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

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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[®], 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[®] *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[®], 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[®] isolation and purification
209 protocol for skua cloacal swabs preserved in RNA NOW[®] , and with the QIAamp cad
210 Pathogen Mini[®] 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[®], 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
439 of the manuscript. All authors contributed substantially to the drafts and gave final approval
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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.,
459 2019).

460 **References**

- 461 Baker, L., Matthiopoulos, J., Müller, T., Freuling, C., & Hampson, K. (2019). Optimizing
462 spatial and seasonal deployment of vaccination campaigns to eliminate wildlife
463 rabies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374,
464 20180280.
- 465 Benhamou, S. (2011). Dynamic approach to space and habitat use based on biased random
466 bridges. *PLOS ONE*, 6, e14592.

467 Benhamou, S., & Riote-Lambert, L. (2012). Beyond the utilization distribution: Identifying
468 home range areas that are intensively exploited or repeatedly visited. *Ecological*
469 *Modelling*, 227, 112–116.

470 Boulinier, T., Kada, S., Ponchon, A., Dupraz, M., Dietrich, M., Gamble, A., ... McCoy, K. D.
471 (2016). Migration, prospecting, dispersal? What host movement matters for infectious
472 agent circulation? *Integrative and Comparative Biology*, 56, 330–342.

473 Bourret, V., Gamble, A., Tornos, J., Jaeger, A., Delord, K., Barbraud, C., ... Boulinier, T.
474 (2018). Vaccination protects endangered albatross chicks against avian cholera.
475 *Conservation Letters*, 11, e12443.

476 Carneiro, A. P. B., Manica, A., Trivelpiece, W. Z., & Phillips, R. A. (2015). Flexibility in
477 foraging strategies of Brown Skuas in response to local and seasonal dietary
478 constraints. *Journal of Ornithology*, 156, 625–633.

479 Carneiro, A. P. B., Manica, A., & Phillips, R. A. (2014). Foraging behaviour and habitat use
480 by brown skuas *Stercorarius lonnbergi* breeding at South Georgia. *Marine Biology*,
481 161, 1755–1764.

482 Caron, A., Cappelle, J., Cumming, G. S., de Garine-Wichatitsky, M., & Gaidet, N. (2015).
483 Bridge hosts, a missing link for disease ecology in multi-host systems. *Veterinary*
484 *Research*, 46, 83.

485 Christensen, J. P., & Bisgaard, M. (2000). Fowl cholera. *Revue Scientifique et Technique*
486 *(International Office of Epizootics)*, 19(2), 626–637.

487 Cleaveland, S., Hess, G. R., Dobson, A., Laurensen, M. K., McCallum, H. I., Roberts, M., &
488 Woodroffe, R. (2002). The role of pathogens in biological conservation. In P. J.
489 Hudson, A. Rizzoli, B. T. Grenfell, & J. A. P. Heesterbeek (Eds.), *The Ecology of*
490 *Wildlife Diseases* (pp. 139–150). Oxford: Oxford University Press.

491 Craft, M. E., Hawthorne, P. L., Packer, C., & Dobson, A. P. (2008). Dynamics of a multihost
492 pathogen in a carnivore community. *Journal of Animal Ecology*, 77, 1257–1264.

493 Curtis, P. E. (1983). Transmission of *Pasteurella multocida* infection from the brown rat
494 (*Rattus norvegicus*) to domestic poultry. *Veterinary Record*, 113, 133–134.

495 Cuthbert, R., Ryan, P. G., Cooper, J., & Hilton, G. (2003). Demography and population
496 trends of the Atlantic yellow-nosed albatross. *The Condor*, 105, 439–452.

497 Daversa, D. R., Fenton, A., Dell, A. I., Garner, T. W. J., & Manica, A. (2017). Infections on
498 the move: how transient phases of host movement influence disease spread.
499 *Proceedings of the Royal Society B: Biological Sciences*, 284, 20171807.

500 de Souza Petersen, E., de Araujo, J., Krüger, L., Seixas, M. M., Ometto, T., Thomazelli, L.
501 M., ... Petry, M. V. (2017). First detection of avian influenza virus (H4N7) in Giant
502 Petrel monitored by geolocators in the Antarctic region. *Marine Biology*, 164, 62.

503 Descamps, S., Jenouvrier, S., Gilchrist, H. G., & Forbes, M. R. (2012). Avian cholera, a
504 threat to the viability of an Arctic seabird colony? *PLOS ONE*, 7, e29659.

505 Dougherty, E. R., Seidel, D. P., Carlson, C. J., Spiegel, O., & Getz, W. M. (2018). Going
506 through the motions: incorporating movement analyses into disease research.
507 *Ecology Letters*, 21, 588-604

508 Duron, Q., Shiels, A. B., & Vidal, E. (2017). Control of invasive rats on islands and priorities
509 for future action: rats on islands. *Conservation Biology*, 31, 761–771.

510 Furness, R. W. (1987). *The Skuas*. A&C Black, London.

511 Gamble, A., Bazire, R., Delord, K., Barbraud, C., Jaeger, A., Gantelet, H., ... Boulinier, T.
512 (2019). ECOPATH: brown skua *Pasteurella multocida* epidemiological data and GPS
513 tracking data (Amsterdam Island, 2015-2017). OSU OREME Repository.
514 <https://doi.org/10.15148/b4b4a2e1-3d00-45b7-b3b2-2ca05d054346>

515 Gamble, A., Garnier, R., Jaeger, A., Gantelet, H., Thibault, E., Tortosa, P., ... Boulinier, T.
516 (2019). Dynamics of antibody levels against avian cholera after natural exposure and
517 vaccination of albatrosses: disease ecology implications. *Oecologia*, 189, 939-949.

518 Garnier, R., Ramos, R., Sanz-Aguilar, A., Poisbleau, M., Weimerskirch, H., Burthe, S., ...
519 Boulinier, T. (2017). Interpreting ELISA analyses from wild animal samples: some
520 recurrent issues and solutions. *Functional Ecology*, 31, 2255–2262.

521 Garnier, R., Ramos, R., Staszewski, V., Militão, T., Lobato, E., González-Solís, J., &
522 Boulinier, T. (2012). Maternal antibody persistence: a neglected life-history trait with
523 implications from albatross conservation to comparative immunology. *Proceedings of*
524 *the Royal Society of London B: Biological Sciences*, 279, 2033–2041.

525 Giles, J. R., Eby, P., Parry, H., Peel, A. J., Plowright, R. K., Westcott, D. A., & McCallum, H.
526 (2018). Environmental drivers of spatiotemporal foraging intensity in fruit bats and
527 implications for Hendra virus ecology. *Scientific Reports*, 8, 9555.

528 Guinet, C., Jouventin, P., & Georges, J. Y. (1994). Long term population changes of fur
529 seals *Arctocephalus gazella* and *Arctocephalus tropicalis* on subantarctic (Crozet)
530 and subtropical (St. Paul and Amsterdam) islands and their possible relationship to El
531 Niño Southern Oscillation. *Antarctic Science*, 6, 473–478.

532 Guzzetta, G., Tagliapietra, V., Perkins, S. E., Hauffe, H. C., Poletti, P., Merler, S., & Rizzoli,
533 A. (2017). Population dynamics of wild rodents induce stochastic fadeouts of a
534 zoonotic pathogen. *Journal of Animal Ecology*, 86, 451–459.

535 Halliday, J. E. ., Meredith, A. L., Knobel, D. L., Shaw, D. J., Bronsvoort, B. M. d. C., &
536 Cleaveland, S. (2007). A framework for evaluating animals as sentinels for infectious
537 disease surveillance. *Journal of The Royal Society Interface*, 4, 973–984.

538 Haydon, D. T., Randall, D. A., Matthews, L., Knobel, D. L., Tallents, L. A., Gravenor, M. B.,
539 ... Laurenson, M. K. (2006). Low-coverage vaccination strategies for the
540 conservation of endangered species. *Nature*, 443, 692–695.

541 Heerah, K., Dias, M. P., Delord, K., Oppel, S., Barbraud, C., Weimerskirch, H., & Bost, C. A.
542 (2019). Important areas and conservation sites for a community of globally
543 threatened marine predators of the Southern Indian Ocean. *Biological Conservation*,
544 234, 192–201.

545 Jaeger, A., Gamble, A., Lagadec, E., Lebarbenchon, C., Bourret, V., Tornos, J., ... Tortosa,
546 P. Exploring the infection dynamics of a bacterial pathogen on a remote oceanic
547 island reveals annual epizootics impacting an albatross population. *BioRxiv*, 711283
548 [Preprint]. July 2019 [cited July 2019].

549 Jaeger, A., Lebarbenchon, C., Bourret, V., Bastien, M., Lagadec, E., Thiebot, J.-B., ...
550 Weimerskirch, H. (2018). Avian cholera outbreaks threaten seabird species on
551 Amsterdam Island. *PLOS ONE*, 13, e0197291.

552 Keith, D. A., Martin, T. G., McDonald-Madden, E., & Walters, C. (2011). Uncertainty and
553 adaptive management for biodiversity conservation. *Biological Conservation*, 144,
554 1175–1178.

555 Klomp, N. I., & Furness, R. W. (1990). Variations in numbers of nonbreeding great skuas
556 attending a colony. *Ornis Scandinavica*, 21, 270-276.

557 Lascelles, B. G., Taylor, P. R., Miller, M. G. R., Dias, M. P., Oppel, S., Torres, L., ... Small,
558 C. (2016). Applying global criteria to tracking data to define important areas for
559 marine conservation. *Diversity and Distributions*, 22, 422–431.

560 Leotta, G. A., Chinen, I., Vigo, G. B., Pecoraro, M., & Rivas, M. (2006). Outbreaks of avian
561 cholera in Hope Bay, Antarctica. *Journal of Wildlife Diseases*, 42, 259–270.

562 Lloyd-Smith, J. O., Cross, P. C., Briggs, C. J., Daugherty, M., Getz, W. M., Latto, J., ... Swei,
563 A. (2005). Should we expect population thresholds for wildlife disease? *Trends in*
564 *Ecology & Evolution*, 20, 511–519.

565 Lloyd-Smith, J. O., Schreiber, S. J., Kopp, P. E., & Getz, W. M. (2005). Superspreading and
566 the effect of individual variation on disease emergence. *Nature*, 438, 355–359.

567 Longmire, J. L., Lewis, A. K., Brown, N. C., Buckingham, J. M., Clark, L. M., Jones, M. D., ...
568 Ray, F. A. (1988). Isolation and molecular characterization of a highly polymorphic
569 centromeric tandem repeat in the family *Falconidae*. *Genomics*, 2, 14–24.

570 Marchand, P., Freycon, P., Herbaux, J.-P., Game, Y., Toïgo, C., Gilot-Fromont, E., ... Hars,
571 J. (2017). Sociospatial structure explains marked variation in brucellosis
572 seroprevalence in an Alpine ibex population. *Scientific Reports*, 7, 15592.

573 Mariën, J., Borremans, B., Kourouma, F., Baforday, J., Rieger, T., Günther, S., ... Fichet-
574 Calvet, E. (2019). Evaluation of rodent control to fight Lassa fever based on field data
575 and mathematical modelling. *Emerging Microbes & Infections*, 8, 640–649.

576 Merkle, J. A., Cross, P. C., Scurlock, B. M., Cole, E. K., Courtemanch, A. B., Dewey, S. R., &
577 Kauffman, M. J. (2017). Linking spring phenology with mechanistic models of host
578 movement to predict disease transmission risk. *Journal of Applied Ecology*, 55, 810–
579 819.

580 Micol, T., & Jouventin, P. (1995). Restoration of Amsterdam Island, South Indian Ocean,
581 following control of feral cattle. *Biological Conservation*, 73, 199–206.

582 Navarro, J., Grémillet, D., Afán, I., Miranda, F., Bouten, W., Forero, M. G., & Figuerola, J.
583 (2019). Pathogen transmission risk by opportunistic gulls moving across human
584 landscapes. *Scientific Reports*, 9, 10659.

585 Parmelee, D. F., Maxson, S. J., & Bernstein, N. P. (1979). Fowl cholera outbreak among
586 brown skuas at Palmer Station. *Antarctic Journal of the United States*, 14, 168–169.

587 Paull, S. H., Song, S., McClure, K. M., Sackett, L. C., Kilpatrick, A. M., & Johnson, P. T.
588 (2012). From superspreaders to disease hotspots: linking transmission across hosts
589 and space. *Frontiers in Ecology and the Environment*, 10, 75–82.

590 Pepin, K. M., Davis, A. J., Beasley, J., Boughton, R., Campbell, T., Cooper, S. M., ...
591 VerCauteren, K. C. (2016). Contact heterogeneities in feral swine: implications for
592 disease management and future research. *Ecosphere*, 7, e01230.

593 Pepin, K. M., Kay, S. L., Golas, B. D., Shriner, S. S., Gilbert, A. T., Miller, R. S., ...
594 Buhnerkempe, M. G. (2017). Inferring infection hazard in wildlife populations by
595 linking data across individual and population scales. *Ecology Letters*, 20, 275–292.

596 Pietz, P. J. (1987). Feeding and nesting ecology of sympatric South Polar and brown skuas.
597 *The Auk*, 104, 617–627.

598 Robinson, S. J., Barbieri, M. M., Murphy, S., Baker, J. D., Harting, A. L., Craft, M. E., &
599 Littnan, C. L. (2018). Model recommendations meet management reality:
600 implementation and evaluation of a network-informed vaccination effort for
601 endangered Hawaiian monk seals. *Proceedings of the Royal Society B: Biological*
602 *Sciences*, 285, 20171899.

603 Rolland, V., Barbraud, C., & Weimerskirch, H. (2009). Assessing the impact of fisheries,
604 climate and disease on the dynamics of the Indian yellow-nosed albatross. *Biological*
605 *Conservation*, 142, 1084–1095.

606 Rushmore, J., Caillaud, D., Hall, R. J., Stumpf, R. M., Meyers, L. A., & Altizer, S. (2014).
607 Network-based vaccination improves prospects for disease control in wild
608 chimpanzees. *Journal of the Royal Society Interface*, 11, 20140349.

609 Sage, M. J. L., Towey, B. D., & Brunner, J. L. (2019). Do scavengers prevent or promote
610 disease transmission? The effect of invertebrate scavenging on Ranavirus
611 transmission. *Functional Ecology*, 33, 1342–1350.

612 Samuel, M. D., Shadduck, D. J., Goldberg, D. R., & Johnson, W. P. (2003). Comparison of
613 methods to detect *Pasteurella multocida* in carrier waterfowl. *Journal of Wildlife*
614 *Diseases*, 39, 125–135.

615 Samuel, M. D., Takekawa, J. Y., Baranyuk, V. V., & Orthmeyer, D. L. (1999). Effects of avian
616 cholera on survival of Lesser Snow Geese *Anser caerulescens*: an experimental
617 approach. *Bird Study*, 46, 239–247.

618 Sebastiano, M., Eens, M., Pineau, K., Chastel, O., & Costantini, D. (2019). Food
619 supplementation protects magnificent frigatebird chicks against a fatal viral disease.
620 *Conservation Letters*, e12630.

621 Strona, G., Carstens, C. J., Beck, P. S. A., & Han, B. A. (2018). The intrinsic vulnerability of
622 networks to epidemics. *Ecological Modelling*, 383, 91–97.

623 Thiebot, J.-B., Barbraud, C., Delord, K., Marteau, C., & Weimerskirch, H. (2014). Do
624 introduced mammals chronically impact the breeding success of the world's rarest
625 albatross? *Ornithological Science*, *13*, 41–46.

626 Trivelpiece, W., Butler, R. G., & Volkman, N. J. (1980). Feeding territories of brown skuas
627 (*Catharacta lonnbergi*). *The Auk*, *97*, 669–676.

628 Viana, M., Mancy, R., Biek, R., Cleaveland, S., Cross, P. C., Lloyd-Smith, J. O., & Haydon,
629 D. T. (2014). Assembling evidence for identifying reservoirs of infection. *Trends in*
630 *Ecology & Evolution*, *29*, 270–279.

631 Votier, S. C., Bearhop, S., Ratcliffe, N., & Furness, R. W. (2004). Reproductive
632 consequences for Great Skuas specializing as seabird predators. *The Condor*, *106*,
633 275.

634 Weimerskirch, H. (2004). Diseases threaten Southern Ocean albatrosses. *Polar Biology*, *27*,
635 374–379.

636 Wille, M., McBurney, S., Robertson, G. J., Wilhelm, S. I., Blehert, D. S., Soos, C., ...
637 Whitney, H. (2016). A pelagic outbreak of avian cholera in North American gulls:
638 scavenging as a primary mechanism for transmission? *Journal of Wildlife Diseases*,
639 *52*, 793–802.

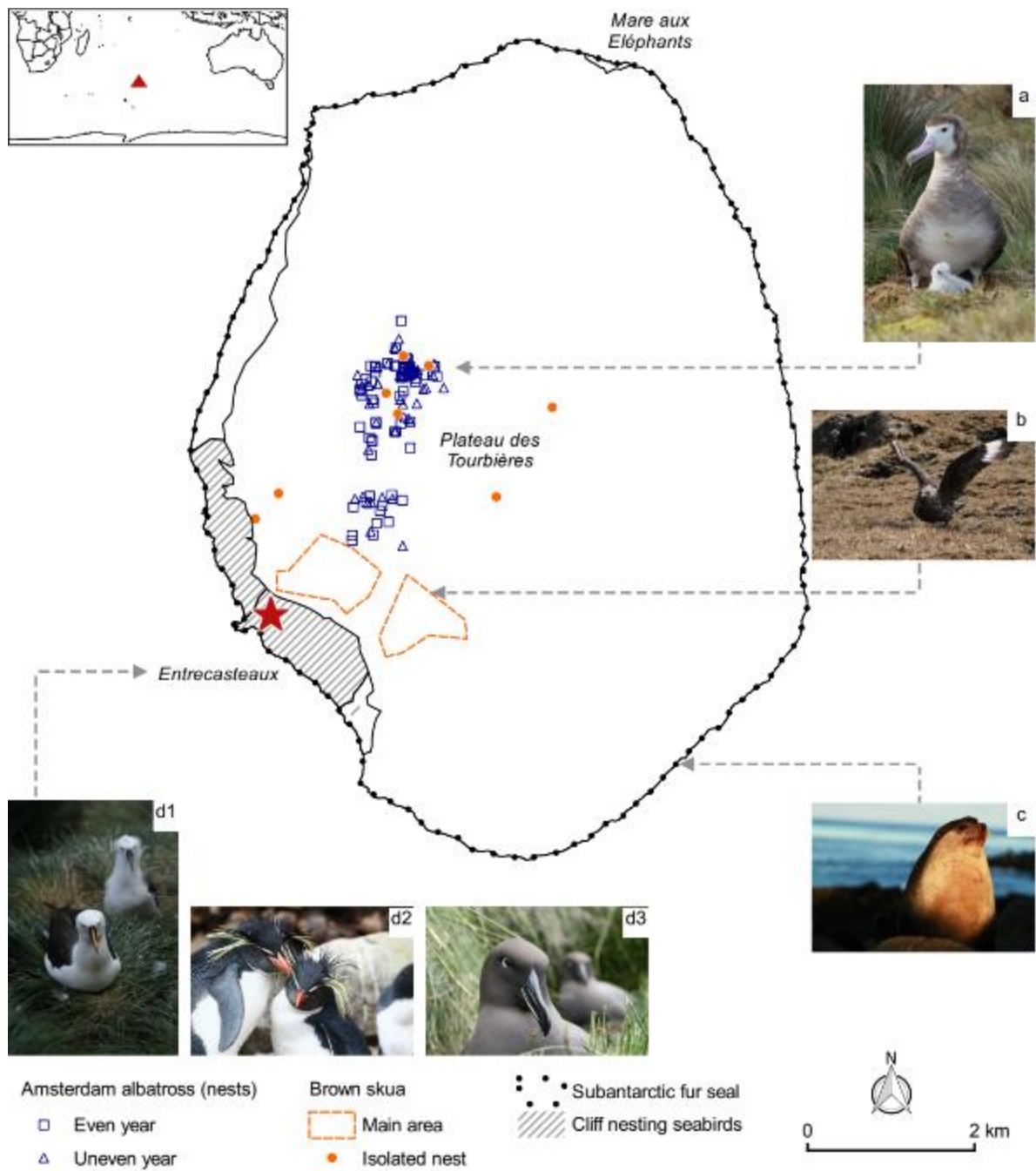
640 Woodroffe, R., & Donnelly, C. A. (2011). Risk of contact between endangered African wild
641 dogs *Lycaon pictus* and domestic dogs: opportunities for pathogen transmission.
642 *Journal of Applied Ecology*, *48*, 1345–1354.

643 Young, H. S., Wood, C. L., Kilpatrick, A. M., Lafferty, K. D., Nunn, C. L., & Vincent, J. R.
644 (2017). Conservation, biodiversity and infectious disease: scientific evidence and
645 policy implications. *Philosophical Transactions of the Royal Society B*, *372*,
646 20160124.

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)

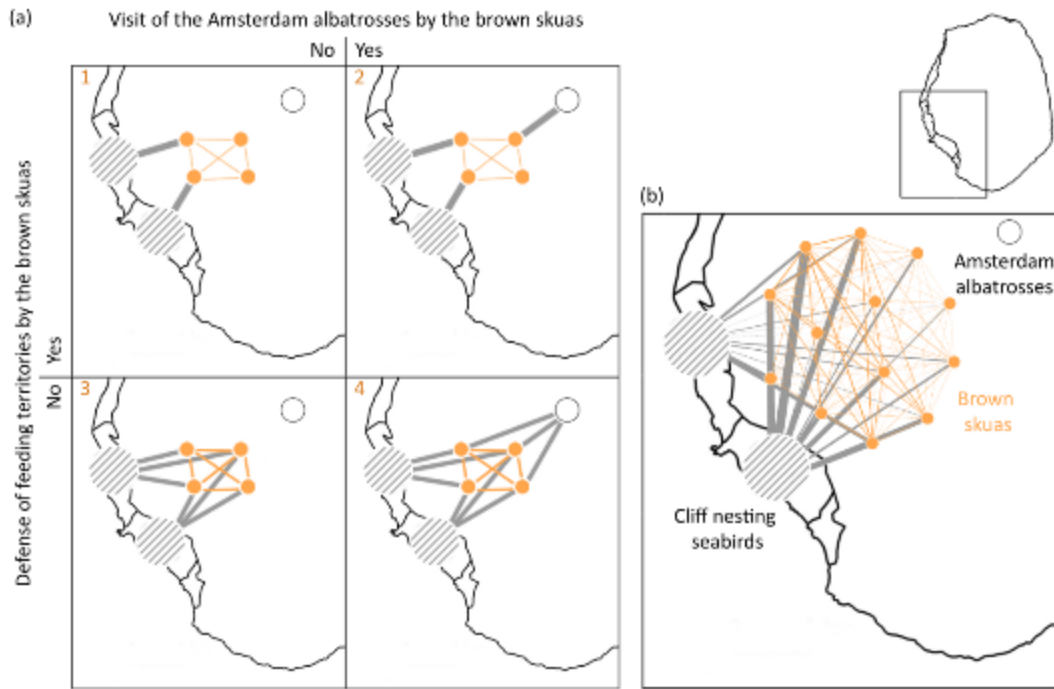
655 mostly nest on the southern part on the inland plateau; subantarctic fur seals (c) breed all

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

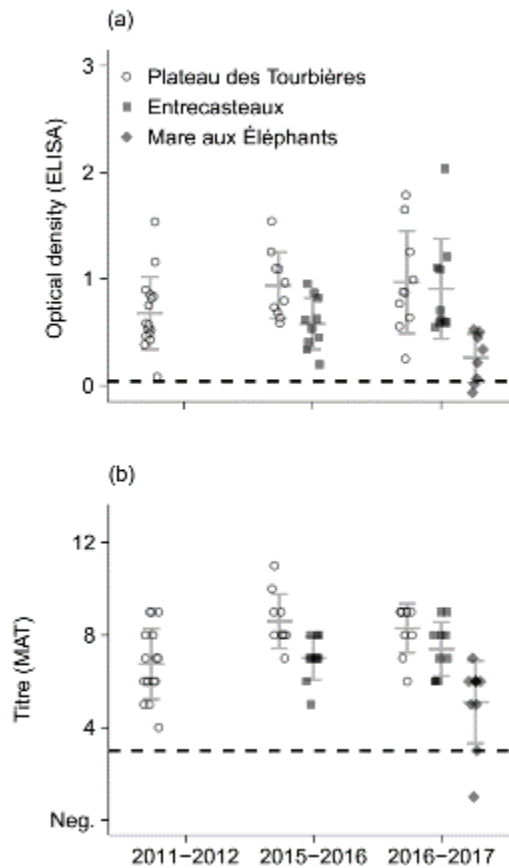
658 denotes the monitored yellow-nosed albatross subcolony. Photos: Romain Bazire, IPEV. Map

659 background: Réserve Naturelle Nationale des Terres Australes Françaises.



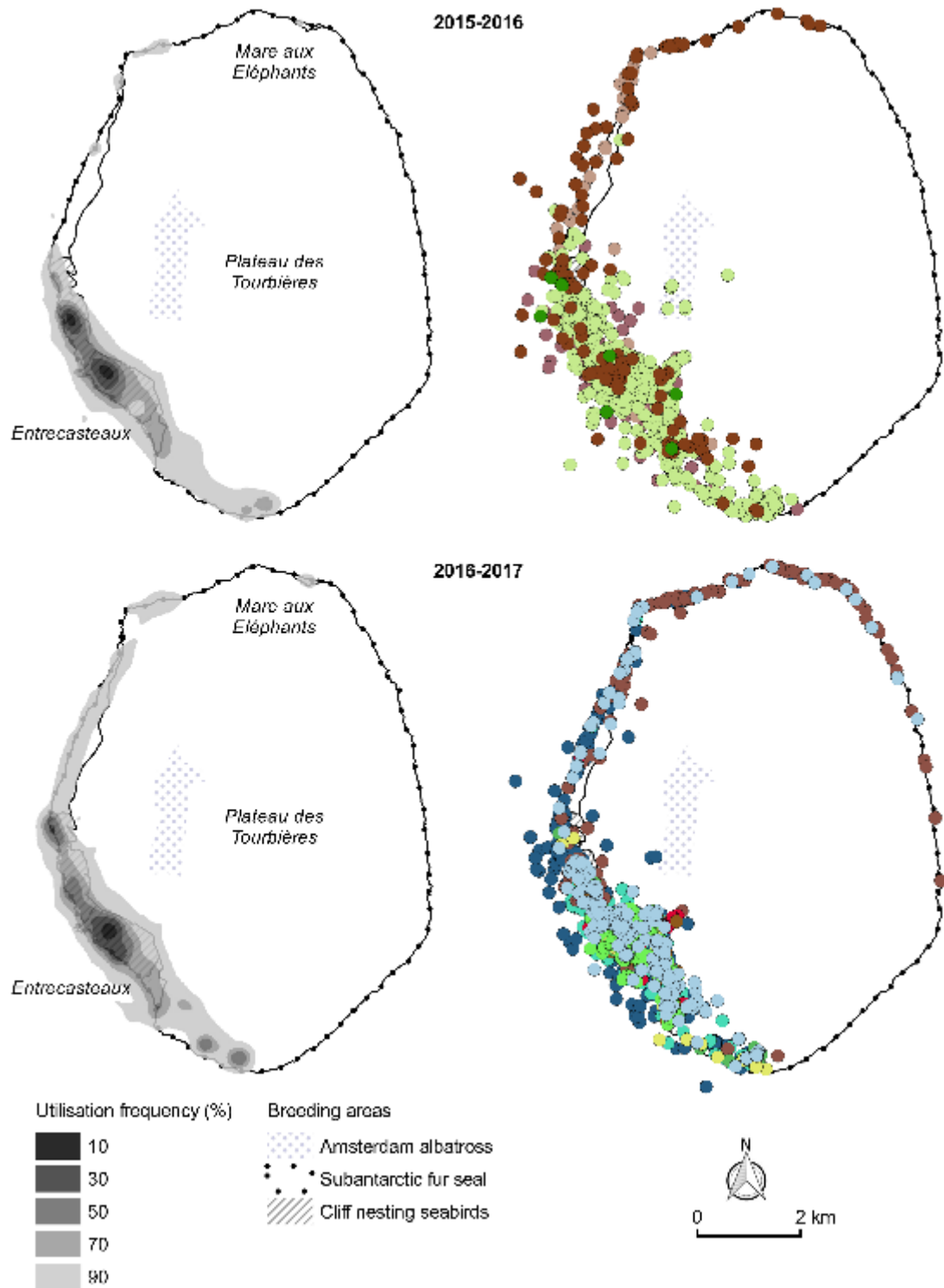
660

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).



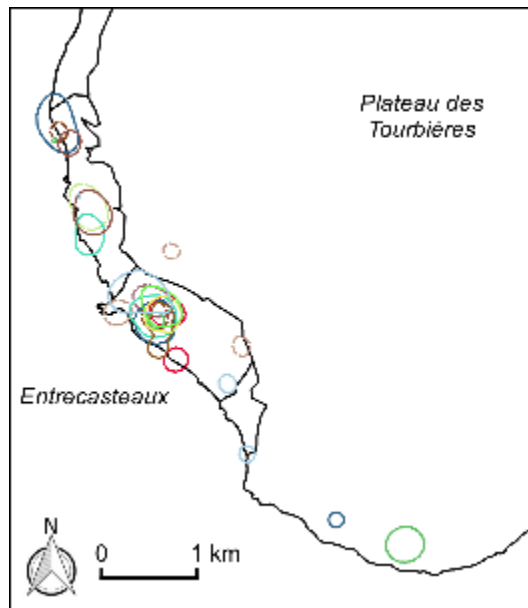
670

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