross	<i>Phoebastria fusca</i>	x	B	x	B
Northern giant petrel	<i>Macronectes halli</i>	x	NB	x	NB
Grey petrel	<i>Procellaria cinerea</i>	x	Unknown	x	B*
Great winged petrel	<i>Pterodroma macroptera</i>	x	B	x	B
Black-winged petrel	<i>Pterodroma nigripennis</i>			x	NB
Soft-plumaged petrel	<i>Pterodroma mollis</i>			x	NB
MacGillivray's prion	<i>Pachyptila macgillivrayi</i>			x	B
Fairy prion	<i>Pachyptila turtur</i>			x	B
Flesh-footed shearwater	<i>Puffinus carneipes</i>	x	B	x	B
Subantarctic little shearwater	<i>Puffinus elegans</i>			x	B
White-bellied storm petrel	<i>Fregatta grallaria</i>			x	B*
Black-bellied storm petrel	<i>Fregatta tropica</i>			x	Unknown
Australasian gannet	<i>Morus serrator</i>	x	B	x	B
Brown skua	<i>Catharacta antarctica</i>	x	NB	x	B
Sooty tern	<i>Sterna fuscata</i>			x	B*
Antarctic tern	<i>Sterna vittata</i>	x	NB	x	B
Red-tailed tropicbird	<i>Phaeton rubricauda</i>			x	NB

Sources: Segonzac (1972); Tollu (1984); Roux (1985); Guinard et al. (1998); Micol and Jouventin (2003) and Thiebot et al. (2010).

albatrosses and Australasian gannets. Although these three species breed in low numbers, this suggests that invasive mammals had no or little negative impact of these species, or that potential population growth was counteracted by other environmental factors. At Amsterdam Island, these two albatross species have been declining in the last decades (Weimerskirch et al., 2018), and declines have mainly been attributed to the impact of diseases (Jaeger et al., 2018, 2020; Rolland et al., 2009). The stability of the sooty albatross population at Saint-Paul over the past 50 years (Segonzac, 1972) may suggest that diseases observed at Amsterdam are not having harmful effects on this species at Saint-Paul. Alternative hypotheses to explain stability in albatrosses and gannets on Saint-Paul could be predation by mice, which are still present on the island, bycatch in longline fisheries and climate (Rolland et al., 2010). Although we did not find any evidence for predation by mice on chicks or adults at Saint-Paul, such predation is known to occur at other localities (Cuthbert & Hilton, 2004; Dillely et al., 2015).

Second, as predicted, we found $\lambda > 1$ for species known to be vulnerable to rat predation (i.e. MacGillivray's prion, fairy prion, great-winged petrel, flesh-footed shearwater, subantarctic little shearwater, white-bellied storm petrel and Antarctic tern). All these species, except great-winged petrels and flesh-footed shearwaters, were only breeding on La Quille prior to the eradication of rats. Earlier seabird surveys identified little shearwater *Puffinus assimilis* as a breeding species on La Quille (but not on Saint Paul; Tollu, 1984). The little shearwater is sometimes considered as conspecific with the subantarctic little shearwater. However, based on dark face and relatively large dark collar of captured birds, they were considered as belonging to *P. elegans* (Onley & Scofield, 2007). Therefore, it is highly likely that birds identified as *P. assimilis* breeding on La Quille belong to *P. elegans* (Brooke, 2004). Species less vulnerable to rat predation, such as albatrosses, had lower population growth rates. Although there were too few counts to estimate pre- and post-eradication λ (Fischer et al., 2020), colonization of Saint-Paul by species that were previously only breeding on La Quille and positive post-eradication λ , clearly indicated that these species highly benefited from rat eradication.

Our third prediction was almost confirmed. Antarctic tern had the second largest increase in breeding population, behind MacGillivray's prion, but all other species had lower population growth. Sooty tern population remained small, but the Saint-Paul breeding population is situated at the limit of the distributional range of the species, as for the Australasian gannet (del Hoyo et al., 1996, 1992; Lequette et al., 1995). This high growth rate for Antarctic terns may result from relatively

lower philopatry than for Procellariiformes (Brooke et al., 2018). However, we think this is unlikely since source populations were situated close to Saint-Paul Island (La Quille) for both MacGillivray's prions and Antarctic terns. A more likely explanation is the higher fecundity and shorter generation time for terns that lay two eggs, whereas Procellariiformes lay a single egg. Nevertheless, this does not explain why MacGillivray's prions had a higher growth rate than Antarctic terns. Environmental factors may partly explain these differences contrary to expectation. During our 2018 survey we observed several (10s) remains of Antarctic terns showing signs of predation by brown skuas, but none was observed for MacGillivray's prions. If predation levels are sufficiently high this could limit population growth (Jiguet et al., 2007). Finally, we note that our extrapolation of Antarctic tern densities to the entire coastal cliffs may be biased since cliffs situated on the northeast coast of the island have a different structure than elsewhere (higher elevation, less steep).

The fourth prediction was confirmed, with a higher λ for all species having a relatively large source population nearby (Antarctic tern, MacGillivray's prion, great-winged petrel). Brooke et al. (2018) found some evidence that distance to and size of a source population resulted in a higher λ after recolonization. Our results are coherent with this finding, since for these three species source populations were larger than for the other species and were situated only 150 m from Saint-Paul. Source populations for some other species (albatrosses, brown skua) are situated on Amsterdam Island, 90 km north of Saint-Paul, or even much further in south west Australia (flesh-footed shearwater). This highlights the importance of maintaining predator free islets for the conservation of seabird species, which can constitute unique population sources following eradication of invasive mammals on larger islands nearby.

As predicted, we found one new breeding species for Saint-Paul that was not breeding on nearby islets, the brown skua, indicating immigration probably from Amsterdam island where ≈ 60 pairs breed (Gamble et al., 2020). Brown skuas were breeding on Saint-Paul until the late 19th century but disappeared thereafter probably following the local extinction of prion and petrel populations as well as of Amsterdam fur seals, which constituted their main prey (Péron, 1824; Vélain, 1877). Incidental observations during our 2018 survey suggest that brown skuas mainly feed on northern rockhopper penguin eggs/chicks, placenta of Amsterdam fur seals and Antarctic terns. Brown skuas have been increasing at Amsterdam from a few breeding pairs in 1970 (Segonzac, 1972) to 63 in 2018 (unpublished data). This species was

persecuted on Amsterdam until the early 1970s (Segonzac, 1972), and it is likely that the observed recent population growth reflects a recovery from past persecution. The population growth may also be partly due to the increase of the Amsterdam fur seal population (Guinet et al., 1994; Pacoureau et al., 2017). The population appears to have stabilized to around 60 breeding pairs since the early 2010s. The recolonization of Saint-Paul by breeding skuas following the eradication of invasive mammals, may indicate that rats had negative effects on skuas through predation on chicks, but also that the increase of food resources (Antarctic terns) due to rat eradication may have directly benefited breeding skuas. Skuas may have also benefited from the increase of the Amsterdam fur seal population, although fur seals were in comparable numbers in the late 1990s as in the late 2010s (\approx 360 breeding females, Guinet et al., 1994). We believe that the hypothesis of predation by rats is the more likely as the population of rabbits was quite high before their eradication and would have fulfilled needs for breeding skuas. Skuas breeding on Saint-Paul probably came from Amsterdam, as a group of 15 nonbreeding individuals was regularly observed on Saint-Paul, including two individuals marked at Amsterdam.

Five species previously breeding on La Quille before eradication were newly recorded breeding on Saint-Paul following eradication. These species thus now breed on the two sites, which lower their local extinction risk. Since surveys pre-eradication were similar to those performed post-eradication were are confident that the species newly found breeding on Saint-Paul represent true colonization of the island rather than species that were missed during pre-eradication surveys. This is particularly the case for conspicuous species such as the brown skua and terns, as well as for species performing intense and strong vocalizations during breeding such as prions and shearwaters.

Compared to Amsterdam Island, some breeding species on Saint-Paul showed opposite population trends. Northern rockhopper penguin and sooty albatross showed major declines on Amsterdam (Barbraud et al., 2020; Weimerskirch et al., 2018) whereas their populations appeared to have increased or remained stable at Saint-Paul (Guinard et al., 1998; this study). Diseases are suspected to be the main cause of population declines at Amsterdam (Jaeger et al., 2018). Therefore, our results suggest that these species are poorly impacted by diseases at Saint-Paul.

The most important population increases following eradication were for prions and flesh-footed shearwaters. This was particularly clear for prions which were not breeding on Saint-Paul prior to rat eradication due to rat predation. Although our population estimates are imprecise, we are quite confident in their accuracy since two independent monitoring methods gave relatively similar results for MacGillivray's prion in colony 2. The CAPTURE estimate indicated around 740 individuals and the adaptive sampling indicated 858 burrows with signs of occupation. At the time the survey was performed MacGillivray's prions were laying their egg. Thus it likely that we captured individuals that were leaving the colony for a foraging trip at sea while their partner stayed in the burrow to incubate the egg (Warham, 1990). Consequently, our CAPTURE estimate is likely a good proxy of the number of breeding pairs. Flesh-footed shearwaters also appear to have benefited from invasive mammal eradication (Lavers, 2014). Earlier surveys suggested that the flesh-footed population was stable between its discovery in 1970 and 1984 (Roux, 1985). Rats were probably preying on eggs and chicks in burrows and it is also possible that rabbits competed for burrows prior to their eradication.

The breeding status of white-bellied storm petrel could not be confirmed, as we observed two burrows with both pair members but without an egg. White-bellied storm petrels lay their egg in January (Marchant & Higgins, 1990), so it is likely that observed birds were occupying their burrow before laying. The black-bellied storm petrel captured in mist-net had an incubation pouch, so it might also be visiting the island just before laying (Marchant & Higgins, 1990). This species was also captured in late December 2017 on Saint-Paul during a brief visit to the island (H. Weimerskirch, pers. comm.).

In conclusion, monitoring of seabirds 20 years after invasive

mammal eradication (rats and rabbits) showed population growth of populations on a remote oceanic island of the Indian Ocean. These findings further highlight the importance of invasive mammal eradication on islands as a conservation tool, despite the fact that our study did not include the effects of the eradication on invertebrates and vegetation. Although mice were not targeted and so not eradicated from Saint-Paul, our results suggest that their impact on seabird populations remained limited until now, although we cannot exclude they had a negative effect on population growth rates through an impact on breeding success. Nevertheless, given the reported negative impact of mice on seabirds elsewhere (Cuthbert & Hilton, 2004; Dilley et al., 2015), we encourage eradication of mice on Saint-Paul as a conservation action to ensure the future of seabird populations on this island. Despite increases, seabird populations on Saint-Paul are still relatively small, and therefore vulnerable to additional impacts or re-introduction of rats. Seabird population recovery on Saint-Paul further reinforces the importance of eradicating invasive mammals (Norway rat *R. norvegicus*, domestic cat *Felis catus*, house mouse) from Amsterdam Island, which is part of the 'top 10' islands ranked in terms of conservation benefit to threatened birds arising from the eradication of alien vertebrates (Brooke et al., 2007; Holmes et al., 2019; Spatz et al., 2017). Results from Saint-Paul indicate that endangered species such as albatrosses and penguins will eventually benefit from eradication of invasive mammals, but this will mainly benefit Antarctic terns and small burrowing petrels including the endangered MacGillivray's prion.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jnc.2021.126049>.

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