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1 **Predator and scavenger movements among and within endangered seabird colonies:**  
2 **opportunities for pathogen spread**

3 Amandine Gamble<sup>1,2</sup>, Romain Bazire<sup>1</sup>, Karine Delord<sup>3</sup>, Christophe Barbraud<sup>3</sup>, Audrey  
4 Jaeger<sup>4,5</sup>, Hubert Gantelet<sup>6</sup>, Eric Thibault<sup>6</sup>, Camille Lebarbenchon<sup>4</sup>, Erwan Lagadec<sup>4,7</sup>, Pablo  
5 Tortosa<sup>4</sup>, Henri Weimerskirch<sup>3</sup>, Jean-Baptiste Thiebot<sup>3,7,8</sup>, Romain Garnier<sup>9</sup>, Jérémy Tornos<sup>1,6</sup>  
6 & Thierry Boulinier<sup>1</sup>

7 <sup>1</sup> Centre d'Écologie Fonctionnelle et Évolutive (CEFE), UMR CNRS 5175, University of  
8 Montpellier, EPHE, University Paul Valéry Montpellier 3, IRD, Montpellier, France

9 <sup>2</sup>Department of Ecology and Evolutionary Biology, University of California, Los Angeles, USA

10 <sup>3</sup> Centre d'Études Biologiques de Chizé (CEBC), UMR CNRS 7372, Université La Rochelle,  
11 Villiers en Bois, France

12 <sup>4</sup> Université de la Réunion, UMR Processus Infectieux en Milieu Insulaire Tropical (PIMIT),  
13 CNRS 9192, INSERM 1187, IRD 249, GIP CYROI, Saint Denis, La Réunion, France

14 <sup>5</sup> Université de la Réunion, Écologie Marine Tropicale des Océans Pacifique et Indien  
15 (ENTROPIE), UMR UR-IRD-CNRS, Saint Denis, La Réunion, France

16 <sup>6</sup> Ceva Biovac, Beaucouzé, France

17 <sup>7</sup> Réserve Naturelle Nationale des Terres Australes Française, Saint Pierre, La Réunion,  
18 France

19 <sup>8</sup> National Institute of Polar Research, 10-3 Midori-cho, Tachikawa, 190-8518 Tokyo, Japan

20 <sup>9</sup> Department of Biology, Georgetown University, Washington, D.C., USA

21 Author for correspondence: Amandine Gamble. E-mail: amandine.gamble@gmail.com.

22 Phone: 0033676995983

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28 **Abstract**

29 **1.** The spatial structure of host communities is expected to constrain pathogen spread.  
30 However, predators and/or scavengers may connect distant host (sub)populations when  
31 foraging. Determining whether some individuals or populations play a prominent role in the  
32 spread of pathogens is critical to inform management measures.

33 **2.** We explored movements and epidemiological status of brown skuas (*Stercorarius*  
34 *antarcticus*), the only avian terrestrial consumer native of Amsterdam Island (Indian Ocean),  
35 to assess whether and how they could be involved in the spread of the bacterium *Pasteurella*  
36 *multocida*, which recurrently causes avian cholera outbreaks in endangered albatross and  
37 penguin species breeding on the island.

38 **3.** High proportions of seropositive and DNA-positive individuals for *P. multocida* indicated that  
39 skuas are highly exposed to the pathogen and may be able to transmit it. Movement tracking  
40 revealed that the foraging ranges of breeding skuas largely overlap among individuals and  
41 expand all along the coasts where albatrosses and penguins nest, but not on the inland  
42 plateau hosting the endemic Amsterdam albatross (*Diomedea amsterdamensis*).

43 **4.** Considering the epidemiological and movement data, skua movements may provide  
44 opportunity for pathogen spread among and within seabird colonies.

45 **5. Synthesis and applications.** This work highlights the importance of considering the  
46 behaviour and epidemiological status of predators and scavengers in disease dynamics  
47 because the foraging movements of individuals of such species can potentially limit the  
48 efficiency of local management measures in spatially-structured host communities. Such  
49 species could thus represent priority vaccination targets to implement efficient management  
50 measures aiming at limiting pathogen spread and also be used as sentinels to monitor  
51 pathogen circulation and evaluate the effectiveness of management measures.

52 **Résumé**

53 **1.** La circulation d'agents infectieux dans les populations sauvages peut être fortement  
54 contrainte par la structuration spatiale de leurs communautés d'hôtes. Cependant, de par leurs  
55 comportements alimentaires, certains prédateurs et/ou charognards peuvent connecter des  
56 (sous-)populations spatialement éloignées. Identifier les individus ou populations susceptibles  
57 de jouer un rôle prépondérant dans la dissémination d'agents infectieux pathogènes est un  
58 élément clé pour la compréhension, et éventuellement le contrôle, des dynamiques  
59 épidémiologiques dans les populations sauvages.

60 **2.** Dans ce contexte, nous avons suivi les déplacements et statuts épidémiologiques de labbes  
61 subantarctiques (*Stercorarius antarcticus*), uniques prédateurs et charognards terrestres  
62 aviaires natifs de l'île Amsterdam (Océan Indien), afin d'évaluer leur implication dans la  
63 dissémination de *Pasteurella multocida*, la bactérie responsable d'épizooties récurrentes de  
64 choléra aviaire affectant les albatros et gorfous de l'île.

65 **3.** Les fortes proportions d'individus positifs à *P. multocida* par sérologie et PCR indiquent que  
66 les labbes sont très exposés à la bactérie et susceptibles de la transmettre. Par ailleurs le  
67 suivi des déplacements d'individus reproducteurs a révélé que les zones de recherche  
68 alimentaire individuelles des labbes se superposent et s'étendent tout le long de la partie de  
69 côte occupée par les albatros et les gorfous. Au contraire, le plateau central où se reproduit  
70 l'albatros d'Amsterdam (*Diomedea amsterdamensis*), espèce endémique de l'île, ne semble  
71 pas visité par les labbes en reproduction.

72 **4.** Compte tenu des données épidémiologiques et écologiques présentées les labbes sont  
73 susceptibles de contribuer à dissémination d'agents infectieux au sein et entre des colonies  
74 d'oiseaux marins menacés d'extinction.

75 **5. Synthèse et applications.** Cette étude met en évidence l'importance de prendre en  
76 considération le comportement et le statut épidémiologique des prédateurs et charognards  
77 lors de la mise en place de programmes de contrôle de dynamiques épidémiologiques. En

78 effet le comportement alimentaire de telles espèces peut limiter l'efficacité des mesures  
79 locales malgré l'apparente structuration spatiale des populations affectée. Prédateurs et  
80 charognards peuvent ainsi représenter des cibles prioritaires pour les programmes de  
81 vaccination visant à limiter la dissémination d'agents infectieux pathogènes mais également  
82 être utilisés comme sentinelles pour en suivre la circulation et évaluer l'efficacité des  
83 programmes de contrôle.

84 **Keywords:** conservation biology, disease ecology, dynamic space utilisation, individual  
85 heterogeneity, movement ecology, *Pasteurella multocida*, sentinel species, serology

## 86 **Introduction**

87 Infectious diseases threaten populations of many endangered wild species and are  
88 now recognized as a main threat relevant to conservation biology (Young et al., 2017). The  
89 structure of contact networks among hosts of infectious agents can strongly impact  
90 epidemiological dynamics (Craft et al., 2008; Strona et al., 2018), hence extinction probabilities  
91 (Cleaveland et al., 2002). Some individuals or populations may occupy key positions in contact  
92 networks and contribute more than others to spreading infectious agents through their  
93 behaviour (Lloyd-Smith, Schreiber, et al., 2005; Paull et al., 2012; Dougherty et al., 2018),  
94 notably in multi-host systems (Craft et al., 2008). Such individuals or populations may thus  
95 constitute particularly relevant targets for disease control protocols aiming at interrupting  
96 transmission chains (Rushmore et al., 2014; Pepin et al., 2016; Robinson et al., 2018).

97 Terrestrial predators and scavengers may effectively connect otherwise isolated  
98 colonies or social groups when foraging, potentially contributing to pathogen spread with  
99 conservation (Craft et al., 2008), public health (Navarro et al., 2019) or fundamental  
100 implications (Boulinier et al., 2016). In wild communities subject to infectious disease  
101 outbreaks, deciphering the contact structure and examining the hosts' respective contributions  
102 in epidemiological dynamics is thus critical to develop control measures. The role of predator  
103 and/or scavenger species as potential spreaders of infectious agents is poorly documented

104 because it requires targeted field efforts at the often unpredictable time of outbreaks (Daverson  
105 et al., 2017). For instance, the role of scavengers has been suspected in avian cholera, caused  
106 by the bacterium *Pasteurella multocida* (*Pm*), outbreaks (Wille et al., 2016), but their actual  
107 contribution as spreaders still requires proper examination.

108         The recurrent outbreaks of avian cholera in seabirds on remote Amsterdam Island  
109 (Indian Ocean, 37°49'S, 77°33'E; Weimerskirch, 2004; Jaeger et al., 2018) provide a unique  
110 opportunity to better understand the potential epidemiological role of a predator and scavenger  
111 species within a relatively simple host community (Figure 1). Avian cholera is a widespread  
112 disease severely threatening the viability of several avian populations (Samuel et al., 1999;  
113 Descamps et al., 2012). On Amsterdam Island, Indian yellow-nosed albatrosses  
114 (*Thalassarche carteri*) have been recurrently hit by avian cholera outbreaks since the mid-  
115 eighties, potentially following the introduction of the pathogen through past human activities,  
116 such as animal farming, or accidental rodent introduction from visiting ships (Micol &  
117 Jouventin, 1995; Jaeger et al., 2018). Infection by *Pm* causes septicaemia in nestlings, leading  
118 to their rapid death (Bourret et al., 2018; Jaeger et al., 2018) with important consequences on  
119 the breeding success of the local yellow-nosed albatross population. For instance, on Gough  
120 Island (which is rodent infested but considered avian cholera free), the breeding success of  
121 the Atlantic yellow-nosed albatross (*Thalassarche chlororhynchos*) is as high as 70%  
122 (Cuthbert et al., 2003), while it has been below 10% most of the past twenty years on  
123 Amsterdam Island for the Indian yellow-nosed albatross (Jaeger et al., 2018). This example  
124 and others (e.g., Sebastiano et al., 2019), illustrate that infectious diseases can represent an  
125 important, but often neglected, threat to seabird population viability. Avian cholera outbreaks  
126 on Amsterdam Island not only affect this globally-significant yellow-nosed albatross population  
127 (Weimerskirch, 2004), but are also suspected to cause mortality in two other endangered  
128 species: the sooty albatross (*Phoebastria fusca*) and the northern rockhopper penguin  
129 (*Eudyptes moseleyi*; Jaeger et al., 2018).

130           Despite the strong impact of avian cholera outbreaks on the endangered seabirds of  
131 Amsterdam Island (Jaeger et al., 2018) and the availability of a vaccine proven to protect  
132 albatross nestlings (Bourret et al., 2018), no control measure has been implemented besides  
133 basic biosecurity measures. Indeed, relying on vaccination of nestlings to maintain the local  
134 yellow-nosed albatross population to its current size (~22000 pairs; Heerah et al., 2019) would  
135 require to vaccinate thousands of nestlings every year, and may thus not represent an efficient  
136 conservation strategy. In contrast, interrupting transmission chains by treating individuals  
137 responsible for the among-colony circulation of the bacterium may help to protect some  
138 colonies with minimal efforts. Since *Pm* transmission occurs primarily through an oro-faecal  
139 route (Samuel et al., 2003), it is unclear how *Pm* circulates locally. Indeed, seabirds on  
140 Amsterdam Island breed in spatially structured, mostly mono-specific, colonies (Figure  
141 S1.A.1) and albatrosses and penguins forage exclusively at sea (Heerah et al., 2019). Hence,  
142 although contacts may be frequent within dense seabird colonies, contacts between  
143 individuals from different colonies may thus be rare besides potential limited prospecting  
144 movements (Boulinier et al., 2016).

145           Terrestrial predators and scavengers could however spread *Pm* across the island while  
146 foraging among seabird colonies undergoing outbreaks. Notably, the small population of  
147 brown skuas (*Stercorarius antarcticus*), the sole terrestrial vertebrate predators and  
148 scavengers native to the island, could disseminate the bacterium when foraging through  
149 shedding and/or by moving infected albatrosses and penguins (Pietz, 1987). Introduced brown  
150 rats (*Rattus norvegicus*) and house mice (*Mus musculus*; Micol & Jouventin, 1995) could also  
151 carry and shed the bacterium, notably as they prey and scavenge on seabird chicks (Figure  
152 S1.A.2; Thiebot et al., 2014), although the distribution of resources and geographical barriers  
153 created by the island relief probably constrain the spatial scale of their contribution. In addition,  
154 the endemic Amsterdam albatross (*Diomedea amsterdamensis*) could also be at risk of  
155 exposure to *Pm* via foraging skuas because it nests a few kilometres inland from the yellow-



156 nosed albatross colonies, although nestling die-offs have seldom been recorded in this  
157 species (Jaeger et al., 2018).

158         Considering the wide range of feeding habits of skuas and the potential heterogeneity  
159 of foraging strategies among individuals (Furness, 1987), some individuals could play a  
160 prominent role in the circulation of infectious agents. In the skua population of Amsterdam  
161 Island, we examined the extent to which the individuals (1) are exposed to *Pm*, (2) forage on  
162 coastal *versus* inland areas, and (3) exploit exclusive feeding territories within the seabird  
163 colonies. We expected the skuas to forage mostly on the coasts where prey species breed in  
164 dense colonies (Figure 2a, scenarios 1 and 3), maximising feeding opportunities (Figure  
165 S1.A.2a), but also exposure risks to *Pm*. Further, we expected skuas to hold exclusive  
166 individual feeding territories (Figure 2a, scenarios 1 and 2; Pietz, 1987; Trivelpiece et al., 1980;  
167 Votier et al., 2004), with restricted movements of some individuals potentially inducing  
168 heterogeneity in exposure to *Pm* and limited contacts among skuas (outside pairs, contacts  
169 are expected to occur mostly on foraging sites and clubs, i.e., sites where individuals gather  
170 outside breeding territories; Klomp & Furness, 1990). Testing these hypotheses should bring  
171 new insights on pathogen circulation in spatially structured host communities and help  
172 managers to design and implement efficient disease control protocols.

## 173 **Materials and Methods**

### 174 **Study population**

175         Around 60 pairs of brown skuas breed at low density yearly on Amsterdam Island's  
176 "Plateau des Tourbières" (PDT; Figure 1). Breeders generally lay two eggs in  
177 October/November and nestlings hatch in late November/early December and fledge 40-50  
178 days later. Skuas attend clubs notably in the north ("Mare aux Éléphants" [MAE]) and the  
179 south-west (bottom of "Entrecasteaux" cliffs). Amsterdam island holds important populations  
180 of Indian yellow-nosed albatrosses, sooty albatrosses (~400 pairs; Heerah et al., 2019) and  
181 northern rockhopper penguins (~12000 pairs), all breeding in mostly mono-specific colonies

182 on the south-west coastal cliffs between August and May (Figure 1). The 40-50 pairs of  
183 Amsterdam albatrosses nest biennially further inland, on the northern part of the PDT (Figure  
184 1). A few small *Procellariiformes* are also present on the island in very low numbers (Micol &  
185 Jouventin, 1995). All around the island, subantarctic fur seals (*Arctocephalus tropicalis*) calve  
186 on the beaches in December (Guinet, Jouventin, & Georges, 1994), also providing food  
187 opportunities for skuas (placentas and dead pups). Introduced brown rats and house mice are  
188 often observed in seabird colonies (Figure S1.A.2). Feral cats (*Felis catus*) were also  
189 introduced on the island (Micol & Jouventin, 1995), but are rarely observed in seabird colonies.

## 190 **Field sampling**

191 During three breeding seasons (2011-2012, 2015-2016, 2016-2017), blood samples  
192 (1 mL from the metatarsal vein using heparinized syringes) and cloacal swabs (using sterile  
193 cotton tips) were collected from 66 adults and 9 nestlings of brown skuas captured on their  
194 nests in the southern part of PDT or in clubs at Entrecasteaux and MAE between November  
195 and January (Table 1). Breeders handled in 2015-2016 and breeders and club attendants  
196 handled in 2016-2017 were marked with leg rings for individual identification. Red blood cells  
197 and plasma were separated by centrifugation a few hours after collection. Swabs were stored  
198 in 0.5 mL of a lysis buffer (RNA NOW<sup>®</sup>, BIOGENTEX, USA, in 2011-2012; Longmire buffer  
199 the following years; Longmire et al., 1988). Samples were kept at -20°C in the field, then stored  
200 at -20°C (plasma) or -80°C (swabs) until analysis.

## 201 **Immunological assays**

202 *Pm*-specific antibody levels in plasma samples of skuas were measured using two  
203 immunoassays in order to ascertain past exposure to *Pm*: an enzyme-linked immunosorbent  
204 assay (ELISA; ID Screen<sup>®</sup> *Pasteurella multocida* Chicken and Turkey Indirect, IDvet, France;  
205 with the positivity threshold determined following Garnier et al., 2017) and a microagglutination  
206 test (MAT; SEROPAST<sup>®</sup>, Ceva-Biovac, France). Technical details are given in Appendix S1.B.

207 **Molecular detection of *Pm***

208 Total nucleic acids were extracted following the RNA NOW<sup>®</sup> isolation and purification  
209 protocol for skua cloacal swabs preserved in RNA NOW<sup>®</sup> , and with the QIAamp cad  
210 Pathogen Mini<sup>®</sup> kit (QIAGEN, USA) for skua cloacal swabs preserved in Longmire lysis buffer.  
211 *Pm* DNA was detected with a real-time polymerase chain reaction (RT-PCR) targeting the  
212 strain previously detected in a dead sooty albatross on Amsterdam Island (Jaeger et al., 2019).  
213 Technical details are given in Appendix S1.B.

214 **Movement tracking**

215 In 2015-2016 and 2016-2017, 18 breeding skuas captured on the southern PDT were  
216 also equipped with solar-powered GPS-UHF devices with a remote data download link (GPS-  
217 UHF Harrier-L<sup>®</sup>, Ecotone, Poland). The GPS acquisition frequency was set at 2 to 5 min and  
218 altitude above sea level was also recorded in 2015-2016 (see Appendix S1.C for more details).  
219 Loggers were deployed during the early chick-rearing period (late November/early December),  
220 when skuas' energetic needs are at their highest (Furness, 1987) and avian cholera outbreaks  
221 occur in albatross colonies (Weimerskirch, 2004; Bourret et al., 2018). Sufficient data for  
222 spatial analysis (> 24h) were collected from 13 individuals, with data spanning 12-102 days  
223 (median [25 and 75% quartiles] = 54 [47;85]; Table S1.C.1), covering most of the chick-rearing  
224 period for the majority of the tracked individuals. A bootstrap analysis estimated this sample  
225 to adequately represent space use of the skua population breeding on southern PDT during  
226 this period (Lascelles et al., 2016; see Appendix S1.C and Figure S1.C .1).

227 Using the GPS data, the intensity (spatial distribution of the mean residence time per  
228 visit of each area, *i.e.*, areas where an individual tends to spend more time) and recursion  
229 (spatial distribution of the number of visits in each area, *i.e.*, areas that an individual tends to  
230 repeatedly visit) distributions were computed to get a dynamic picture of space utilisation  
231 (Benhamou & Riotte-Lambert, 2012). The overlap of the patches recursively used by different  
232 individuals was visually examined to inform on the existence of exclusive feeding territories in

233 this population. To estimate the intensity and recursion distributions, non-overlapping virtual  
234 circles of 50m in radius (referred to as “areas”) were delimited. A new visit to an area occurred  
235 each time the tracked individual re-entered it after a time lag spent outside the area longer  
236 than 10 min and remained in that area for at least 15 min (to exclude cases in which birds  
237 went through an area without using it) using the BRB|MKDE program (for Biased Random  
238 Bridges for Movement-based Kernel Density Estimation; Benhamou, 2011). All data were  
239 analysed and represented after exclusion of locations recorded within the nesting area of the  
240 tracked individuals unless indicated otherwise. Resulting distributions were visualized in QGIS  
241 2.18.21.

## 242 **Monitoring of yellow-nosed albatrosses**

243 In order to assess whether skuas were present in coastal seabird colonies during avian  
244 cholera epizootics, the proportions of yellow-nosed albatross nestlings surviving and excreting  
245 *Pm* DNA in a subcolony of Entrecasteaux were used as a proxy for the progress of the  
246 epizootics. *Pm* DNA excretion was assessed using the same design used in brown skuas.  
247 Details and sample sizes are given in Appendix S1.D.

## 248 **Statistical analyses**

249 All statistical analyses were run using R 3.6.1 and the script available in Appendix S3.  
250 Seroprevalences were calculated as the proportion of seropositive individuals among tested  
251 individuals each year. Differences in antibody levels among locations within a year or among  
252 years in a location were investigated using Wilcoxon tests with a Bonferroni correction and a  
253 5% significance level.

## 254 **Results**

### 255 **Detection of *Pm* and anti-*Pm* antibodies**

256 Specific antibodies were detected in all but two plasma samples from adult brown  
257 skuas by both MAT and ELISA, resulting in seroprevalence varying between 80% and 100%  
258 depending on the site and year (Table 1). In 2016-2017, based on the ELISA results, antibody  
259 levels were significantly lower in MAE than in Entrecasteaux and PDT (both  $p < 0.01$ ; Table  
260 S1.B.1). All other pairwise comparisons were not statistically different (Figure 3). The same  
261 results were obtained from the MAT data. *Pm* DNA was detected in cloacal swabs of adults  
262 from PDT and Entrecasteaux, but not from MAE (Table 1). The proportion of *Pm* positive  
263 samples was generally low ( $\leq 33\%$ ), except for PDT in 2016-2017 with 8/10 positive individuals.  
264 Regarding nestlings, neither specific antibodies nor *Pm* DNA were detected in samples from  
265 2011-2012. In 2016-2017, *Pm* DNA was detected in three seronegative nestlings; one other  
266 nestling was seropositive but not excreting *Pm* DNA (Table 1; Figure S1.E.1).

#### 267 **Individual movement tracking**

268 Both years, breeding skuas moved along the western coast (south to north-east) of the  
269 island, where fur seals, albatrosses and penguins breed (Figure 4). Some individuals visited  
270 the whole western coast within 24 hours (Figure S1.C.3, Appendix S2). Breeding skuas visited  
271 the surroundings of Entrecasteaux and MAE clubs. When travelling along the cliffs, skuas  
272 exploited a large altitudinal gradient, suggesting that they potentially visited fur seals, penguins  
273 and albatross colonies (Figures S1.C.2, S1.C.3). However, none of the tracked individuals  
274 visited the Amsterdam albatross breeding area.

275 Recursively exploited areas largely overlapped among the tracked individuals (Figures  
276 5, S1.C.4). Entrecasteaux cliffs were intensively and recursively exploited by all the tracked  
277 individuals (Figures 5, S1.C.4, S1.C.5, Table S1.C.2), notably during avian cholera outbreaks  
278 (Figure S1.D.1), and represented the only recursively visited site for four of them. Other sites  
279 recursively visited included the northern part of the south-west cliff, harbouring large seabird  
280 and fur seal colonies, the north coast, hosting another large fur seal colony, and the south  
281 plain where seabirds and fur seals are rare, but rodent populations may be present. Note that

282 all the tracked individuals were seropositive and *Pm* DNA was detected in 8/13 birds (Table  
283 S1.C.2) at the time of logger deployment.

## 284 **Discussion**

285 Here, we explored different scenarios of foraging strategies of a predator and  
286 scavenger, the brown skua, in relation to the circulation of a pathogen within a spatially-  
287 structured community of endangered seabirds. Movement data suggest that skuas may inter-  
288 connect several seabird colonies during avian cholera epizootics, potentially contributing to  
289 pathogen spread. Our study allowed to characterise biological processes relevant to pathogen  
290 circulation, such as the fact that skuas do not hold foraging territories, a necessary first step  
291 to build mechanistic models of eco-epidemiological dynamics and explore potential control  
292 measures (Daversa et al., 2017; Dougherty et al., 2018).

### 293 **Skua exposure and infection by *Pm* and implications for epidemiological surveillance**

294 We report the first detection of anti-*Pm* antibodies in skuas and show that the  
295 population of brown skuas from Amsterdam Island is highly exposed to this bacterium. The  
296 proximity of Entrecasteaux cliffs, where skuas may be exposed to *Pm* through feeding on  
297 infected albatrosses and penguins (Figure S1.A.2a), may intensify exposure and explain the  
298 high specific antibody levels measured in individuals sampled at the Entrecasteaux club or  
299 breeding on PDT (Pepin et al., 2017). Because detailed antibody kinetics are not available, it  
300 is not possible to estimate the timing of infection from serological data. Nevertheless, the  
301 detection of PCR-positive birds at Entrecasteaux club or breeding on PDT reveals ongoing  
302 infection at the time of sampling. In contrast, skuas attending the MAE club may forage  
303 preferentially on nearby fur seal colonies, potentially minimising their exposure to *Pm*, which  
304 would explain their lower antibody levels and the absence of PCR-positive birds at this site.  
305 More generally, the important proportion of seropositive but PCR-negative adult skuas  
306 suggests that specific antibodies may persist past the infection period, as commonly observed  
307 in acute infections (Pepin et al., 2017).

308 Jaeger et al. (2018) reported the circulation of a unique *Pm* strain among sooty and  
309 yellow-nosed albatrosses, but technical constraints for field microbiology (e.g. low availability  
310 of fresh carcasses, difficulty to obtain bacterial isolates from non-invasive approaches) limited  
311 the sample sizes. While it is not possible to confirm that the epizootic *Pm* strain killing  
312 albatrosses is circulating in skuas, our current understanding of the system supports the  
313 circulation of a common *Pm* strain circulating in the different species of the island. Future  
314 works should aim at sequencing more *Pm* isolates from different species of the island to  
315 confirm this hypothesis.

316 Interestingly, detection of specific antibodies in the majority of PCR-negative adults  
317 also suggests that a large proportion may survive *Pm* exposure, contrasting with the high  
318 mortality rate reported during previous outbreaks in Antarctica (Parmelee, Maxson, &  
319 Bernstein, 1979; Leotta et al., 2006). This heterogeneity is not surprising given the known  
320 variability of *Pm* virulence in different hosts (Christensen & Bisgaard, 2000). Moreover, the  
321 low mortality rate of adult skuas on Amsterdam Island is similar to that of adult yellow-nosed  
322 albatrosses on that island (Rolland et al., 2009; Gamble, Ganier et al., 2019), but the higher  
323 seroprevalence in skuas suggests different rates of exposure and/or persistence of antibody  
324 levels. If skuas are highly exposed but resistant or tolerant to infection by *Pm*, they could also  
325 be involved in the maintenance of the pathogen on the island. This result also shows that  
326 skuas are potentially good sentinels to detect the circulation of *Pm*, especially using serology  
327 (Halliday et al., 2007). Hence, implementing long-term serosurveys targeting such species can  
328 be especially useful for the acquisition of baseline data on (pathogenic and non-pathogenic)  
329 infectious agent circulation and for the early detection of pathogen circulation. Indeed, in long-  
330 lived species such as seabirds, monitoring protocols based only on breeding pair counts can  
331 take several years before capturing juvenile mortality events because of late recruitment.

### 332 **Movements and disease transmission in structured communities**

333 Apex predator movements have been well studied in relation to foraging during the  
334 breeding season, but their implications for infectious agent circulation have only recently been  
335 considered (Boulinier et al., 2016; de Souza Petersen et al., 2017). As observed elsewhere  
336 (Carneiro et al., 2014; Pietz, 1987), skuas breeding on Amsterdam Island foraged almost  
337 exclusively onshore, mostly along the coastal cliffs harbouring dense seabird colonies with  
338 high feeding opportunities. This population may thus regularly be in contact with yellow-nosed  
339 and sooty albatrosses, rockhopper penguins and subantarctic fur seals during avian cholera  
340 outbreaks. Interestingly, several individuals recursively used different patches along the  
341 western coasts, corresponding to different seabird and fur seal colonies: this may reflect  
342 particular opportunities for the dissemination of infectious agents. In addition, as opposed to  
343 other populations (Trivelpiece et al., 1980; Pietz, 1987; Votier et al., 2004; but see Carneiro et  
344 al., 2014), breeding skuas on Amsterdam Island did not seem to hold individual-exclusive  
345 feeding territories, as supported by the large space utilisation overlap among individuals. The  
346 high food availability in large breeding colonies of vertebrates may explain the absence of  
347 such territories on Amsterdam Island. Accordingly, the absence of individual-exclusive feeding  
348 territories associated with high seroprevalences suggests that, if breeding individuals  
349 contribute to *Pm* circulation on the island, their role could be rather homogeneous (Figure 2),  
350 contrary to other systems (Marchand et al., 2017; Dougherty et al., 2018). However, other  
351 possible sources of heterogeneity among individuals remains to be explored, such as  
352 variations in the duration or intensity of shedding.

353 We did not observe breeding skuas foraging in the small and low-density breeding  
354 population of the Amsterdam albatross, suggesting that they may not connect this population  
355 to others (Figure 2b). This is consistent with the high breeding success of this albatross  
356 population over the last decades (Jaeger et al., 2018). Although a few skua pairs nest among  
357 Amsterdam albatrosses (Figure 1), contacts between the two species may be rare if skuas  
358 forage only on the coast, as movements around the nests are usually limited. However,  
359 considering the flexibility of skuas' foraging behaviour and potential behavioural differences



360 between breeders and non-breeders, some individuals may occasionally visit this colony,  
361 especially if environmental conditions and food availability change (Carneiro et al., 2015).  
362 Such changes, modifying the host space-utilisation, can have important consequences on the  
363 dynamics of infectious agents (Merkle et al., 2017; Giles et al., 2018). Long-term monitoring  
364 of these dynamics is essential to better understand pathogen circulation, and design robust  
365 management options.

### 366 **Maintenance and circulation of infectious agent**

367 The population of brown skuas may play a key role in the circulation of *Pm* on  
368 Amsterdam Island, but the complete maintenance community (*i.e.*, the set of connected host  
369 populations that together can maintain the pathogen over the long term, notably in winter when  
370 most seabirds are absent of the island; Viana et al., 2014) remains to be functionally  
371 characterized. Rodents may be good candidates as local maintenance hosts of *Pm*, but little  
372 data are yet available to examine this hypothesis. Rodents can reach high densities and are  
373 present year-round; they may feed on dead seabird nestlings and are preyed upon by skuas  
374 (Figure S1.A.2b, d). In addition, as observed in poultry (Curtis, 1983), rodents may directly  
375 transmit *Pm* through movements within colonies and biting of live nestlings (Thiebot et al.,  
376 2014; Figure S1.A.2c). Hence, spatio-temporal aspects of rodent exposure to *Pm* and  
377 subsequent shedding need to be explored from an eco-epidemiological standpoint (Lloyd-  
378 Smith, Cross, et al., 2005; Guzzetta et al., 2017). Because the home range radius of rodents  
379 is likely much smaller than that of skuas, rodents could be important in the within-colony  
380 spreading of *Pm*, while skuas may play a key role at a larger spatial scale. These elements  
381 suggest potentially complex epidemiological networks involving several bridge hosts (Caron  
382 et al., 2015) linking cliff-nesting seabirds to Amsterdam albatrosses. Skuas could move *Pm*  
383 from the costal cliffs to PDT, where a few breed in proximity to Amsterdam albatrosses.  
384 Foraging rodents could then move the bacterium from those skuas to the Amsterdam  
385 albatrosses. More generally, this stresses the importance of considering processes occurring  
386 at nested spatial scales, and epidemiological networks in their entirety when exploring chains

387 of transmission (Boulinier et al., 2016; Daversa et al., 2017). In the case of Amsterdam Island,  
388 future work should examine the role of introduced rodents in the maintenance and small-scale  
389 circulation of avian pathogens.

### 390 **Implications for conservation**

391 Our study revealed that the movements of potential bridge hosts (here, skuas and  
392 potentially rodents) may reduce the efficiency of local actions aiming at controlling multi-host  
393 infectious agents. For instance, locally intensive vaccination programs targeting albatrosses  
394 (e.g., Bourret et al., 2018; Gamble, Garnier et al., 2019) combined to rodent population control  
395 would seem feasible in accessible seabird colonies. However, such attempts would likely fail  
396 to control the pathogen because, although the system appears highly spatially structured,  
397 skuas could re-introduce the pathogen from inaccessible, hence non-treated, seabird  
398 colonies. In such a system, efficient disease control measures would likely need to interrupt  
399 the transmission network by targeting bridge hosts by, for instance, vaccinating native  
400 terrestrial predators (here skuas) with a vaccine blocking transmission and eradicating  
401 introduced rodents. However, we do not recommend culling native terrestrial predators as  
402 there are growing evidences that scavenging contribute in disease controls (e.g., Sage et al.,  
403 2019) and the culling of a native species would raise strong ethical issues. In the case of avian  
404 cholera on Amsterdam island, an autogenous vaccine has proven efficient to protect yellow-  
405 nosed albatross nestlings (Bourret et al., 2018), but whether it blocks transmission remains to  
406 be investigated. The direct negative impact of introduced rodents on seabird populations is  
407 well documented and their eradication is seen as a priority for seabird conservation (see  
408 Duron, Shiels & Vidal, 2017 for a review). In contrast, their role in epidemiological dynamics  
409 has rarely been explored, but its potential is highlighted by our results. Implementing the  
410 eradication of introduced rodent populations on Amsterdam Island in parallel to the  
411 epidemiological monitoring of seabird populations, would provide a unique opportunity to  
412 semi-experimentally assess their role in the eco-epidemiological dynamics while representing  
413 a significant management action in itself.

414           When deciding what management measure to implement in a situation such as the  
415 one on Amsterdam Island, modelling approaches can enable the stakeholder to clearly outline  
416 the management objectives, the available means to reach them, and the level of uncertainty  
417 in the parameters underlying the dynamics of the system. Indeed, comparing the potential  
418 benefits of different management strategies is not as straightforward as it may seem and we  
419 encourage stakeholders to work hand in hand with disease ecologists and modellers, even in  
420 an apparently simple situation such as that on Amsterdam Island. For instance,  
421 compartmented epidemiological models represent attractive options to assess the necessary  
422 level of rodent population control (Mariën et al., 2019) or vaccination coverage and protocols  
423 (Haydon et al., 2006; Baker et al., 2019) to efficiently benefit endangered species while  
424 accounting for their particular life-history traits (Garnier et al., 2012). Network models based  
425 on (direct or indirect) contact networks at the inter-specific (Craft et al., 2008; Woodroffe &  
426 Donnelly, 2011) and intra-specific levels (Rushmore et al., 2014; Pepin et al., 2016; Robinson  
427 et al., 2018) could be used to explore the benefits of targeting potential super-spreading  
428 individuals or group of individuals for vaccination or population control. Models also allow to  
429 explore sources of heterogeneity in pathogen maintenance and transmission (Marchand et  
430 al., 2017; Dougherty et al., 2018; Robinson et al., 2018). Finally, management should ideally  
431 be conducted in an adaptive dynamic framework (Keith et al., 2011), requiring a design  
432 allowing to track eco-epidemiological variables, notably through the monitoring of sentinel  
433 species (Halliday et al., 2007), before and after interventions (Viana et al., 2014). The present  
434 paper provide key elements to fuel such modelling approaches.

435 **Authors' contributions.** TB conceived the idea of this work; TB, JT, HW, KD and CB  
436 designed the study; JT, AG and J-BT collected the data; HG and ET developed the MAT; AG,  
437 AJ, CL, PT and EL performed the serology and molecular analyses; AG analysed the  
438 epidemiological data; AG, RB and J-BT analysed the tracking data; AG and TB led the writing  
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455 **Supporting Information.** Appendices S1: text and figures; S2: tracking data animation; S3:  
456 R notebook.

457 **Data availability statement.** Data are available on the OSU-OREME Repository  
458 <https://doi.oreme.org/b4b4a2e1-3d00-45b7-b3b2-2ca05d054346> (Gamble, Bazire et al.,  
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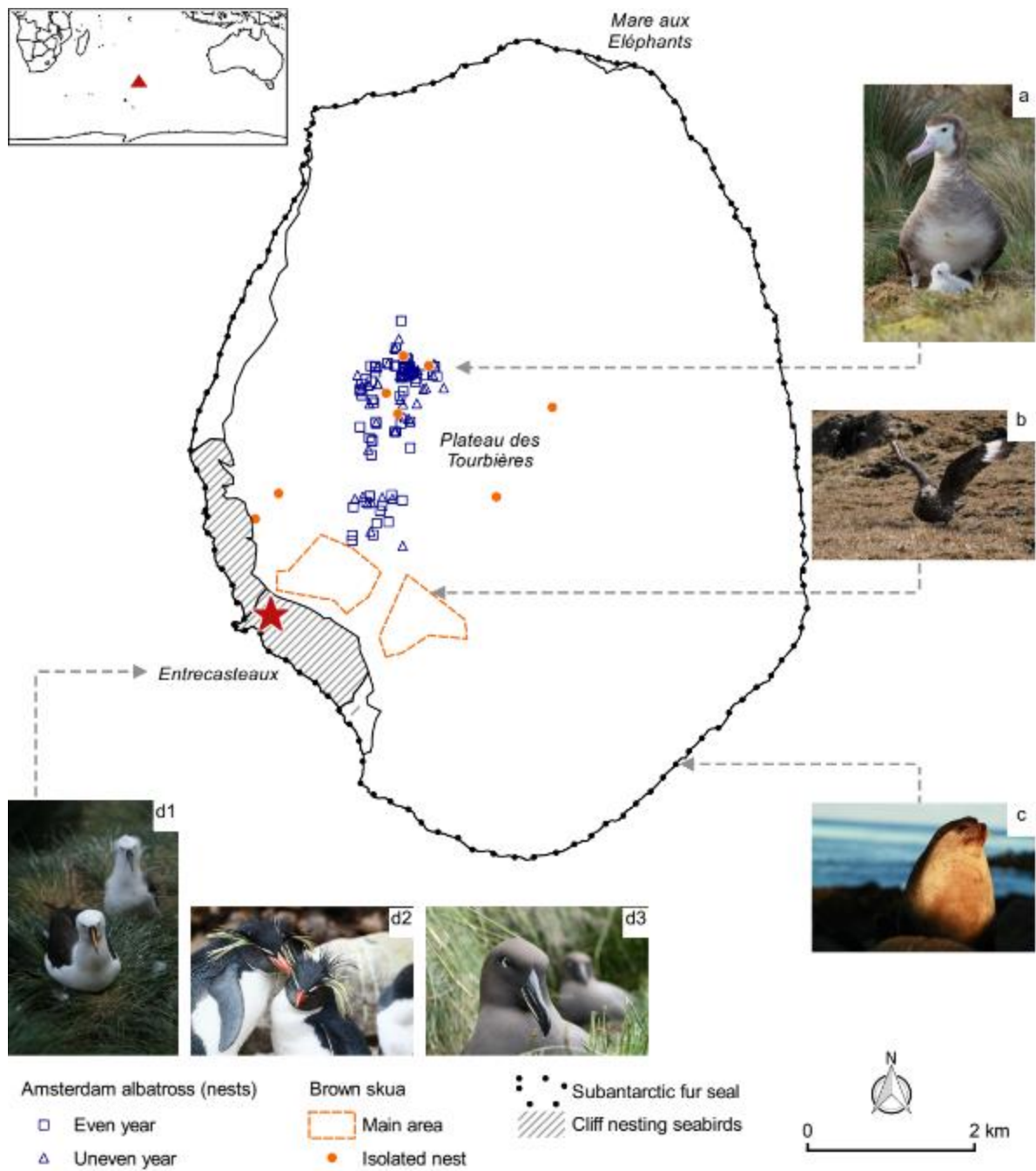
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647 **Table 1.** Proportions of brown skuas from Amsterdam Island positive for anti-*Pm* antibodies  
648 according to MAT and ELISA and for *Pm* DNA according to PCR or RT-PCR from cloacal  
649 swabs. Clopper-Pearson 95% confidence intervals are indicated between brackets and  
650 numbers of positive/tested individuals between parentheses.

Site	Stage	2011-2012			2015-2016			2016-2017		
		MAT	ELISA	PCR	MAT	ELISA	RT-PCR	MAT	ELISA	RT-PCR
Plateau des Tourbières	Breeding adults	1.00 [0.79;1.00] (16/16)	1.00 [0.79;1.00] (16/16)	0.06 [0.00;0.30] (1/16)	1.00 [0.69;1.00] (10/10)	1.00 [0.69;1.00] (10/10)	0.10 [0.00;0.45] (1/10)	1.00 [0.69;1.00] (10/10)	1.00 [0.69;1.00] (10/10)	0.80 [0.44;0.97] (8/10)
	Nestlings	0.00 [0.00;0.71] (0/3)	0.00 [0.04;0.78] (0/3)	0.00 [0.00;0.31] (0/10)	-	-	-	0.17 [0.00;0.64] (1/6)	0.17 [0.00;0.64] (1/6)	0.50 [0.12;0.88] (3/6)
Entrecasteaux	Club attendants	-	-	-	1.00 [0.69;1.00] (10/10)	1.00 [0.69;1.00] (10/10)	0.33 [0.07;0.65] (3/10)	1.00 [0.69;1.00] (10/10)	1.00 [0.69;1.00] (10/10)	0.20 [0.03;0.56] (2/10)
Mare aux Éléphants	Club attendants	-	-	-	-	-	-	0.80 [0.44;0.97] (8/10)	0.75 [0.35;0.97] (6/8)	0.00 [0.00;0.31] (0/10)

651



652

653 Figure 1. Breeding sites of colonial vertebrates on Amsterdam Island (37°49'S, 77°33'E).

654 Amsterdam albatrosses (a) nest on the northern part of the inland plateau; brown skuas (b)

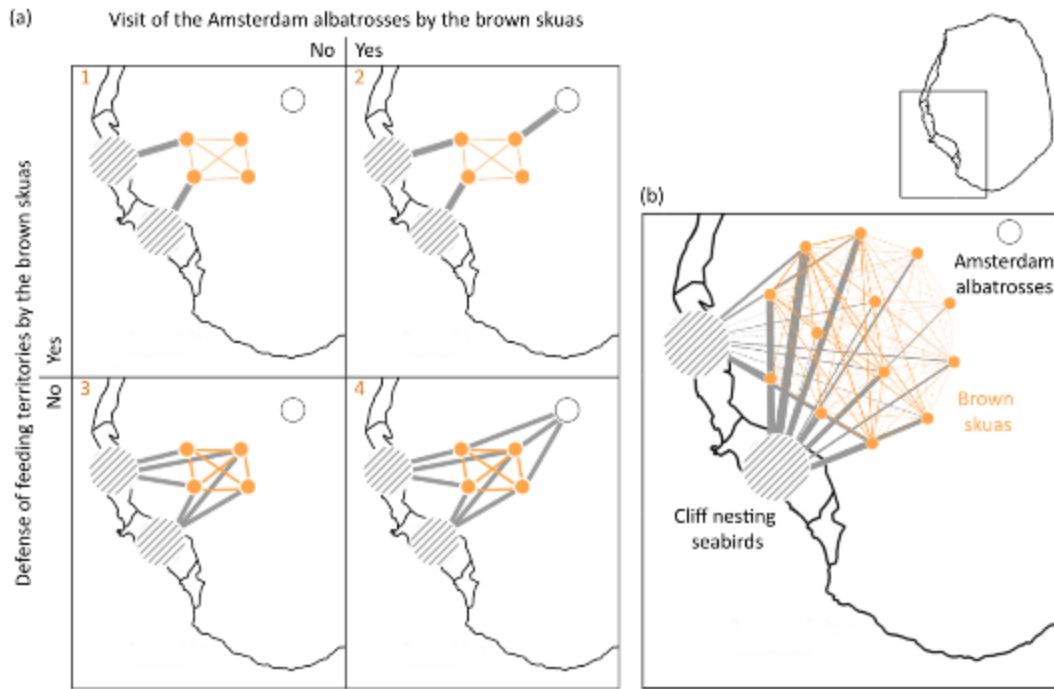
655 mostly nest on the southern part on the inland plateau; subantarctic fur seals (c) breed all

656 around the island; Indian yellow-nosed albatrosses (d1), northern rockhopper penguins (d2)

657 and sooty albatrosses (d3) nest in the high cliffs laying south-west of the island. The red star

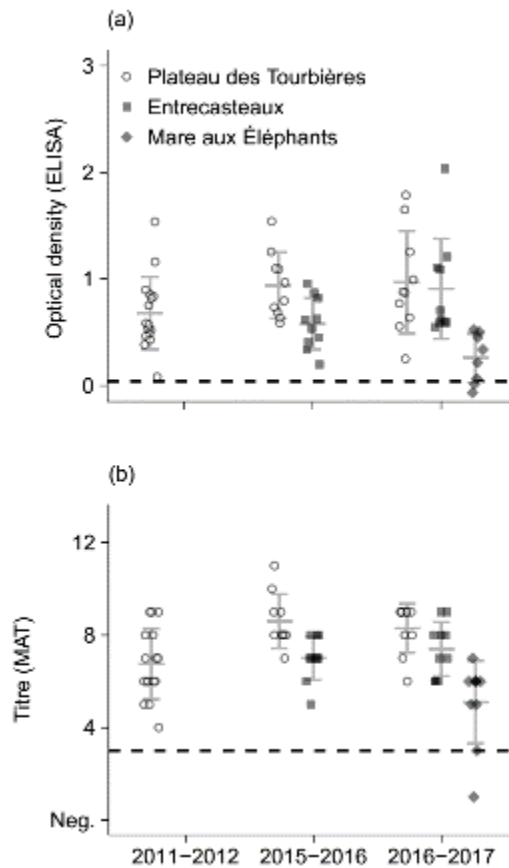
658 denotes the monitored yellow-nosed albatross subcolony. Photos: Romain Bazire, IPEV. Map

659 background: Réserve Naturelle Nationale des Terres Australes Françaises.



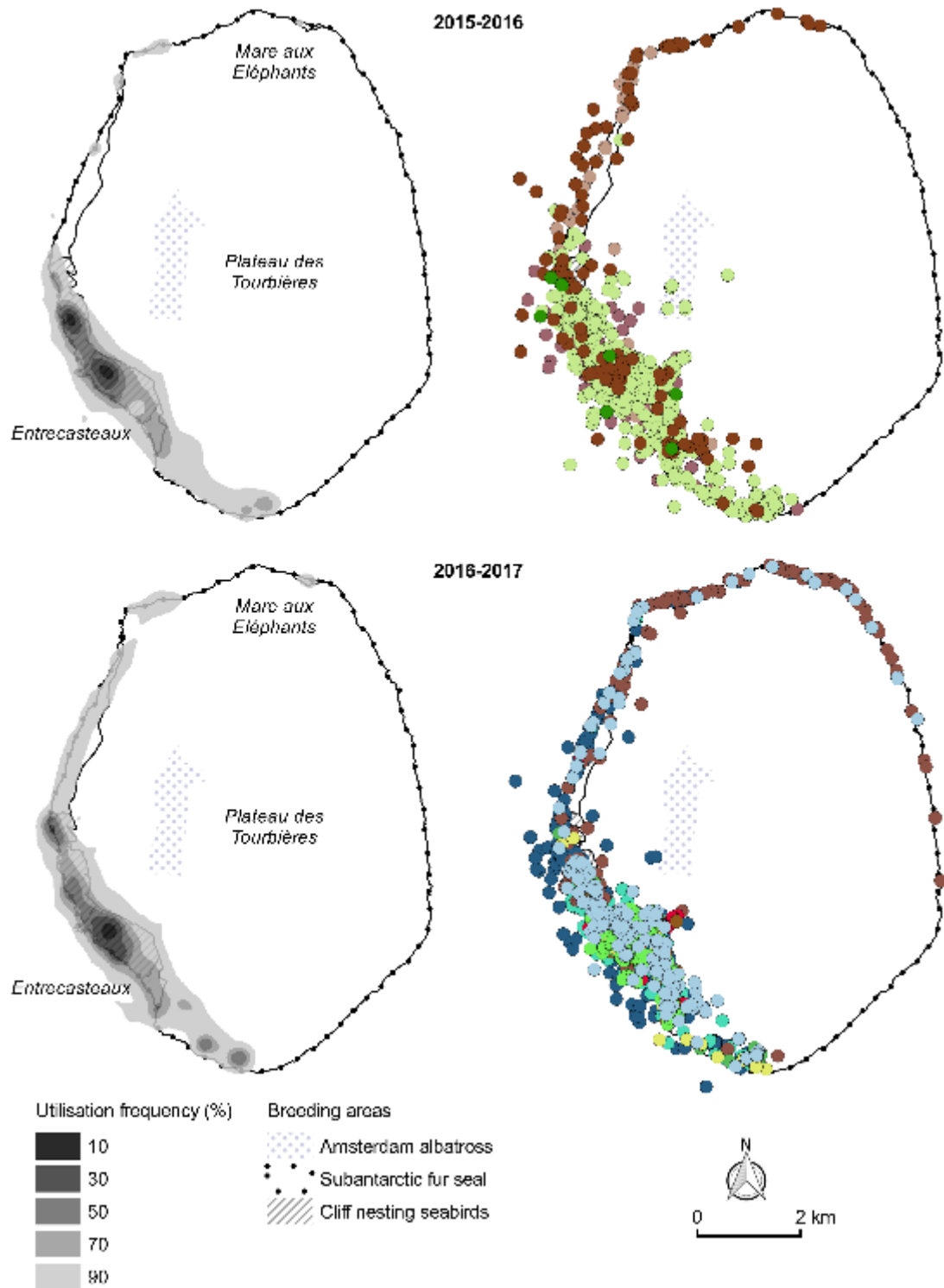
660

661 Figure 2. Hypothetical (a) and observed (b) epidemiological networks linking seabirds on  
 662 Amsterdam Island based on breeding brown skua movements. Each orange node represents  
 663 an individual skua. The hatched and white nodes represent grouped subpopulations of cliff  
 664 nesting birds (*i.e.*, yellow-nosed albatrosses, rockhopper penguins and sooty albatrosses) and  
 665 Amsterdam albatrosses respectively. Edge widths between skuas and other species represent  
 666 the relative time spent in each potential foraging area. Panel b was built based on data  
 667 collected on skuas breeding in the Southern part of PDT and presented in Figure 4. Edge  
 668 widths between two skuas represent the probability of two individuals being present in the  
 669 same potential foraging area at the same time (see Appendix S1.F for calculation details).



670

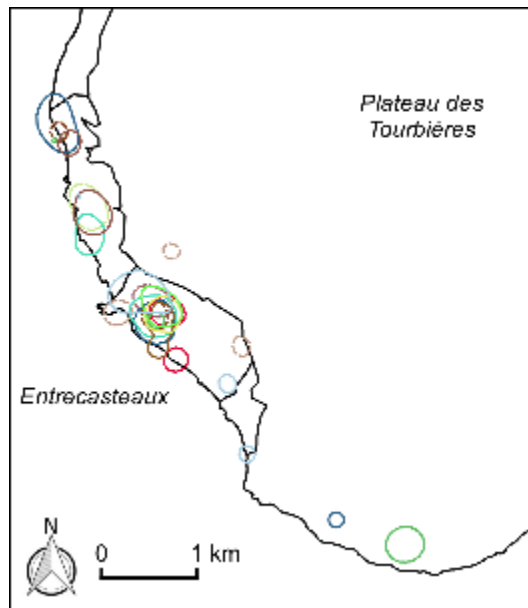
671 Figure 3. Evidence of high exposure of brown skuas to *Pasteurella multocida*: anti-Pm  
 672 antibody levels for skuas measured by ELISA (a) and MAT (b) over three years on Plateau  
 673 des Tourbières (the main skua breeding ground on Amsterdam Island), and two clubs  
 674 (Entrecasteaux and Mare aux Éléphants). Mean  $\pm$  standard deviation are shown in grey. The  
 675 dashed lines represent the seropositivity thresholds. For ease of visualisation, data points  
 676 were horizontally jittered.



677

678 Figure 4. Space utilisation by breeding brown skuas. Left: distribution of space utilisation  
 679 outside of their breeding area by all individuals equipped with GPS-UHF loggers during the  
 680 chick rearing period on Amsterdam Island in 2016-2017 and 2015-2016. Right: corresponding  
 681 unfiltered raw locations; each colour represents an individual.





682

683 Figure 5. Recursive space utilisation by breeding brown skuas equipped with GPS-UHF  
684 loggers during the chick rearing period on Amsterdam Island. The contours correspond to the  
685 individual 50% recursion distribution isopleths; each colour represents an individual with  
686 dashed and solid lines for individuals tracked in 2015-2016 and 2016-2017 respectively. See  
687 Figure S1.C.4 for individual data.

688