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RESEARCH ARTICLE

Predator and scavenger movements among and within endangered seabird colonies: Opportunities for pathogen spread

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Abstract

1. The spatial structure of host communities is expected to constrain pathogen spread. However, predators and/or scavengers may connect distant host (sub) populations when foraging. Determining whether some individuals or populations play a prominent role in the spread of pathogens is critical to inform management measures.
2. We explored movements and epidemiological status of brown skuas *Stercorarius antarcticus*, the only avian terrestrial consumer native of Amsterdam Island (Indian Ocean), to assess whether and how they could be involved in the spread of the bacterium *Pasteurella multocida*, which recurrently causes avian cholera outbreaks in endangered albatross and penguin species breeding on the island.
3. High proportions of seropositive and DNA-positive individuals for *P. multocida* indicated that skuas are highly exposed to the pathogen and may be able to transmit it. Movement tracking revealed that the foraging ranges of breeding skuas largely overlap among individuals and expand all along the coasts where albatrosses and penguins nest, but not on the inland plateau hosting the endemic Amsterdam albatross *Diomedea amsterdamensis*.
4. Considering the epidemiological and movement data, skua movements may provide opportunity for pathogen spread among and within seabird colonies.
5. *Synthesis and applications.* This work highlights the importance of considering the behaviour and epidemiological status of predators and scavengers in disease dynamics because the foraging movements of individuals of such species can potentially limit the efficiency of local management measures in spatially structured host communities. Such species could thus represent priority vaccination targets

to implement efficient management measures aiming at limiting pathogen spread and also be used as sentinels to monitor pathogen circulation and evaluate the effectiveness of management measures.

KEYWORDS

conservation biology, disease ecology, dynamic space utilization, individual heterogeneity, movement ecology, *Pasteurella multocida*, sentinel species, serology

1 | INTRODUCTION

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

Terrestrial predators and scavengers may effectively connect otherwise isolated colonies or social groups when foraging, potentially contributing to pathogen spread with conservation (Craft et al., 2008), public health (Navarro et al., 2019) or fundamental implications (Boulinier et al., 2016). In wild communities subject to infectious disease outbreaks, deciphering the contact structure and examining the hosts' respective contributions in epidemiological dynamics are thus critical to develop control measures. The role of predator and/or scavenger species as potential spreaders of infectious agents is poorly documented because it requires targeted field efforts at the often unpredictable time of outbreaks (Daversa, Fenton, Dell, Garner, & Manica, 2017). For instance, the role of scavengers has been suspected in avian cholera, caused by the bacterium *Pasteurella multocida* (*Pm*), outbreaks (Wille et al., 2016), but their actual contribution as spreaders still requires proper examination.

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

Despite the strong impact of avian cholera outbreaks on the endangered seabirds of Amsterdam Island (Jaeger et al., 2018) and the availability of a vaccine proven to protect albatross nestlings (Bourret et al., 2018), no control measure has been implemented besides basic biosecurity measures. Indeed, relying on vaccination of nestlings to maintain the local yellow-nosed albatross population to its current size (~22,000 pairs; Heerah et al., 2019) would require to vaccinate thousands of nestlings every year and may thus not represent an efficient conservation strategy. In contrast, interrupting transmission chains by treating individuals responsible for the among-colony circulation of the bacterium may help to protect some colonies with minimal efforts. Since *Pm* transmission occurs primarily through an oro-faecal route (Samuel, Shadduck, Goldberg, & Johnson, 2003), it is unclear how *Pm* circulates locally. Indeed, seabirds on Amsterdam Island breed in spatially structured, mostly mono-specific, colonies (Figure S1.A.1) and albatrosses and penguins forage exclusively at sea (Heerah et al., 2019). Hence, although contacts may be frequent within dense seabird colonies, contacts between individuals from different colonies may thus be rare besides potential limited prospecting movements (Boulinier et al., 2016).

Terrestrial predators and scavengers could, however, spread *Pm* across the island while foraging among seabird colonies undergoing

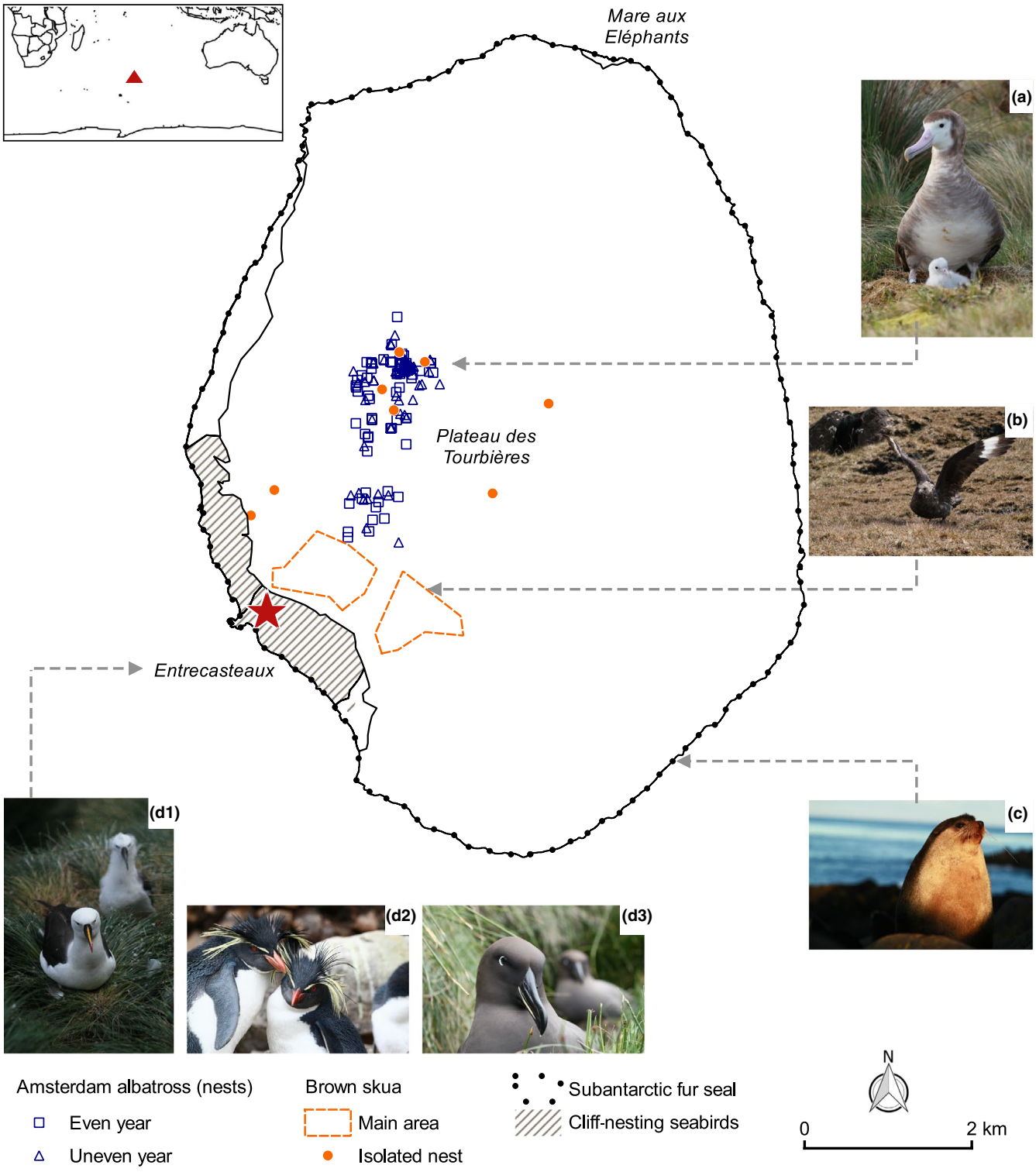

FIGURE 1 Breeding sites of colonial vertebrates on Amsterdam Island (37°49′S, 77°33′E). Amsterdam albatrosses (a) nest on the northern part of the inland plateau; brown skuas (b) mostly nest on the southern part on the inland plateau; subantarctic fur seals (c) breed all around the island; Indian yellow-nosed albatrosses (d1), northern rockhopper penguins (d2) and sooty albatrosses (d3) nest in the high cliffs laying south-west of the island. The red star denotes the monitored yellow-nosed albatross subcolony. Photos: Romain Bazire, IPEV. Map background: Réserve Naturelle Nationale des Terres Australes Françaises

outbreaks. Notably, the small population of brown skuas *Stercorarius antarcticus*, the sole terrestrial vertebrate predators and scavengers native to the island, could disseminate the bacterium when foraging through shedding and/or by moving infected albatrosses and penguins (Pietz, 1987). Introduced brown rats *Rattus norvegicus* and house mice *Mus musculus* (Micol & Jouventin, 1995) could also

carry and shed the bacterium, notably as they prey and scavenge on seabird chicks (Figure S1.A.2; Thiebot, Barbraud, Delord, Marteau, & Weimerskirch, 2014), although the distribution of resources and geographical barriers created by the island relief probably constrain the spatial scale of their contribution. In addition, the endemic Amsterdam albatross *Diomedea amsterdamensis* could also be at risk of exposure to *Pm* via foraging skuas because it nests a few kilometres inland from the yellow-nosed albatross colonies, although nestling die-offs have seldom been recorded in this species (Jaeger et al., 2018).

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

2 | MATERIALS AND METHODS

2.1 | Study population

Around 60 pairs of brown skuas breed at low density yearly on Amsterdam Island's 'Plateau des Tourbières' (PDT; Figure 1). Breeders generally lay two eggs in October/November, and nestlings hatch in late November/early December and fledge 40–50 days later. Skuas attend clubs notably in the north ('Mare aux Éléphants' [MAE]) and

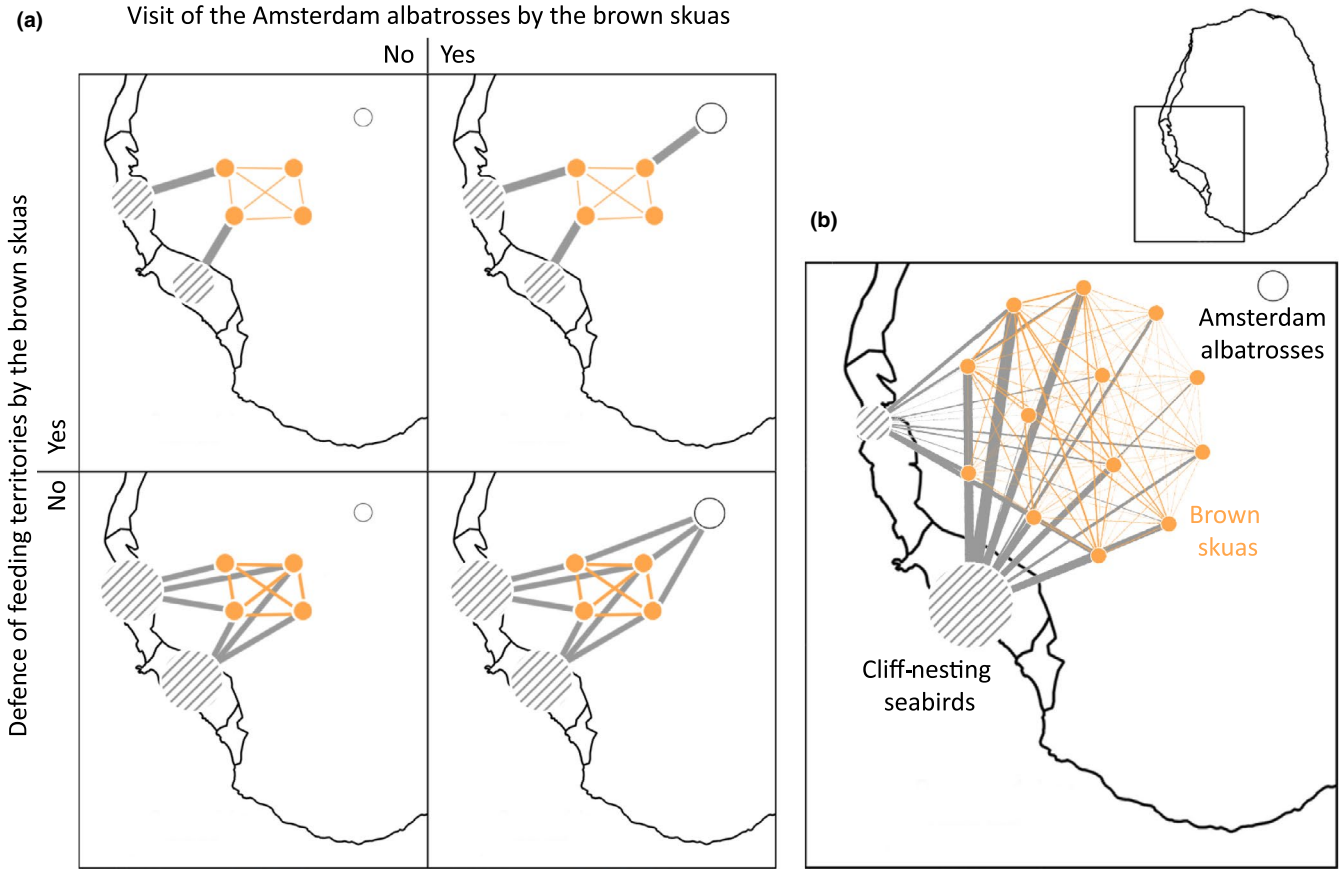

FIGURE 2 Hypothetical (a) and observed (b) epidemiological networks linking seabirds on Amsterdam Island based on breeding brown skua movements. Each orange node represents an individual skua. The hatched and white nodes represent grouped subpopulations of cliff-nesting birds (i.e. yellow-nosed albatrosses,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

the south-west (bottom of 'Entrecasteaux' cliffs). Amsterdam Island holds important populations of Indian yellow-nosed albatrosses, sooty albatrosses (~400 pairs; Heerah et al., 2019) and northern rockhopper penguins (~12,000 pairs), all breeding in mostly monospecific colonies on the south-west coastal cliffs between August and May (Figure 1). The 40–50 pairs of Amsterdam albatrosses nest biennially further inland, on the northern part of the PDT (Figure 1). A few small *Procellariiformes* are also present on the island in very low numbers (Micol & Jouventin, 1995). All around the island, subantarctic fur seals *Arctocephalus tropicalis* calve on the beaches in December (Guinet, Jouventin, & Georges, 1994), also providing food opportunities for skuas (placentas and dead pups). Introduced brown rats and house mice are often observed in seabird colonies (Figure S1.A.2). Feral cats *Felis catus* were also introduced on the island (Micol & Jouventin, 1995), but are rarely observed in seabird colonies.

2.2 | Field sampling

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

2.3 | Immunological assays

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

2.4 | Molecular detection of *Pm*

Total nucleic acids were extracted following the RNA NOW® isolation and purification protocol for skua cloacal swabs preserved in RNA NOW®, and with the QIAamp cador Pathogen Mini® Kit (QIAGEN) for skua cloacal swabs preserved in Longmire lysis buffer. *Pm* DNA

TABLE 1 Proportions of brown skuas from Amsterdam Island positive for anti-*Pm* antibodies according to MAT and ELISA and for *Pm* DNA according to PCR or RT-PCR from cloacal swabs. Clopper–Pearson 95% confidence intervals are indicated between brackets and numbers of positive/tested individuals between parentheses

		2011–2012			2015–2016			2016–2017		
Site	Stage	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)

Abbreviations: ELISA, enzyme-linked immunosorbent assay; MAT, microagglutination test; PCR, polymerase chain reaction; RT-PCR, real-time polymerase chain reaction.

was detected with a real-time polymerase chain reaction (RT-PCR) targeting the strain previously detected in a dead sooty albatross on Amsterdam Island (Jaeger et al., 2019). Technical details are given in Appendix S1.B.

2.5 | Movement tracking

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

Using the GPS data, the intensity (spatial distribution of the mean residence time per visit of each area, i.e. areas where an individual tends to spend more time) and recursion (spatial distribution of the number of visits in each area, i.e. areas that an individual tends to repeatedly visit) distributions were computed to get a dynamic picture of space utilization (Benhamou & Riotte-Lambert, 2012). The overlap of the patches recursively used by different individuals was visually examined to inform on the existence of exclusive feeding territories in this population. To estimate the intensity and recursion distributions, non-overlapping virtual circles of 50 m in radius (referred to as 'areas') were delimited. A new visit to an area occurred each time the tracked individual re-entered it after a time-lag spent outside the area longer than 10 min and remained in that area for at least 15 min (to exclude cases in which birds went through an area without using it) using the BRB|MKDE program (for Biased Random Bridges for Movement-based Kernel Density Estimation; Benhamou, 2011). All data were analysed and represented after exclusion of locations recorded within the nesting area of the tracked individuals unless indicated otherwise. Resulting distributions were visualized in QGIS 2.18.21.

2.6 | Monitoring of yellow-nosed albatrosses

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

2.7 | Statistical analyses

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

3 | RESULTS

3.1 | Detection of *Pm* and anti-*Pm* antibodies

Specific antibodies were detected in all but two plasma samples from adult brown skuas by both MAT and ELISA, resulting in seroprevalence varying between 80% and 100% depending on the site and year (Table 1). In 2016–2017, based on the ELISA results, antibody levels were significantly lower in MAE than in Entrecasteaux and PDT (both $p < .01$; Table S1.B.1). All other pairwise comparisons were not statistically different (Figure 3). The same results were obtained from the MAT data. *Pm* DNA was detected in cloacal swabs of adults from PDT and Entrecasteaux, but not from MAE (Table 1). The proportion of *Pm* positive samples was generally low (≤33%), except for PDT in 2016–2017 with 8/10 positive individuals. Regarding nestlings, neither specific antibodies nor *Pm* DNA was detected in samples from 2011 to 2012. In 2016–2017, *Pm* DNA was detected in three seronegative nestlings; one other nestling was seropositive but not excreting *Pm* DNA (Table 1; Figure S1.E.1).

3.2 | Individual movement tracking

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

Recursively exploited areas largely overlapped among the tracked individuals (Figure 5; Figure S1.C.4). Entrecasteaux cliffs were intensively and recursively exploited by all the tracked individuals (Figure 5, Figures S1.C.4, S1.C.5, Table S1.C.2), notably during avian cholera outbreaks (Figure S1.D.1), and represented the only recursively visited site for four of them. Other sites recursively visited included the northern part of the south-west cliff, harbouring large seabird and fur seal colonies, the north coast, hosting another large fur seal colony, and the south plain where seabirds and fur seals

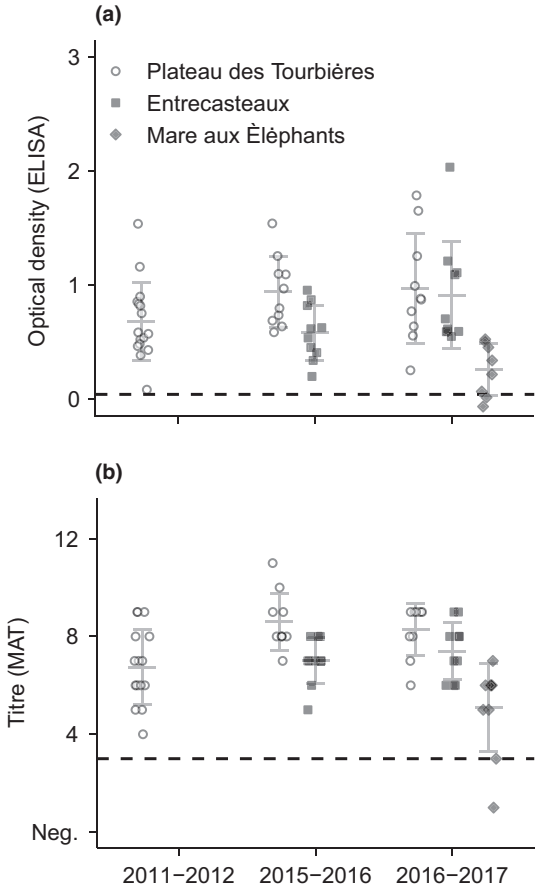

FIGURE 3 Evidence of high exposure of brown skuas to *Pasteurella multocida*: anti-Pm antibody levels for skuas measured by ELISA (a) and MAT (b) over three years on Plateau des Tourbières (the main skua breeding ground on Amsterdam Island), and two clubs (Entrecasteaux and Mare aux Éléphants). Mean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

are rare, but rodent populations may be present. Note that all the tracked individuals were seropositive and *Pm* DNA was detected in 8/13 birds (Table S1C.2) at the time of logger deployment.

4 | DISCUSSION

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

4.1 | Skua exposure and infection by *Pm* and implications for epidemiological surveillance

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

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

Interestingly, detection of specific antibodies in the majority of PCR-negative adults also suggests that a large proportion may survive *Pm* exposure, contrasting with the high mortality rate reported during previous outbreaks in Antarctica (Leotta, Chinen, Vigo, Pecoraro, & Rivas, 2006; Parmelee, Maxson, & Bernstein, 1979). This heterogeneity is not surprising given the known variability of *Pm* virulence in different hosts (Christensen & Bisgaard, 2000). Moreover, the low mortality rate of adult skuas on Amsterdam Island is similar to that of adult yellow-nosed albatrosses on that island (Gamble, Garnier, et al., 2019; Rolland, Barbraud, & Weimerskirch, 2009), but the higher seroprevalence in skuas suggests different rates of exposure and/or persistence of antibody levels. If skuas are highly exposed but resistant or tolerant to infection by *Pm*, they could also be involved in the maintenance of the pathogen on the island. This result also shows that skuas are potentially good sentinels to detect the circulation of *Pm*, especially using serology (Halliday et al., 2007). Hence, implementing long-term serosurveys targeting such species can be especially useful for the acquisition of baseline data on (pathogenic and non-pathogenic) infectious agent circulation and for the early detection of pathogen circulation. Indeed, in long-lived species

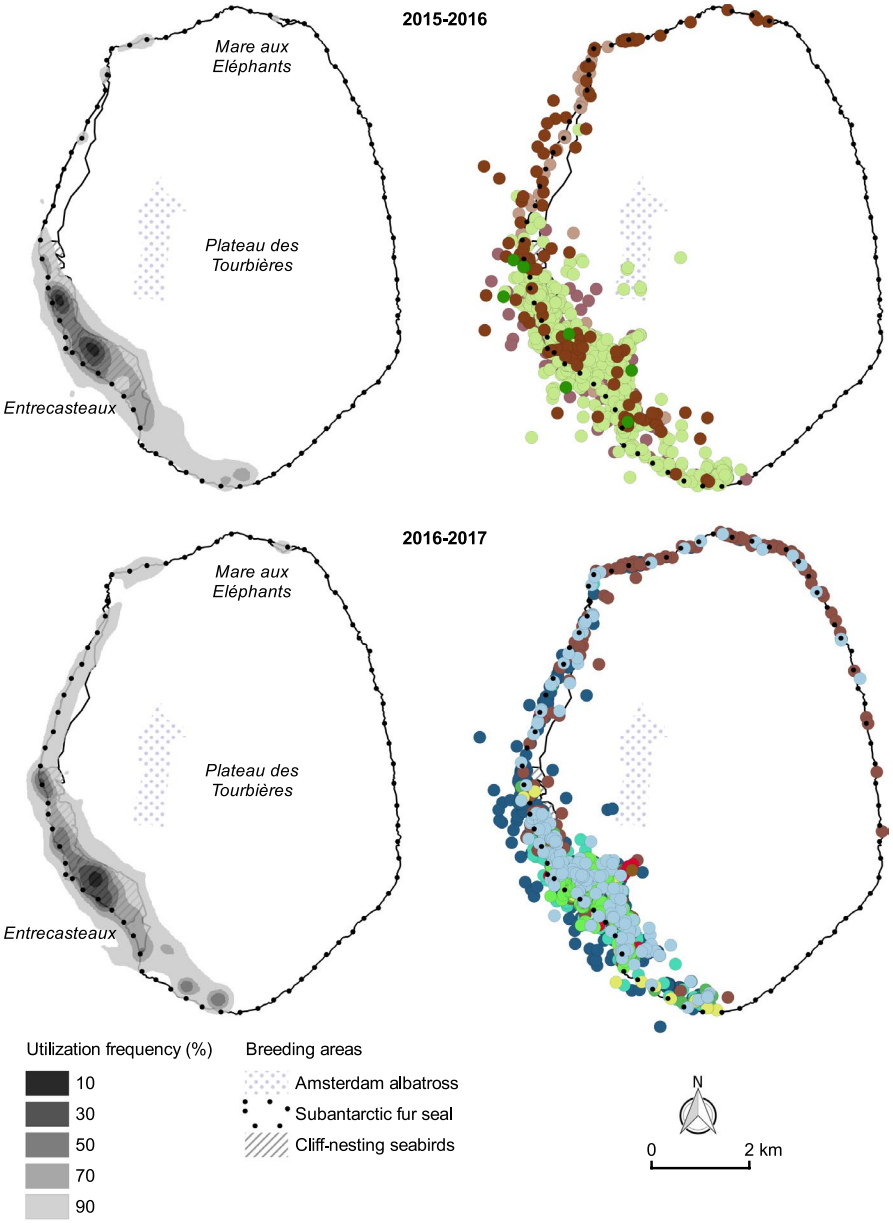

FIGURE 4 Space utilization by breeding brown skuas. Left: distribution of space utilization outside of their breeding area by all individuals equipped with GPS-UHF loggers during the chick-rearing period on Amsterdam Island in 2016–2017 and 2015–2016. Right: corresponding unfiltered raw locations; each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

such as seabirds, monitoring protocols based only on breeding pair counts can take several years before capturing juvenile mortality events because of late recruitment.

4.2 | Movements and disease transmission in structured communities

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

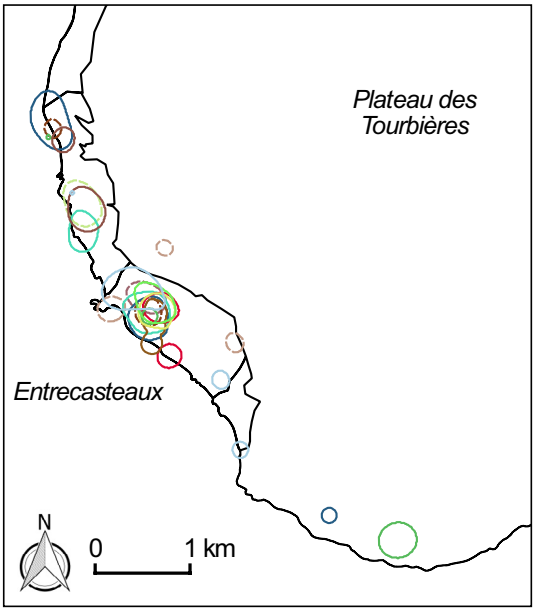

FIGURE 5 Recursive space utilization by breeding brown skuas equipped with GPS-UHF loggers during the chick-rearing period on Amsterdam Island. The contours correspond to the individual 50% recursion distribution isopleths; each colour represents an individual with dashed and solid lines for individuals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

sources of heterogeneity among individuals remain to be explored, such as variations in the duration or intensity of shedding.

We did not observe breeding skuas foraging in the small- and low-density breeding population of the Amsterdam albatross, suggesting that they may not connect this population to others (Figure 2b). This is consistent with the high breeding success of this albatross population over the last decades (Jaeger et al., 2018). Although a few skua pairs nest among Amsterdam albatrosses (Figure 1), contacts between the two species may be rare if skuas forage only on the coast, as movements around the nests are usually limited. However, considering the flexibility of skuas' foraging behaviour and potential behavioural differences between breeders and non-breeders, some individuals may occasionally visit this colony, especially if environmental conditions and food availability change (Carneiro, Manica, Trivelpiece, & Phillips, 2015). Such changes, modifying the host space utilization, can have important consequences on the dynamics of infectious agents (Giles et al., 2018; Merkle et al., 2017). Long-term monitoring of these dynamics is essential to better understand pathogen circulation and design robust management options.

4.3 | Maintenance and circulation of infectious agent

The population of brown skuas may play a key role in the circulation of *Pm* on Amsterdam Island, but the complete maintenance community (i.e. the set of connected host populations that together can maintain the pathogen over the long term, notably in winter when most seabirds are absent of the island; Viana et al., 2014) remains to be functionally characterized. Rodents may be good candidates as local maintenance hosts of *Pm*, but little data are yet available to examine this hypothesis. Rodents can reach high densities and are present year-round; they may feed on dead seabird nestlings and are preyed upon by skuas (Figure S1.A.2b,d). In addition, as observed in poultry (Curtis, 1983), rodents may directly transmit *Pm* through movements within colonies and biting of live nestlings (Thiebot et al., 2014; Figure S1.A.2c). Hence, spatio-temporal aspects of rodent exposure to *Pm* and subsequent shedding need to be explored from an eco-epidemiological standpoint (Guzzetta et al., 2017; Lloyd-Smith, Cross, et al., 2005). Because the home range radius of rodents is likely much smaller than that of skuas, rodents could be important in the within-colony spreading of *Pm*, while skuas may play a key role at a larger spatial scale. These elements suggest potentially complex epidemiological networks involving several bridge hosts (Caron, Cappelle, Cumming, Garine-Wichatitsky, & Gaidet, 2015) linking cliff-nesting seabirds to Amsterdam albatrosses. Skuas could move *Pm* from the coastal cliffs to PDT, where a few breed in proximity to Amsterdam albatrosses. Foraging rodents could then move the bacterium from those skuas to the Amsterdam albatrosses. More generally, this stresses the importance of considering processes occurring at nested spatial scales and epidemiological networks in their entirety when exploring chains of transmission (Boulinier et al., 2016; Daversa et al., 2017). In the case of Amsterdam Island, future work should examine the role of introduced rodents in the maintenance and small-scale circulation of avian pathogens.

4.4 | Implications for conservation

Our study revealed that the movements of potential bridge hosts (here, skuas and potentially rodents) may reduce the efficiency of local actions aiming at controlling multi-host infectious agents. For instance, locally intensive vaccination programmes targeting albatrosses (e.g. Bourret et al., 2018; Gamble, Garnier, et al., 2019) combined to rodent population control would seem feasible in accessible seabird colonies. However, such attempts would likely fail to control the pathogen because, although the system appears highly spatially structured, skuas could re-introduce the pathogen from inaccessible, hence non-treated, seabird colonies. In such a system, efficient disease control measures would likely need to interrupt the transmission network by targeting bridge hosts by, for instance, vaccinating native terrestrial predators (here skuas) with a vaccine blocking transmission and eradicating introduced rodents. However, we do not recommend culling native terrestrial predators as there are growing evidences that scavenging contribute in disease controls (e.g. Le Sage, Towey, & Brunner, 2019) and the culling of a native species would raise strong ethical issues. In the case of avian cholera on Amsterdam Island, an autogenous vaccine has proven efficient to protect yellow-nosed albatross nestlings (Bourret et al., 2018), but whether it blocks transmission remains to be investigated. The direct negative impact of introduced rodents on seabird populations

is well documented, and their eradication is seen as a priority for seabird conservation (see Duron, Shiels, & Vidal, 2017 for a review). In contrast, their role in epidemiological dynamics has rarely been explored, but its potential is highlighted by our results. Implementing the eradication of introduced rodent populations on Amsterdam Island in parallel to the epidemiological monitoring of seabird populations would provide a unique opportunity to semi-experimentally assess their role in the eco-epidemiological dynamics while representing a significant management action in itself.

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

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AUTHORS' CONTRIBUTIONS

T.B. conceived the idea of this work; T.B., J.T., H.W., K.D. and C.B. designed the study; J.T., A.G. and J.-B.T. collected the data; H.G. and E.T. developed the MAT; A.G., A.J., C.L., P.T. and E.L. performed the serology and molecular analyses; A.G. analysed the epidemiological data; A.G., R.B. and J.-B.T. analysed the tracking data; A.G. and T.B. led the writing of the manuscript. All authors contributed substantially to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available on the OSU-OREME Repository https://doi.oreme.org/b4b4a2e1-3d00-45b7-b3b2-2ca05d054346 (Gamble, Bazire, et al., 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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