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1 **Seabird population changes following mammal eradication at oceanic**

2 **Saint-Paul Island, Indian Ocean**

3

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5 Christophe Barbraud^a, Karine Delord^a, Fabrice Le Bouard^b, Roald Harivel^b,

6 Jérémie Demay^{a,c}, Adrien Chaigne^b, Thierry Micol^{b,d}

7

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

9 ^b *Réserve Naturelle Nationale des Terres Australes Françaises, TAAF, rue Gabriel Dejean,*
10 *97458 Saint-Pierre, France*

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

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

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18 Seabird population change after rat eradication

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20 Corresponding author :

21 Christophe Barbraud, barbraud@cebc.cnrs.fr

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25

26 **Abstract**

27 The eradication of invasive mammals on islands is important for protecting seabird
28 populations and insular ecosystems. However, the impacts of such eradications are
29 insufficiently known because monitoring of potentially beneficiary species is often sporadic
30 and limited. We performed a survey of all seabird species on Saint-Paul Island, southern
31 Indian Ocean, 20 years after successful eradication of invasive black rat (*Rattus rattus*) and
32 European rabbit (*Oryctolagus cuniculus*). Using complementary sampling designs including
33 adaptive cluster sampling, stratified random sampling and entire sampling, we estimated
34 population changes and colonization by new seabird species. A total of 13 seabird species
35 were found breeding on Saint-Paul post-eradication compared to six before the eradication.
36 Among the seven species that colonized the island, five (MacGillivray's prion *Pachyptila*
37 *macgillivrayi*, fairy prion *P. turtur*, white-bellied storm petrel *Fregetta grallaria*, Antarctic
38 tern *Sterna vittata*, sooty tern *Onychoprion fuscatus*) had relictual populations breeding on a
39 nearby islet, and one (brown skua *Stercorarius lonnbergi*) was a new breeding species. We
40 also found breeding subantarctic little shearwaters *Puffinus elegans*. For species that were
41 breeding on the Saint Paul pre-eradication, the mean annual population growth rate was 1.030
42 ± 0.093 (SE). Species known to be vulnerable to rat predation (prions, great-winged petrel
43 *Pterodroma macroptera*, flesh-footed shearwater *Puffinus carneipes*, subantarctic little
44 shearwater, white-bellied storm petrel, Antarctic tern) had the highest population growth
45 rates. Two decades after the eradication of invasive mammals on a remote oceanic island,
46 seabird populations were high beneficiaries. These findings further highlight the importance
47 of invasive mammal eradication on islands as a conservation tool. Results are encouraging for
48 the planned eradication of invasive mammals from nearby Amsterdam Island, and suggest this
49 will mainly benefit terns and small burrowing petrels.

50

51 **Keywords**

52 Rats; island restoration; petrels; population growth rate; shearwaters; terns

53

54 **1. Introduction**

55 Insular ecosystems, those that are small and naturally fragmented, warrant a high priority
56 in biodiversity conservation as they host more than 15% of terrestrial species, and 61% of all
57 recently extinct species and 37% of all critically endangered species are endemic to
58 islands(Kier et al., 2009; Tershy et al., 2015). High levels of endemism richness and high
59 extinction rates have motivated increasing conservation efforts on islands, such as the
60 eradication of invasive mammals which was successfully undertaken on >850 islands
61 worldwide (DIISE, 2018). Indeed, invasive nonnative mammals are the main cause of animal
62 extinction on islands and one of the most important threats to insular biodiversity (Clavero &
63 García-Berthou, 2005; Szabo et al., 2012). However, the impacts of eradication of invasive
64 mammals on islands are insufficiently known because monitoring of eradication outcomes,
65 such as recolonization or population growth of potentially beneficiary species, is often
66 sporadic and limited (Lavers, Wilcox, & Donlan, 2010; Jones et al., 2016; Towns, 2018).
67 These deficiencies with outcome monitoring are particularly acute for seabirds (Brooke et al.,
68 2018). For example, in their review Brooke et al. (2018) were able to estimate seabird
69 population growth rate post-eradication for only 61 islands. This is partly due to several
70 factors (Towns, 2018). First, due to the slow life-histories and long generation time of
71 seabirds, there is a delay in population growth following eradication of invasive mammals.
72 Monitoring for at least 10 years, and preferably longer, after eradication is needed to identify
73 population changes for seabirds due to their long generation time, slow life-histories, and low
74 immigration rates (Brooke et al., 2018). Such long timescales are often beyond the remit of
75 funding agencies and are incompatible with projects funded from short-term calls. Second,

76 there are also logistical challenges (and associated costs) of reaching remote locations for
77 undertaking surveys, and repeatable monitoring designs allowing to quantify population
78 growth are not undertaken systematically. Third, assumptions are often made that positive
79 outcomes at one locality will repeat on those nearby, even when communities differ. Other
80 impediments to reporting eradication outcomes are unmeasurable claims of potential response
81 by target species, and the unavailability of economical ways to measure the speed and scale of
82 changes at the ecosystem level.

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

89 Black rats (*Rattus rattus*) and European rabbits (*Oryctolagus cuniculus*), but not house
90 mouse (*Mus musculus*), were successfully eradicated from Saint-Paul Island, Indian Ocean, in
91 the late 1990's (from 1997 to 1999; Micol & Jouventin, 2002). Absence of sightings or rat
92 signs since then confirmed that the island is still rat free, and a maintenance program of bait
93 stations disposed near landings points ensured that it remains rat free. Rats and mice were
94 introduced between 1792 and 1874, and rabbits probably during the early 19th century
95 (Segonzac, 1972). Despite encouraging recolonization signs by seabirds early after
96 eradication (Micol & Jouventin, 2002), no systematic survey has been undertaken since
97 eradication of rats and rabbits was confirmed. However, Saint-Paul was predicted as a site
98 with highly threatened beneficiary species from invasive mammal eradication (Jones et al.,
99 2016), with three potentially beneficiary endangered seabird species (northern rockhopper

100 penguin *Eudyptes moseleyi*, sooty albatross *Phoebetria fusca* and Indian yellow-nosed
101 albatross *Thalassarche carteri*).

102 The aim of our study was therefore to perform a comprehensive survey of all seabird
103 species on Saint-Paul nearly 20 years after successful invasive rat and rabbit eradication, and
104 to estimate population changes and colonization by new seabird species. Based on results
105 obtained by Jones et al. (2016), who found that invasive mammal eradication benefited
106 terrestrial insular fauna on 181 islands, and by Brooke et al. (2018), who examined what
107 factors influence rates of population recovery for 181 seabird populations of 69 species
108 following successful eradication projects, we made the following predictions. First, we
109 expected positive population growth for seabird species that were reported to breed on Saint-
110 Paul and a nearby islet and were known to be vulnerable to rats. Second, we predicted
111 positive growth for seabird species that were not able to breed due to predation. For Saint-
112 Paul this concerned small to medium size burrowing petrels such as MacGillivray's prion,
113 fairy prion *P. turtur*, great-winged petrel *Pterodroma macroptera*, flesh-footed shearwater
114 *Puffinus carneipes*, little shearwater *P. assimilis*, and white-bellied storm petrel *Fregatta*
115 *grallaria*, as well as the surface nesting Antarctic tern *Sterna vittata*, all known to breed on
116 Saint-Paul and on an islet situated nearby (Tollu, 1984). Third, we expected faster growth
117 rates for terns, as identified by Brooke et al., (2018) in a comparative study. Fourth, we
118 predicted faster population growth if large source populations were nearby. La Quille is a
119 mammal free predator islet situated 150 meters offshore Saint-Paul. Until the eradication of
120 invasive mammals on Saint-Paul it constituted the only refuge for breeding seabirds that
121 formerly bred on Saint-Paul (Tollu, 1984). Before eradication the most abundant species
122 breeding on La Quille were Antarctic terns (\approx 200 breeding pairs, Segonzac, 1972),
123 MacGillivray's prion (\approx 150 breeding pairs, Tollu, 1984) and great-winged petrels (\approx 40-60
124 breeding pairs, Micol & Jouventin, 2002). Four other species were breeding on La Quille but

125 in very low numbers (Tollu, 1984). We thus predicted higher population growth rates for the
126 three most abundant species on La Quille (Antarctic terns, MacGillivray's prion and great-
127 winged petrels). Finally, Brooke et al. (2018) identified immigration as an important factor for
128 colony growth. Because new species were previously observed as nonbreeding at Saint-Paul
129 following eradication (Thiebot et al., 2010), thus constituting potential immigrants, and given
130 that new species have been recorded as breeding on islands following rodent eradication
131 (Croll et al., 2016), we expected new breeding species for Saint-Paul.

132

133 **2. Methods**

134 *2.1. Study site*

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

145 Before the eradication, rats, mice and rabbits were the only remaining exotic mammals on
146 Saint-Paul Island as cats, pigs and goats had disappeared decades ago. To evaluate the impact
147 of the rat eradication on Saint-Paul seabird populations we conducted a variety of surveys in
148 March/April 2005, 2006, 2012 and 2013 to coincide with breeding activities of winter
149 breeding seabirds, and in December 2018 to coincide with breeding activities of summer

150 breeding seabirds. Different survey types combining various sampling designs and
151 enumeration methods were utilized to provide an abundance estimate of seabirds that occur on
152 the island and to detect presence of rare species. Survey types were selected according to
153 species-specific breeding habits, densities and site accessibility to fieldworkers, but the same
154 methods were used in different years for consistency. Table 1 describes the sampling designs
155 and enumeration methods used for each species. Burrows were assigned to species or groups
156 of species according to identification of individuals captured in burrows and to burrow
157 dimensions indicated in Table S1 (see Supplementary material).

158

159 *2.2. Adaptive cluster sampling*

160 Because we anticipated low densities of breeding burrowing petrels on the island, and
161 since burrowing petrels often breed in clusters, we used systematic adaptive cluster sampling
162 to estimate abundance of burrowing petrels (Thompson, 1992; Thompson & Seber, 1996).
163 The systematic adaptive cluster sampling consisted of two steps. In the first step systematic
164 sampling was applied, yielding an initial set of U sampling units (primary plots). Primary
165 plots were positioned on transects with 100 m between each plot and 300 m between each
166 transect (Fig. 1). Because from breeding ecology of the species, we expected higher
167 colonization of coastal areas, a complementary coastal transect was established with 100 m
168 between each primary plot. Each sampling primary plot consisted in a 10 m radius circle. In
169 each plot, the presence of petrel burrows was determined by two experienced observers
170 searching meticulously within the plot. If no burrow was present, the next primary plot was
171 searched for. If at least one burrow was present, the second step adds neighboring circular
172 plots (secondary plots) to this primary plot (and thus to the sample). The presence of at least
173 one burrow in each one of these secondary plots was determined. If positive, further
174 neighboring plots were added (tertiary plots). Plots were added repeatedly until no additional

175 plots contained a burrow anymore. This procedure for selection in adaptive designs depends
176 upon population numbers observed in the field (see Supplementary material).

177

178 *2.3. Stratified random sampling*

179 During successive visits and qualitative searches for petrel burrows on the island, two
180 relatively small areas of high density of MacGillivray's and fairy prions were found
181 (thereafter named colony 1 and colony 2). To avoid over-sampling these areas using the
182 adaptive cluster sampling approach (which could occur when the final sample size is many
183 multiples of the initial sample size), we used stratified random sampling in high-density areas
184 for MacGillivray's and fairy prions (see Supplementary material).

185

186 *2.4. Entire sampling*

187 Previous surveys showed that flesh-footed shearwaters breed in a colony situated on the
188 northwest coastal area of Saint-Paul where nest densities are high (Segonzac, 1972; Roux,
189 1985). To avoid over-sampling this area using the adaptive cluster sampling approach, and
190 since the flesh-footed shearwater colony is settled in a well-defined narrow coastal band
191 northwest of Saint-Paul, we performed a true survey of the entire colony (i.e. the entire
192 sampling frame was covered, see Supplementary material).

193 Entire sampling was also used for conspicuous surface nesting species: northern
194 rockhopper penguin, Indian yellow-nosed albatross, sooty albatross, brown skua (*Stercorarius*
195 *lonnbergi*), sooty tern (*Onychoprion fuscatus*), Antarctic terns, and Australasian gannet
196 (*Morus serrator*). At the time of our last survey (December 2018), rockhopper penguins were
197 ending their breeding cycle and chicks were preparing for departure at sea. We thus counted
198 the number of chicks by direct counts. Indian yellow-nosed albatrosses, sooty albatrosses and
199 Australasian gannets were incubating, so we counted the number of adults occupying a nest

200 site. For brown skuas our visit corresponded to the chick rearing period, so we counted the
201 number of nests with chicks and the number of pairs defending a territory. For terns, which
202 breed in coastal cliffs (Segonzac, 1972), we counted territorial pairs when moving between
203 plots situated on the coastal transect of the adaptive cluster sampling.

204

205 *2.5. Mist-netting*

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

211

212 *2.6. Incidental observations*

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

216

217 *2.7. Estimating population growth rates*

218 Following Brooke et al. (2018) we estimated an annual rate of population change (λ) for
219 each species for which populations were different from zero at the time of eradication. λ was
220 not estimated for northern rockhopper penguins since only chicks counts were available in
221 2018. We used the most recent population estimate (N_{init}) before or at the time of the
222 eradication program and our population estimate obtained from the 2018 survey (N_{2018}). Then,
223 λ was calculated as $\left(\frac{N_{2018}}{N_{init}}\right)^{(1/T)}$, T being the number of years separating the two estimates. λ
224 < 1 represents a population decline, $\lambda > 1$ a population increase, and $\lambda = 1$ a stable population.

225 Survey methods pre- and post-eradication were similar which makes us confident in the
226 validity of the comparisons pre- and post-eradication (see Supplementary material).

227

228 **3. Results**

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

238

239 *3.1. Adaptive cluster sampling*

240 In April 2012, a total of 30 burrows were detected on the coastal transect, none within the
241 caldera, and only two burrows were detected on the land transects. Out of 154 primary plots
242 on the coastal transect, nine had at least one burrow with signs of occupation. The number of
243 secondary, tertiary and quaternary plots with at least one burrow showing signs of occupation
244 was five, one and one, respectively. The average number of burrows per plot (all plots
245 confounded) was 1.9 ± 0.8 (SD).

246 In December 2018, a total of 48 burrows were detected on the coastal transect, including
247 seven within the caldera. Out of 154 primary plots on the coastal transect, 11 had at least one
248 burrow with signs of occupation. The number of secondary and tertiary plots with at least one
249 burrow showing signs of occupation was eight and one, respectively. The average number of

250 burrows per plot was 1.5 ± 0.8 . Among these 48 burrows, five (10.4%) were assigned to
251 prions, one (2.1%) to subantarctic little shearwaters, 22 (45.8%) to medium sized petrels (i.e.
252 such as great-winged petrels), 18 (37.5%) to flesh-footed shearwaters, and two (4.2%) to
253 storm petrels.

254 Estimates of abundance from coastal transects were 126 ± 37 (SD) burrows (95%
255 confidence interval estimated assuming a normal distribution: 52-200) and 198 ± 41 burrows
256 (95% CI: 116-280) in 2012 and 2018, respectively. Assuming burrow assignment was correct
257 and representative, and given the species-specific proportions above, there were 21 burrows
258 of prions, four burrows of subantarctic little shearwaters, 91 burrows of medium size petrels,
259 74 burrows of flesh-footed shearwaters, and eight burrows of storm petrels in 2018.

260

261 3.2. Stratified random sampling

262 We found a total of 49 burrows of MacGillivray's or fairy prion in random sampling
263 points. Mean densities of burrows of prions were 0.230 ± 0.025 (SD) burrow.m⁻² and $0.424 \pm$
264 0.177 burrow.m⁻² in colony 1 and colony 2, respectively (surface area of colonies: 1432 m²
265 and 2079 m², respectively). Mean densities of burrows that showed signs of occupations or
266 were occupied were 0.177 ± 0.035 burrow.m⁻² and 0.413 ± 0.112 burrow.m⁻² in colony 1 and
267 colony 2, respectively. This yielded a total number of prion (both MacGillivray's and fairy)
268 burrows of 1212 (95% CI estimated assuming a normal distribution: 746-1678) and a total
269 number of burrows with signs of occupation of 1112 (95% CI: 554-1669; 253 for colony 1
270 and 858 for colony 2). The proportion of burrows that showed signs of occupations or were
271 occupied was 91.7%.

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

275

276 *3.3. Mist-netting*

277 Four species were captured in mist-nets: MacGillivray's prion, fairy prion, white-bellied
278 storm petrel and black-bellied storm petrel (see Table S2 for measurements in Supplementary
279 material). Very few capture-mark-recapture data were available for storm petrels so we only
280 used capture-mark-recapture models for estimating population sizes of prions. The
281 proportions of prion species caught in mist-nets were 77.2% for MacGillivray's prion and
282 22.8% for fairy prion.

283 For MacGillivray's prions, model selection criteria in program CAPTURE selected model
284 Mtb as the best model. This model assumes a behavioral response to capture and temporal
285 variation in both initial capture and recapture probabilities. The model estimated a total of 737
286 individuals in colony 2, albeit with high uncertainty (95% CI estimated from CAPTURE: 64-
287 7651). Closure test suggested that the closure assumption was not fulfilled (closure test: $\chi^2 =$
288 28.2, $df = 11$, $P = 0.003$). However, this lack of fit was mainly due to one capture occasion
289 during which a high number of new individuals were captured. The closure assumption was
290 fulfilled when excluding this capture occasion ($\chi^2 = 17.1$, $df = 10$, $P = 0.072$).

291 For fairy prions, model selection criteria selected model Mo and model Mh as the best
292 models. These models assume constant capture probabilities and heterogeneity in capture
293 probabilities, respectively. Model Mo and Mh estimated a total of 84 (95% CI: 36-280) and
294 91 (95% CI: 36-331) individuals in colony 2, respectively. Closure test suggested that the
295 closure assumption was fulfilled (closure test: $\chi^2 = 3.6$, $df = 5$, $P = 0.61$).

296

297 *3.4. Entire sampling*

298 In 2018, for flesh-footed shearwaters a total of 1003 and 481 burrows were counted in rush
299 and denuded habitats in the coastal colony, respectively. Burrow detection probability differed

300 between rush and denuded habitats and was 0.640 ± 0.065 (SD) and 0.905 ± 0.047 ,
301 respectively. Thus, the total number of burrows was 2098 (95% CI assuming a normal
302 distribution: 1782-2415). The proportion of burrows with signs of occupation was $0.919 \pm$
303 0.024 . Therefore, the total number of burrows with signs of occupation in the colony was
304 1928 (95% CI: 1659-2197).

305 Northern rockhopper penguins were breeding in two colonies (Fig. 2, $38^{\circ}43'52.30''\text{S}$ –
306 $77^{\circ}30'40.45''\text{E}$ and $38^{\circ}42'44.51''\text{S}$ – $77^{\circ}31'44.48''\text{E}$), one in the caldera and one south of the
307 Terrasse des Pingouins with 3942 and 260 chicks, respectively.

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

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

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

314 Four sooty terns with territorial behaviors were observed in coastal cliffs facing La Quille,
315 but breeding status could not be confirmed since sites were inaccessible.

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

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

322

323 *3.5. Incidental observations*

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

331

332 **4. Discussion**

333 Our results clearly show that 20 years after the eradication of invasive mammals on Saint-
334 Paul seabird populations were high beneficiaries. Most seabird populations grew following
335 eradication, and all predictions were generally confirmed. First, all seabird populations had
336 positive growth rates, except for Indian yellow-nosed albatrosses, sooty albatrosses and
337 Australasian gannets. Although these three species breed in low numbers, this suggests that
338 invasive mammals had no or little negative impact of these species, or that potential
339 population growth was counteracted by other environmental factors. At Amsterdam Island,
340 these two albatross species have been declining in the last decades (Weimerskirch et al.,
341 2018), and declines have mainly been attributed to the impact of diseases (Rolland, Barbraud,
342 & Weimerskirch, 2009; Jaeger et al., 2018, 2020). The stability of the sooty albatross
343 population at Saint-Paul over the past 50 years (Segonzac, 1972) may suggest that diseases
344 observed at Amsterdam are not having harmful effects on this species at Saint-Paul.
345 Alternative hypotheses to explain stability in albatrosses and gannets on Saint-Paul could be
346 predation by mice, which are still present on the island, bycatch in longline fisheries and
347 climate (Rolland et al., 2010). Although we did not find any evidence for predation by mice

348 on chicks or adults at Saint-Paul, such predation is known to occur at other localities
349 (Cuthbert & Hilton, 2004; Dilley et al., 2015).

350 Second, as predicted, we found $\lambda > 1$ for species known to be vulnerable to rat predation
351 (i.e. MacGillivray's prion, fairy prion, great-winged petrel, flesh-footed shearwater,
352 subantarctic little shearwater, white-bellied storm petrel and Antarctic tern). All these species,
353 except great-winged petrels and flesh-footed shearwaters, were only breeding on La Quille
354 prior to the eradication of rats. Earlier seabird surveys identified little shearwater *Puffinus*
355 *assimilis* as a breeding species on La Quille (but not on Saint Paul; Tollu, 1984). The little
356 shearwater is sometimes considered as conspecific with the subantarctic little shearwater.
357 However, based on dark face and relatively large dark collar of captured birds, they were
358 considered as belonging to *P. elegans* (Onley & Scofield, 2007). Therefore, it is highly likely
359 that birds identified as *P. assimilis* breeding on La Quille belong to *P. elegans* (Brooke,
360 2004). Species less vulnerable to rat predation, such as albatrosses, had lower population
361 growth rates. Although there were too few counts to estimate pre- and post-eradication λ
362 (Fischer et al., 2020), colonization of Saint-Paul by species that were previously only
363 breeding on La Quille and positive post-eradication λ , clearly indicated that these species
364 highly benefited from rat eradication.

365 Our third prediction was almost confirmed. Antarctic tern had the second largest increase
366 in breeding population, behind MacGillivray's prion, but all other species had lower
367 population growth. Sooty tern population remained small, but the Saint-Paul breeding
368 population is situated at the limit of the distributional range of the species, as for the
369 Australasian gannet (del Hoyo et al., 1992; Lequette, Berteaux, & Judas, 1995; del Hoyo,
370 Elliott, & Sargatal, 1996). This high growth rate for Antarctic terns may result from relatively
371 lower philopatry than for Procellariiformes (Brooke et al., 2018). However, we think this is
372 unlikely since source populations were situated close to Saint-Paul Island (La Quille) for both

373 MacGillivray's prions and Antarctic terns. A more likely explanation is the higher fecundity
374 and shorter generation time for terns that lay two eggs, whereas Procellariiformes lay a single
375 egg. Nevertheless, this does not explain why MacGillivray's prions had a higher growth rate
376 than Antarctic terns. Environmental factors may partly explain these differences contrary to
377 expectation. During our 2018 survey we observed several (10s) remains of Antarctic terns
378 showing signs of predation by brown skuas, but none was observed for MacGillivray's prions.
379 If predation levels are sufficiently high this could limit population growth (Jiguet et al., 2007).
380 Finally, we note that our extrapolation of Antarctic tern densities to the entire coastal cliffs
381 may be biased since cliffs situated on the northeast coast of the island have a different
382 structure than elsewhere (higher elevation, less steep).

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

393 As predicted, we found one new breeding species for Saint-Paul that was not breeding on
394 nearby islets, the brown skua, indicating immigration probably from Amsterdam island where
395 ≈ 60 pairs breed (Gamble et al., 2020). Brown skuas were breeding on Saint-Paul until the late
396 19th century but disappeared thereafter probably following the local extinction of prion and
397 petrel populations as well as of Amsterdam fur seals, which constituted their main prey

398 (Péron, 1824; Vélain, 1877). Incidental observations during our 2018 survey suggest that
399 brown skuas mainly feed on northern rockhopper penguin eggs/chicks, placenta of
400 Amsterdam fur seals and Antarctic terns. Brown skuas have been increasing at Amsterdam
401 from a few breeding pairs in 1970 (Segonzac, 1972) to 63 in 2018 (unpublished data). This
402 species was persecuted on Amsterdam until the early 1970s (Segonzac, 1972), and it is likely
403 that the observed recent population growth reflects a recovery from past persecution. The
404 population growth may also be partly due to the increase of the Amsterdam fur seal
405 population (Guinet, Jouventin, & Georges, 1994; Pacoureau et al., 2017). The population
406 appears to have stabilized to around 60 breeding pairs since the early 2010s. The
407 recolonization of Saint-Paul by breeding skuas following the eradication of invasive
408 mammals, may indicate that rats had negative effects on skuas through predation on chicks,
409 but also that the increase of food resources (Antarctic terns) due to rat eradication may have
410 directly benefited breeding skuas. Skuas may have also benefited from the increase of the
411 Amsterdam fur seal population, although fur seals were in comparable numbers in the late
412 1990s as in the late 2010s (\approx 360 breeding females, Guinet et al., 1994;). We believe that the
413 hypothesis of predation by rats is the more likely as the population of rabbits was quite high
414 before their eradication and would have fulfill needs for breeding skuas. Skuas breeding on
415 Saint-Paul probably came from Amsterdam, as a group of 15 nonbreeding individuals was
416 regularly observed on Saint-Paul, including two individuals marked at Amsterdam.

417 Five species previously breeding on La Quille before eradication were newly recorded
418 breeding on Saint-Paul following eradication. These species thus now breed on the two sites,
419 which lower their local extinction risk. Since surveys pre-eradication were similar to those
420 performed post-eradication we are confident that the species newly found breeding on
421 Saint-Paul represent true colonization of the island rather than species that were missed during
422 pre-eradication surveys. This is particularly the case for conspicuous species such as the

423 brown skua and terns, as well as for species performing intense and strong vocalizations
424 during breeding such as prions and shearwaters.

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

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

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

454 In conclusion, monitoring of seabirds 20 years after invasive mammal eradication (rats and
455 rabbits) showed population growth of populations on a remote oceanic island of the Indian
456 Ocean. These findings further highlight the importance of invasive mammal eradication on
457 islands as a conservation tool, despite the fact that our study did not include the effects of the
458 eradication on invertebrates and vegetation. Although mice were not targeted and so not
459 eradicated from Saint-Paul, our results suggest that their impact on seabird populations
460 remained limited until now, although we cannot exclude they had a negative effect on
461 population growth rates through an impact on breeding success. Nevertheless, given the
462 reported negative impact of mice on seabirds elsewhere (Cuthbert & Hilton, 2004; Dilley et
463 al., 2015), we encourage eradication of mice on Saint-Paul as a conservation action to ensure
464 the future of seabird populations on this island. Despite increases, seabird populations on
465 Saint-Paul are still relatively small, and therefore vulnerable to additional impacts or re-
466 introduction of rats. Seabird population recovery on Saint-Paul further reinforces the
467 importance of eradicating invasive mammals (Norway rat *R. norvegicus*, domestic cat *Felis*
468 *catus*, house mouse) from Amsterdam Island, which is part of the ‘top 10’ islands ranked in
469 terms of conservation benefit to threatened birds arising from the eradication of alien
470 vertebrates (Brooke, Hilton, & Martins, 2007; Spatz et al., 2017; Holmes et al., 2019). Results
471 from Saint-Paul indicate that endangered species such as albatrosses and penguins will

472 eventually benefit from eradication of invasive mammals, but this will mainly benefit
473 Antarctic terns and small burrowing petrels including the endangered MacGillivray's prion.

474

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487

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613 **Table 1**

614 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
Entire sampling	Entire sampling	Capture-recapture	Capture-recapture	Elusive, high density	Prions
Entire sampling	Entire sampling	Complete counts	Incomplete counts	Elusive, high density	Flesh-footed shearwater
		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

615 **Table 2**

616 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
 617 (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}
 618 (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 <i>et al.</i> , 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 <i>et al.</i> , 1995	2	1.00	0

619 ^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%
 620 and a number of breeding pairs of 9023.

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

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

625 ^e estimated from a total number of burrows with signs of occupation obtained from adaptive cluster sampling (i.e. 74) and entire sampling (i.e.
 626 1928). Note that the N_{init} estimate does not account for burrow detection probability. λ estimated using the observed number of burrows in 2018
 627 (1484, i.e. without correction for detection probability) was 1.03.

628 ^e estimated from a total number of burrows with signs of occupation obtained from adaptive cluster sampling and random sampling.
629 ^f includes all territorial pairs (breeding and nonbreeding).
630 ^g estimated from the extrapolated numbers obtained from the coastal transects (i.e. 526) and numbers estimated in the caldera (i.e. 5).
631 ^h indicates positive growth rate that could not be explicitly calculated since $N_{init} = 0$.
632 ¹Tollu (1984); ²Micol & Jouventin (2002); ³Segonzac (1972).

633 **Table 3**

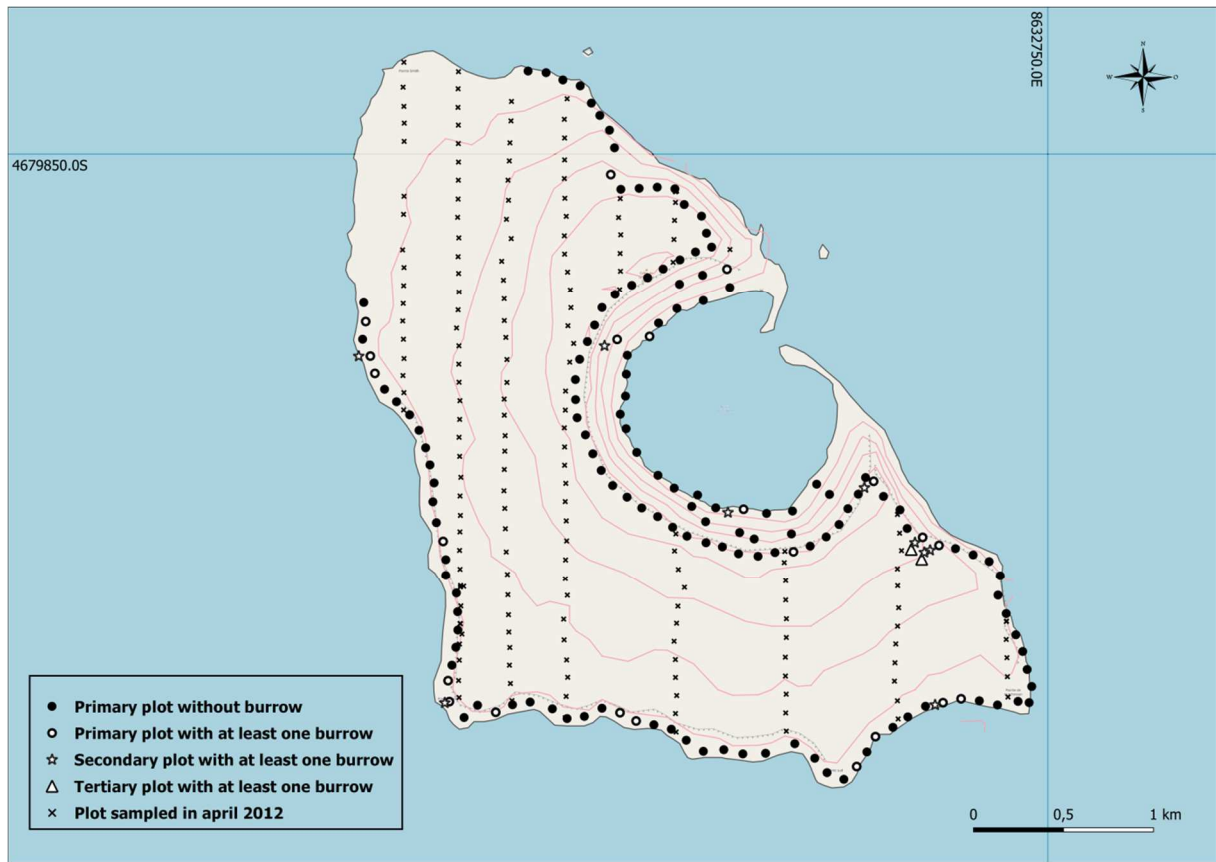
634 Seabird species observed on land at Saint-Paul Island (excluding La Quille) during surveys or as incidental observations. B: confirmed breeder,

635 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>Fregetta grallaria</i>			x	B*
Black-bellied storm petrel	<i>Fregetta tropica</i>			x	Unknown
Australasian gannet	<i>Morus serrator</i>	x	B	x	B
Brown skua	<i>Stercorarius antarcticus</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

636 Sources: Segonzac, 1972; Tollu, 1984; Roux, 1985; Guinard et al., 1998; Micol & Jouventin, 2002; Thiebot et al., 2010

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



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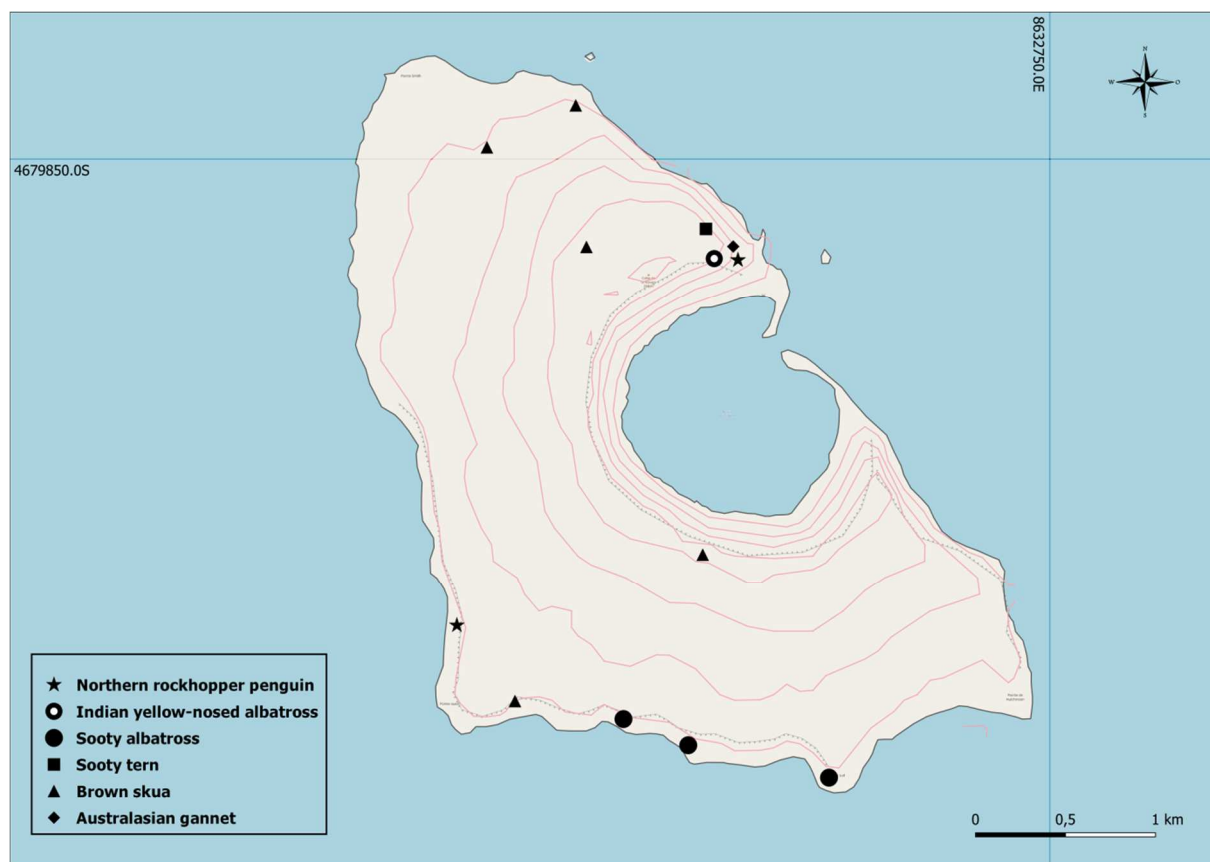
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650 **Fig. 2.** Map showing the localization of breeding penguins, albatrosses, terns, skuas, and
651 gannets on Saint Paul Island in 2018.



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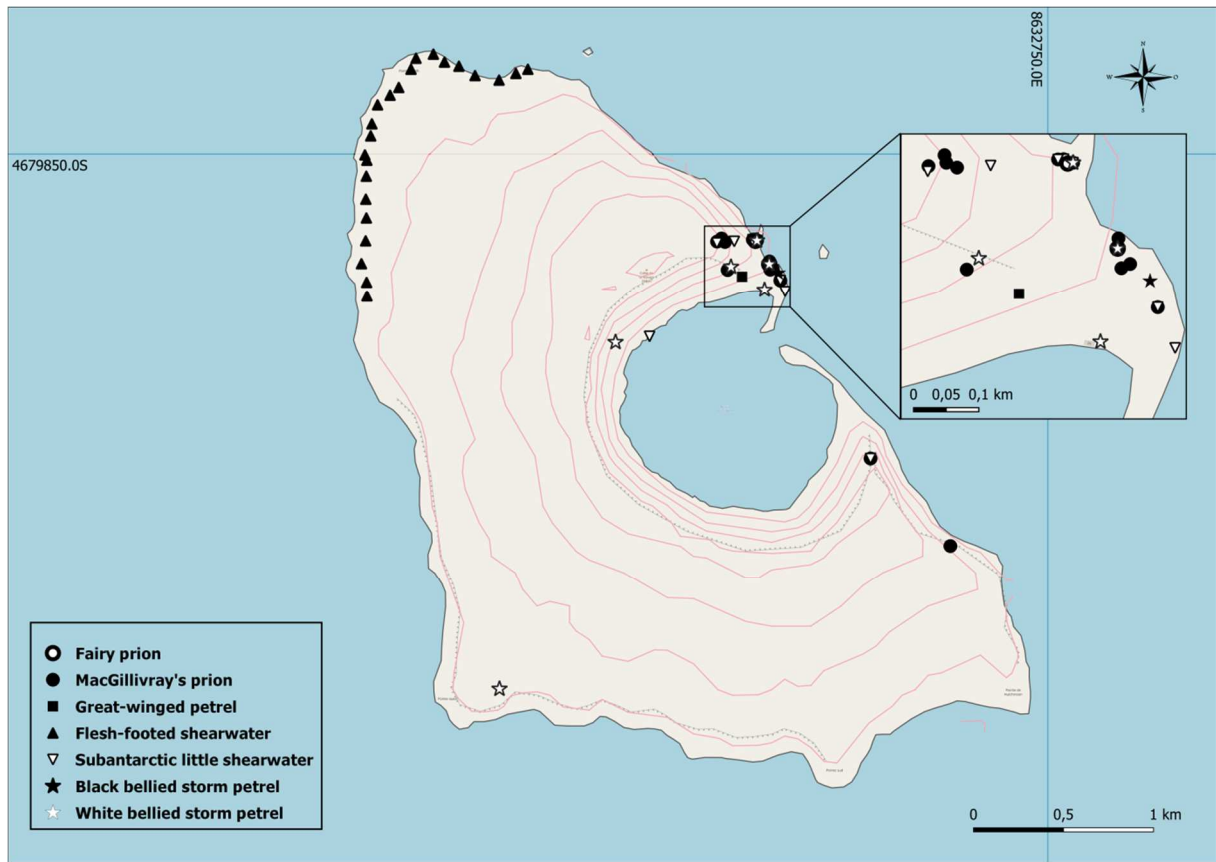
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663 **Fig. 3.** Map showing the localization of breeding burrowing petrels, shearwaters and storm
664 petrels on Saint Paul Island in 2018.



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