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RESEARCH ARTICLE

Hanging out at the club: Breeding status and territoriality affect individual space use, multi-species overlap and pathogen transmission risk at a seabird colony

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Abstract

1. Wildlife movement ecology often focuses on breeders, whose territorial attachments facilitate trapping and following individuals over time. This leads to incomplete understanding of movements of individuals not actively breeding due to age, breeding failure, subordinance, and other factors. These individuals are often present in breeding populations and contribute to processes such as competition and pathogen spread. Therefore, excluding them from movement ecology studies could bias or mask important spatial dynamics.
2. Loafing areas offer an alternative to breeding sites for capturing and tracking individuals. Such sites may allow for sampling individuals regardless of breeding status, while also avoiding disturbance of sensitive breeding areas. However, little is known about the breeding status of individuals attending loafing sites, or how their movements compare to those of breeders captured at nests.
3. We captured a seabird, the brown skua, attending either nests or loafing areas ('clubs') at a multi-species seabird breeding site on Amsterdam Island (southern Indian Ocean). We outfitted skuas with GPS-UHF transmitters and inferred breeding statuses of individuals captured at clubs using movement patterns of breeders captured at nests. We then compared space use and activity patterns between breeders and nonbreeders.
4. Both breeding and nonbreeding skuas attended clubs. Nonbreeders ranged more widely, were more active, and overlapped more with other seabirds and marine mammals than did breeders. Moreover, some nonbreeders occupied fixed territories and displayed more restricted movements than those without territories. Nonbreeders became less active over the breeding season, while activity of breeders remained stable. Nonbreeding skuas were exposed to the agent of avian cholera at similar rates to breeders but were more likely to forage

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in breeding areas of the endangered endemic Amsterdam albatross, increasing opportunities for interspecific pathogen transmission.

5. Our results show that inference based only on breeders fails to capture important aspects of population-wide movement patterns. Capturing nonbreeders as well as breeders would help to improve population-level representation of movement patterns, elucidate and predict effects of external changes and conservation interventions (e.g. rat eradication) on movement patterns and pathogen spread, and develop strategies to manage outbreaks of diseases such as highly pathogenic avian influenza.

KEYWORDS
Diomedea amsterdamensis, dynamic space utilization, floaters, foraging, infectious disease, nonbreeding, *Stercorarius antarcticus*

1 | INTRODUCTION

Many key processes underlying wildlife population dynamics are spatially structured. These include habitat and resource selection (Aebischer et al., 1993), intra- and interspecific interactions (Laundré et al., 2010), migratory connectivity (Amstrup et al., 2004), pathogen transmission (White et al., 2018) and exposure to risk (Hays et al., 2019). Ultimately, linking demographic outcomes to spatially explicit processes requires detailed knowledge of individual variation in movement patterns and distribution (Morales et al., 2010). Due the cost, labour and disturbance involved in obtaining individual movement data, however, the sample of individuals included in movement studies often represents only a small fraction of the overall population. To minimize bias in inferences and maximize power to describe population-level variation, tracking studies must therefore sample a sufficiently diverse population to effectively capture patterns and processes of interest.

To directly link habitat conditions and movement decisions to demographic outcomes, studies of wildlife movement frequently target breeding individuals (e.g. Hinam & St. Clair, 2008; Schofield et al., 2010). In species with altricial young, breeders occupy a restricted habitat area during breeding and often return to the same breeding site year after year, which may make them easier to capture and follow over time than individuals of unknown breeding status (Cooper & Marra, 2020; Votier et al., 2011). However, not all individuals present at or near breeding sites at any given time are actively breeding (e.g. nonbreeding adults, sub-adults, failed breeders). Nonbreeding individuals, also called floaters, may be present in wildlife breeding areas for a variety of reasons including delayed sexual maturity, resource competition or breeding failure, and their presence and distribution affect multiple aspects of population dynamics (Pardo et al., 2013; Penteriani et al., 2011; Ponchon et al., 2013). Nonbreeders can directly enhance survival or reproductive success of breeders by diluting predation, assisting in breeding, or participating in social foraging or defence (Branconi et al., 2020), and provide a reservoir of potential breeders in case adult survival decreases (Klomp & Furness, 1992). Conversely, nonbreeders attending breeding areas may depress reproductive success and survival by increasing density-dependent pressures including resource competition, aggression and pathogen transmission (Bretagnolle et al., 2008). Assessing the relative importance of these positive and negative effects requires understanding the prevalence, distribution, and interactions of nonbreeders with the breeding population.

In addition to their potential demographic effects, nonbreeders often range more widely than breeders, affecting their interactions with species and environments at the landscape scale (Mayer et al., 2017; Webb et al., 2011). For example, nonbreeders may make more frequent exploratory movements and visit a greater variety of breeding areas than established or successful breeders (Ponchon et al., 2015; Votier et al., 2011). In addition, nonbreeders may feed on different resources during (Borghello et al., 2019; McInnes et al., 2016) and after the breeding season (Clay et al., 2016), which may affect their exposure to environmental conditions and interactions with other species. Consequently, individuals not producing or raising young can play important roles in transferring information, propagules, contaminants, genes and pathogens within and among breeding populations and species (Boulinier et al., 2016). Movement studies that exclude such individuals therefore risk mischaracterizing movement patterns and distribution of the overall population, potentially influencing the evaluation of demographic parameters and risk factors (Cooper & Marra, 2020).

The brown skua *Stercorarius antarcticus*, a colonially-breeding seabird, provides an opportunity to compare breeding and nonbreeding individuals under similar environmental conditions. Both breeding and nonbreeding brown skuas are often present at breeding colonies, where they feed on other seabirds and mammals via predation, scavenging and kleptoparasitism (Furness et al., 2020). This behaviour brings them into frequent contact with a variety of native and introduced bird and mammal species

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as well as anthropogenic discards (Hemmings, 1990). As scavengers, skuas may also act as reservoirs for pathogen accumulation and transmission, making them a useful sentinel for assessing pathogen dynamics in remote areas (Miller et al., 2008; Vicente & VerCauteren, 2019; Wille et al., 2016). Brown skuas are potential spreaders of pathogens to other seabirds breeding in remote colonies (Gamble et al., 2020), where cyclic outbreaks of diseases such as avian cholera (due to *Pasteurella multocida*; *Pm*) threaten the long-term viability of endangered seabirds, including endemic species (Bourret et al., 2018; Jaeger et al., 2018). Thus, understanding interactions of skuas with sympatric species is required to accurately measure, monitor and predict dynamics of interspecific pathogen transmission and spread (Gamble et al., 2020). While previous studies have examined foraging patterns of breeding skuas during the breeding season (e.g. Carneiro et al., 2015; Gamble et al., 2020; Schultz et al., 2021), little information is available on movements of nonbreeders during this period. Both breeding and nonbreeding skuas attend and defend territories at common loafing areas (hereafter, clubs) during the breeding period (Borghello et al., 2019), offering an opportunity to capture a broad cross-section of individuals and examine the role of nonbreeders in spatially structured processes and interactions (Furness, 2015; Klomp & Furness, 1992). However, it is necessary to validate the use of these sites by a broad cross-section of individuals and assess potential biases in populations available for sampling. In addition, since breeding status of seabirds captured away from nest sites is unknown and may be difficult to assess (McFarlane Tranquilla et al., 2003), a reliable method is needed to determine reproductive status of individuals captured at clubs.

To assess how skua movement patterns and habitat use vary with breeding status, we captured and tracked brown skuas attending a sub-tropical breeding colony, at either nest sites (i.e. known breeders) or clubs (i.e. individuals of unknown breeding status). We fitted both groups with GPS-UHF transmitters to infer breeding status and measure movement frequency and distance, habitat use, and overlap with other species. Our principal research question was whether space use of skuas captured at clubs would differ from that of breeders captured at nests. More specifically, we investigated (1) whether movement patterns and distribution differed between breeding and nonbreeding skuas; (2) whether breeding status of skuas affect the frequency or intensity of their use of breeding areas of other species; and (3) whether breeding status affects the likelihood that brown skuas will act as spreaders of infectious agents such as *Pasteurella multocida*.

2 | MATERIALS AND METHODS

2.1 | Study site

We conducted all fieldwork on Amsterdam Island (37°49′S, 77°33′E), a 55 km^2 volcanic island in the southern Indian Ocean hosting large populations of emblematic, globally threatened seabird species (Heerah et al., 2019). The island consists of a mountainous 500–800 m plateau whose western edge is defined by sheer cliffs. Seabirds breed primarily in the southwest quadrat of the island in largely monospecific sub-colonies. The central plateau provides nesting habitat for brown skuas (~60 pairs), along with the entire population of the endemic, endangered Amsterdam albatross *Diomedea amsterdamensis* (40–50 pairs) (Gamble et al., 2020; Figure 1). Beaches and cliffs are used by three additional species of endangered seabirds: yellow-nosed albatrosses *Thalassarche carteri*

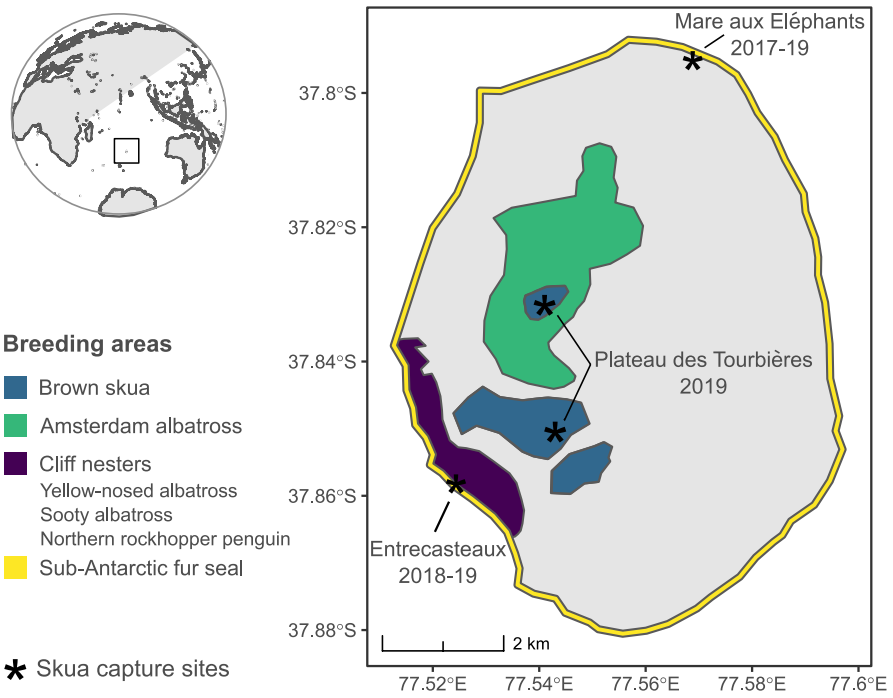

FIGURE 1 Seabird and seal breeding areas and brown skua capture locations on Amsterdam Island, 2017–2020.

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(~22,000 pairs), sooty albatrosses *Phoebetria fusca* (~400 pairs) and northern rockhopper penguins *Eudyptes moseleyi* (~12,000 pairs) (Figure 1). Sub-Antarctic fur seals *Arctocephalus tropicalis* breed in large numbers (~6400 pups; Guinet et al., 1994) along the perimeter of the island (Figure 1). Nonnative mammal species occur throughout the island, including house mice *Mus musculus*, brown rats *Rattus norvegicus*, and feral cats *Felis catus* (Micol & Jouventin, 1995).

Brown skuas breed annually on Amsterdam Island from October–January, including a month-long incubation period (October–November) and 40–50-day chick-rearing period beginning in late November (Furness et al., 2020). Nests occur throughout the central plateau (Plateau des Tourbières), most densely in the southwestern quadrant (Figure 1). Breeding and nonbreeding skuas congregate throughout the breeding season in communal loafing areas (clubs) at the base of the western cliffs (Entrecasteaux), close to small lakes on the central plateau, and in the northeast quadrat of the island (Mare aux Eléphants; Figure 1). Prior data suggest that breeding skuas on Amsterdam Island occupy terrestrial habitats during the breeding season (Gamble et al., 2020).

2.2 | Capture and tagging

We captured skuas during three austral summers (i.e. breeding seasons) using noose poles, leg nooses, or by hand. Cohorts 1 (2017–2018) and 2 (2018–2019) included adult skuas of unknown breeding status captured at club sites (Entrecasteaux and Mare aux Eléphants; Figure 1) during the late chick rearing period (18 December–20 January). Cohort 3 (2019–2020) included individuals from both club sites, as well as breeding skuas captured on nests during late incubation and early chick-rearing (8 November–8 December).

Upon capture, we collected physical measurements, blood samples, and oral and cloacal swabs, verified nest contents where applicable, banded birds with unique markers (metal and alphanumeric Darvic rings), and attached remote-downloading, solar-powered GPS transmitters (GPS-UHF Harrier-L, Ecotone Telemetry, Gdynia, Poland; 13 g) to scapular feathers—that is, upper back between the wings—using waterproof cloth adhesive tape (tesa Extra Power: Hamburg, Germany). Because prior tracking efforts documented limited nocturnal movement in this population (Gamble et al., 2020), we chose to collect only diurnal locations and conserve battery life during periods without solar recharging. Thus, transmitters recorded locations every 5 min during daylight (05:00–22:00 UTC +5) and lasted 0–100 days (average: 48 days). To ensure enough data to accurately estimate home ranges and characterize behaviour, we excluded individuals whose transmitters collected <24 h of continuous data from further analysis; all remaining transmitters were active for at least 6 days. Receiving antennas were placed near loafing sites, in a yellow-nosed albatross colony on Entrecasteaux cliff, and on the margin of the skua breeding area. Because of difficulties accessing skua nests in a strictly protected area, breeding success could not be directly monitored; however, tracking data confirmed that all individuals captured at nests continued attending their nest sites after release. Experimental design was approved by the Regional Animal Experimentation Ethical Committee (French Ministry of Research permit #10257-2018011712301381v6) and by the Comité de l'Environnement Polaire (A-2017-97, A-2017-111, A-2018-123, A 2018–139, A-2019-69, 2019–121, A-2019-132 and A-2019-135).

2.3 | Determination of epidemiological status and sex

Upon capture, blood samples (1 ml from the metatarsal vein using heparinized syringes), and oral and cloacal swabs were collected to explore epidemiological status of individual skuas with respect to the agent of avian cholera *Pasteurella multocida* (*Pm*), as in a previous study in the same population (Gamble et al., 2020). 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 (Longmire buffer; Longmire et al., 1988). Samples were kept at −20°C in the field, then stored at −20°C (plasma) or −80°C (swabs) until analysis.

To assess past exposure to *Pm*, we measured specific antibody levels against the bacteria in plasma samples of a subsample of captured skuas using a microagglutination test (MAT) using the D2C *Pm* isolate from Amsterdam Island (SEROPAST®, Ceva Biovac, France; see Gamble et al., 2020). To assess infection status at capture, total nucleic acids were extracted from oral and cloacal swabs using the QuantiNova Probe PCR kit (QIAGEN, USA) and screened for *Pm* DNA by real-time polymerase chain reaction (RT-PCR) using primers and protocols from Townsend et al. (1998). To compare the current study with previous epidemiology results, we incorporated an additional dataset of antibody titres and *Pm* DNA presence from breeding and nonbreeding skuas on Amsterdam Island sampled between 2011 and 2017 (Gamble et al., 2019), collected and analysed using the same methods (Gamble et al., 2020).

Since sex of skuas could not be determined visually, we sexed individuals using DNA extracted from red blood cells using the DNeasy Blood and Tissue Kit (QIAGEN, USA). We tested for the presence of the W-chromosome-linked (i.e. female-specific) CHD1W gene via polymerase chain reaction (PCR) using 2550F and 2718R primers as described by Fridolfsson and Ellegren (1999).

2.4 | Data processing and breeding status inference

We conducted all data analysis in R 4.2.0 (R Core Team, 2022). We cleaned data by regularizing tracks to consistent 5-min intervals during each daylight tracking period using the *ltraj* function in package ADEHABITATLT (Calenge, 2006) and removed erroneous locations using a speed filter of 12 km/h, or 1 km between successive locations (van Bemmelen et al., 2018).

To test for differences in *Pm* antibody levels and infections among capture locations, we constructed generalized linear mixed models (GLMM) in the NLME package (Pinheiro et al., 2022) in R 4.2.0 (R Core Team, 2022), with antibody titre (Gaussian) or seropositivity/PCR

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positivity (binomial) as response variables. Models included fixed effects of year and either location type (nest or club) or capture location (Plateau des Tourbieres, Entrecasteaux, or Mare aux Eléphants). We considered fixed effects to differ among groups if the 95% confidence interval of the coefficient estimate did not overlap zero.

To determine the breeding status of skuas captured at clubs, we used the *find_nests* function in the NESTR package (Picardi et al., 2020). We then defined a breeding site as ≥60 points within a radius of 15 m in or near skua breeding habitat (Figure 1). Onsite tests indicated an error rate of ~20 m in GPS fixes at the base of the cliff; we chose a slightly smaller radius to account for the openness of the plateau habitat. We further specified that the area include ≥1 visit per day for ≥3 consecutive days within the week following capture, and limited our analysis to the breeding season (1 November–1 February). We tested the algorithm on known breeders ($n = 6$) to ensure that it correctly identified known nest locations before applying it to individuals of unknown status captured at clubs ($n = 35$). We considered sites that fit the parameters to be breeding sites if they occurred in potential nesting habitat (i.e. excluding known clubs or resting areas). For individuals with more than one site fitting the criteria, we identified the first site occupied post-capture as the primary breeding site.

To compare behavioural patterns among skuas, we processed individual tracks using a three-state Hidden Markov Model in package MOVEHMM (Michelot et al., 2016). The model assigned locations to one of three underlying movement states: resting (turning angles and interlocation distances close to zero), foraging (sharp turning angles and short distances) or commuting (wide turning angles and long distances; see Figure S1).

2.5 | Utilization distributions and multi-species overlap

To compare habitat use by skuas, we calculated individual kernel density estimates and composite estimates by breeding status using the *kde* function in the KS package (Duong, 2020). We used a plugin bandwidth estimator and a grid size of approximately 0.001°. We then generated polygons representing the core (50% utilization distribution, or 50% UD) and full (90% UD) individual and composite home ranges. We projected isopleths using a Lambert Azimuthal Equal Area projection centred on the island and calculated their areas (km^2). To assess seasonal changes in movement, we calculated core and full home range sizes for each individual across a 5-day moving window centred on each day of the season.

To assess the representativeness of our sample relative to the overall population, we calculated inclusion values following the methods of Lascelles et al. (2016). Briefly, for a sample of *N* individuals, inclusion values are calculated by sub-setting random samples of 1:*N* individuals from the tracked population, calculating the utilization distribution using only the subset, and then determining the percentage of locations of individuals not included in the subset that fall within the calculated utilization distribution. After calculating inclusion values for 1:*N* individuals, the asymptote of the nonlinear function relating inclusion and *N* is assumed to be the maximum inclusion value if all individuals in the population were sampled. The representativeness of the overall sample is thus calculated by dividing the inclusion value for *N* by the asymptote. We calculated inclusion of full home ranges (90% UD) for the overall sample as well as for nest and club captures alone, using 50 replicates per sample size.

To compare probability of interaction with other species by breeding status, we overlaid individual locations and home range areas with Amsterdam albatross, cliff-nesting seabird and seal habitat polygons. We then calculated the proportion of individual skua core and full home range polygons that occurred within other species' habitat areas (i.e. 0 = no overlap, 1 = completely overlapping) as well as the proportion of skua locations within other species' habitat areas that were assigned to each behavioural state.

2.6 | Modelling

We used GLMMs to compare tracking duration among breeding statuses and assess differences in behaviour and home range size. We constructed separate models for each of five response variables—core home range area (50% UD; km^2), full home range area (90% UD; km^2), and proportion of locations classified in each of the three behavioural states (resting, foraging and commuting)—both within overall home ranges and in areas overlapping habitats used by Amsterdam albatross, cliff-nesting seabirds and seals.

All models used a Gaussian distribution and identity link and included fixed effects of breeding status, day of season (linear or quadratic), sex, wing chord, capture site and cohort (year), and a random effect of individuals. We tested preliminary models with an additional fixed effect of either tracking duration or number of locations to account for differences in sample size among individuals; however, these additional effects increased the Akaike Information Criterion (AIC) value by >2 points for all models relative to models without these effects and thus did not improve model fit (Burnham & Anderson, 2004).

We considered a predictor variable to significantly improve model fit if the 95% confidence interval of its coefficient estimate did not overlap zero. To obtain final models, we successively dropped nonsignificant terms from models until confidence intervals for all remaining coefficients differed from zero, or until dropping an additional term did not decrease the AIC value by >2 points. We further assessed differences among groups using post-hoc general linear hypothesis tests in the MULTCOMP package (Hothorn et al., 2008).

Tracking data and individual metadata used in this analysis are archived on Zenodo: https://doi.org10.5281/zenodo.7362496 (Lamb et al., 2022).

3 | RESULTS

We deployed transmitters on 50 individuals over three breeding seasons (2017–2021). Forty-one of the transmitters collected

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sufficient data for analysis (i.e. functioned continuously for ≥24 h), including 6/8 transmitters deployed at nest sites and 35/42 transmitters deployed at clubs (see Table S1). The nine remaining transmitters apparently experienced mechanical failure before or shortly after deployment, as individuals carrying these transmitters were observed in the vicinity of antennas after transmitters had stopped functioning. Transmitters lasted an average of 56 days each (range = 10–100). Tracking duration was similar between individuals captured at nests (mean ± standard deviation [SD]: 60.3 ± 26.8 days) and clubs (55.4 ± 29.4 days) (95% CI of coefficient value [β] = −9.11–40.79). Molecular sexing was sufficient to determine sex of 32 tracked skuas (78%). Sex ratios skewed female overall (21/32; 66%) and in all individual years. We did not detect differences in skeletal measurements between sexes (see Table S2); therefore, biometric measurements were not sufficient to sex unknown individuals.

Space use of tracked skuas was highly representative, (97%; see Figure S2), suggesting that our sample size was sufficient to describe movements of the sampled population. Individuals captured at clubs were substantially more representative (90.3%) than nest captures (65.8%; see Figure S2) and had higher inclusion values for all sample sizes (see Figure S2). Composite core home ranges for the two club sites overlapped by 57% (SD: ±7%), and full home ranges overlapped by 76% (SD: ±14%), suggesting use of similar habitats among club sites. Our algorithm correctly identified known breeding locations for 7 of 7 individuals captured at nests, although only 6 provided sufficient data for further analysis. The same algorithm identified likely breeding locations for 3 of 35 (8.6%) individuals captured at clubs. For an additional 8 of 35 (22.9%) individuals, the algorithm identified locations that fit the selection criteria but were located at known clubs or in nonnesting habitat between the main skua breeding areas (see Figure S3). We classified these individuals as territorial nonbreeders (see Table S1 and Table S4). Several breeders occupied secondary territories both during and after the breeding season (see Table S4 and Figure S3).

Behavioural patterns and distributions differed among breeders, territorial nonbreeders and nonterritorial nonbreeders. All groups used broadly similar areas spanning plateau and cliff habitats used by breeding seabirds and, peripherally, coastal areas used by breeding seals. However, composite core and full home range sizes were substantially larger for nonterritorial nonbreeders than for breeders or territorial nonbreeders, which used areas of similar size (Figure 2). Individual core and full home ranges were significantly smaller for breeders than for nonterritorial nonbreeders, while territorial nonbreeders used home ranges of intermediate size (Table 1; Figure 3). Breeders rested more than either territorial or nonterritorial nonbreeders (Figure 3). Among nonbreeders, territorial nonbreeders spent more time foraging, while nonterritorial nonbreeders spent more time commuting (Figure 3). Among variables included in GLMMs, only breeding status and day of season (quadratic) were significant predictors for home range sizes or activity levels (Table 1). Sex, wing chord, capture site, and cohort were not significant predictors and did not improve model fit for any of the five response variables we modelled.

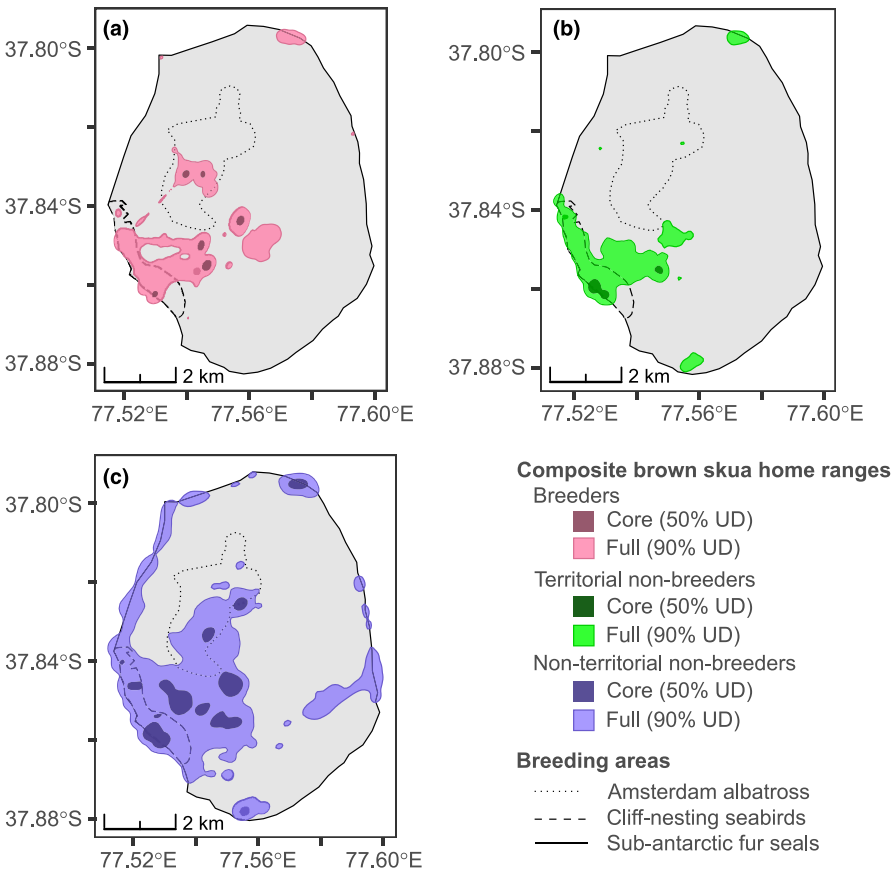

FIGURE 2 Composite core (50% utilization distribution) and full (90% utilization distribution) home ranges for (a) breeding, (b) territorial nonbreeding, and (c) nonterritorial nonbreeding brown skuas on Amsterdam Island, 2017–2020.

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TABLE 1 Coefficient values from GLMMs of core home range size (50% utilization distribution), full home range size (90% utilization distribution), and proportion of resting, foraging and commuting locations for brown skuas on Amsterdam Island, 2017–2020. Bold values indicate coefficients for which the 95% confidence estimate does not overlap zero

		Coefficient values (95% CI)				
	Response	Intercept	Nonterritorial nonbreeders (vs. breeders)	Territorial nonbreeders (vs. breeders)	Day of season (linear)	Day of season (quadratic)
All locations	Core home range	−0.32 to 0.31	**0.11 to 0.84**	−0.33 to 0.56	**−4.83 to −2.99**	−0.60 to 0.92
	Full home range	−1.71 to 2.64	**1.57 to 6.57**	−1.87 to 4.29	**−44.7 to −30.9**	**4.74 to 16.2**
	% Resting	**0.35 to 0.54**	**−0.26 to −0.04**	−0.26 to 0.01	−0.36 to 0.20	−0.27 to 0.20
	% Foraging	**0.32 to 0.39**	−0.10 to 0.06	−0.27 to 0.19	**0.02 to 0.56**	−0.16 to 0.28
	% Commuting	**0.12 to 0.29**	**0.07 to 0.26**	−0.04 to 0.20	−0.49 to 0.03	−0.23 to 0.19
Overlap areas						
Amsterdam albatross	Core home range	**0.01 to 0.02**				
	Full home range	0.02 to 0.09			**−0.50 to −0.23**	**0.08 to 0.31**
	% Resting	**0.16 to 0.66**	−0.39 to 0.16	−0.42 to 0.23	**−1.34 to −0.43**	−0.11 to 0.56
	% Foraging	0.10 to 0.61	−0.29 to 0.27	−0.31 to 0.34		
	% Commuting	**0.04 to 0.41**	−0.07 to 0.34	−0.16 to 0.33		
Cliff-nesting seabirds	Core home range	−0.04 to 0.03	**0.01 to 0.08**	−0.02 to 0.08	**−0.40 to −0.21**	**0.03 to 0.18**
	Full home range	−0.04 to 0.14	**0.18 to 0.40**	**0.08 to 0.34**	**−2.39 to −1.16**	−0.40 to 0.25
	% Resting	**0.05 to 0.31**	−0.13 to 0.16	−0.12 to 0.24	−0.73 to 0.05	**0.87 to 1.50**
	% Foraging	**0.22 to 0.36**	−0.06 to 0.09	**0.02 to 0.21**	**−1.26 to −0.49**	**0.34 to 0.97**
	% Commuting	**0.39 to 0.71**	−0.23 to 0.12	**−0.49 to −0.03**	**0.80 to 1.70**	**−2.22 to −1.49**
Sub-Antarctic fur seals	Core home range	−0.01 to 0.01	**0.01 to 0.03**	−0.01 to 0.03	**−0.16 to −0.11**	**0.03 to 0.07**
	Full home range	**−0.03 to 0.06**	**0.03 to 0.13**	−0.03 to 0.10	**−0.89 to −0.61**	**0.49 to 0.72**
	% Resting	**0.15 to 0.28**			**−1.16 to −0.69**	−0.18 to 0.53
	% Foraging	**0.29 to 0.46**	−0.08 to 0.11	**0.02 to 0.24**	**0.40 to 1.34**	−0.37 to 0.40
	% Commuting	**0.25 to 0.52**	−0.33 to 0.02	**−0.54 to −0.09**		

During the breeding season, home range sizes remained relatively consistent for breeders but declined substantially in both territorial and nonterritorial nonbreeders (Figure 4). Home range sizes of territorial nonbreeders and breeders converged toward the end of the breeding season, while those of nonterritorial nonbreeders remained larger. The proportion of active locations for breeders peaked around chick hatching and then declined, while proportions of active locations for territorial and nonterritorial nonbreeders declined throughout the season but remained higher than in breeders (Figure 4).

Ten of the 41 tracked individuals (24%), including one individual captured at a nest and nine captured at clubs, were positive for *Pm* DNA, suggesting active infection (Table 2). These included 1 breeder, 2 territorial nonbreeders, and 7 nonterritorial nonbreeders. Infection rates in 2017–2020 were similar to 2011–2017 values (22.7%). We further tested a subset of 28 tracked skuas for *Pm* antibodies and detected antibodies in 27 samples (96%), similar to values from 2011–2017 (97%; Table 2). Across all years (2011–2017), including interannual variation as a fixed effect improved models of *Pm* infection rates, but not antibody titres (see Table S3). Antibody titres and infection rates did not differ between nests and clubs; however, titres were lower at MAE than ETX and PDT, while infection rates were similar among sites (see Table S3).

Territorial and nonterritorial nonbreeding skuas used larger proportions of cliff-nesting seabird (full home range) and fur seal breeding habitats (core home range) than breeding individuals (Table 1). Twenty-one of 41 tracked individuals (51%) had home ranges that overlapped both cliff-nesting seabird habitats and Amsterdam albatross nesting areas, including 4/9 breeders (44%), 4/8 territorial nonbreeders (50%), and 13/24 nonterritorial nonbreeders (54%) (see Figure S4). Five of 41 individuals (12%), all nonterritorial nonbreeders, used both cliff and Amsterdam albatross nesting areas as part of their core home ranges. Of skuas with active avian cholera infections (i.e. *Pm* DNA), 9/10 (90%) used both cliff and Amsterdam albatross nesting areas as part of their full home ranges, including 1 breeder, 1 territorial nonbreeder and 7 nonterritorial nonbreeders (Figure 5). Three of these individuals (30%), all nonterritorial nonbreeders, also used both areas as part of their core home ranges (Figure 5).

Within Amsterdam albatross breeding habitat, nonbreeding skuas were more likely than breeders to be engaged in active foraging or commuting behaviour, while breeders were more likely to be resting (Table 1; Figure 6). Among active locations in Amsterdam albatross habitat, an average of 30% per individual (SD: 30%; Range: 0%–89%) were classified as foraging locations, with the remaining 70% representing commuting flights. In cliff-nesting seabird and fur

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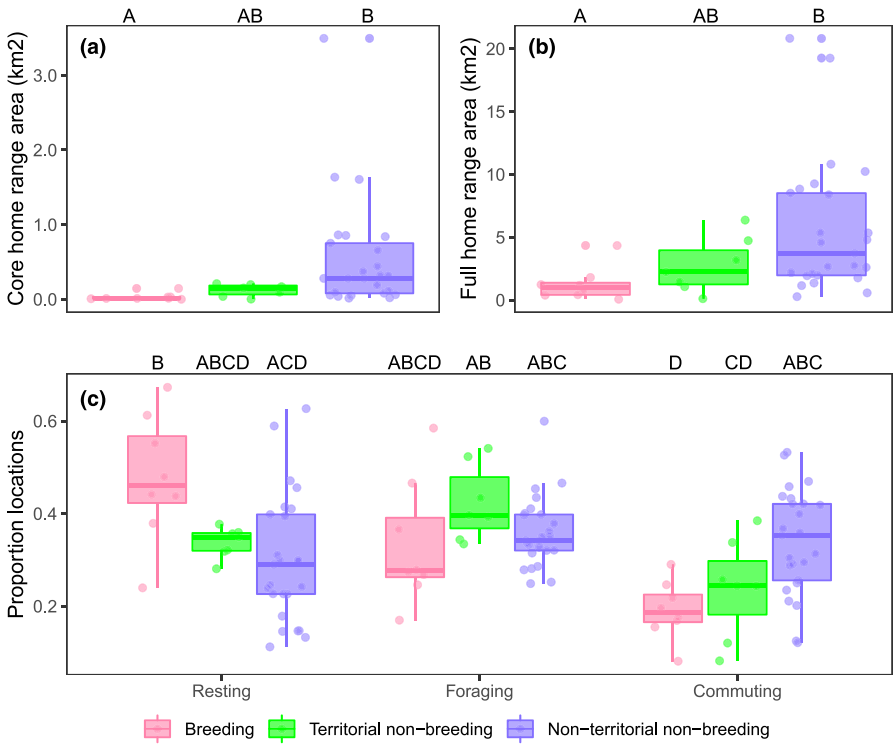

FIGURE 3 Movement parameters for brown skuas on Amsterdam Island, 2017–2020: (a) core home range area (50% utilization distribution); (b) full home range area (90% utilization distribution); and (c) proportion of locations in each behavioural state.

seal breeding habitats, territorial nonbreeding skuas were less active than either breeders or nonterritorial nonbreeders (Figure 6). On average, foraging comprised 47% (SD: 22%; Range: 0%–85%) of individual active locations in cliff-nesting seabird habitat, and 55% (SD: 22%; Range: 0%–92%) of active locations in seal breeding habitat.

4 | DISCUSSION

Our results show substantial differences between the distribution and behaviour of breeding and nonbreeding brown skuas using shared habitats at a multi-species seabird colony during the breeding season. In general, nonbreeders occupied larger areas, spent more time moving among sites, overlapped more with other seabirds and marine mammals, linked nesting areas used by different seabird species, and showed greater variability among individuals and over time than did breeders. Both breeders and nonbreeders showed similarly high rates of prior and ongoing avian cholera infection; however, the wide-ranging and variable movements of nonbreeding skuas create substantially greater opportunities for nonbreeders than breeders to transport pathogens among seabird species. These results highlight the importance of understanding and accounting for individual heterogeneity in movement patterns when evaluating spatially-mediated processes.

We found that including nonbreeding skuas in assessment of space use substantially increased previous estimates derived from breeders alone (Gamble et al., 2020). Nonbreeders have also been observed to coexist with breeders but occupy larger home ranges in at least two other semisocial species of predatory and scavenging birds: crested caracaras *Caracara cheriway* (Dwyer et al., 2013) and black kites *Milvus migrans* (Tanferna et al., 2013). Without the need to return to a central nest site and provision chicks, nonbreeders may be more able to explore prospective feeding areas and adapt to seasonal changes in resource distribution, resulting in wider-ranging movements. Nonbreeders could be less experienced or less efficient foragers, requiring larger areas to meet their energetic needs, or could be excluded by socially dominant breeders from the most productive foraging areas (Hahn & Bauer, 2008). Indeed, our algorithm identified multiple activity centres for six breeding skuas that concurrently occupied both an apparent nest site and a coastal loafing area or club site, suggesting that at least some proportion of the breeding population maintains separate territories in or near prime foraging areas during the breeding season. Nonbreeders with fixed territories (~25% of the nonbreeding sample) also had smaller home range sizes than nonterritorial nonbreeders. Taken together, these results indicate that social hierarchies may allow older or more dominant individuals to occupy and defend productive feeding areas, and potentially meet their resource needs in more stable and compact home ranges.

Nonbreeders in our study spent substantially less time resting and more time foraging or commuting than breeders, despite the elevated provisioning requirements associated with raising chicks. Nonbreeders could be exploiting more movement-intensive foraging strategies (e.g. kleptoparasitism). Activity could also result from territorial exclusion—if nonbreeders are unable to occupy a productive feeding territory, they may need to spend more time foraging or moving among multiple territories to meet their resource needs. Indeed, territorial nonbreeders in our study spent comparatively more time foraging or resting, while nonterritorial nonbreeders spent more time commuting. This suggests that the ability to occupy a territory

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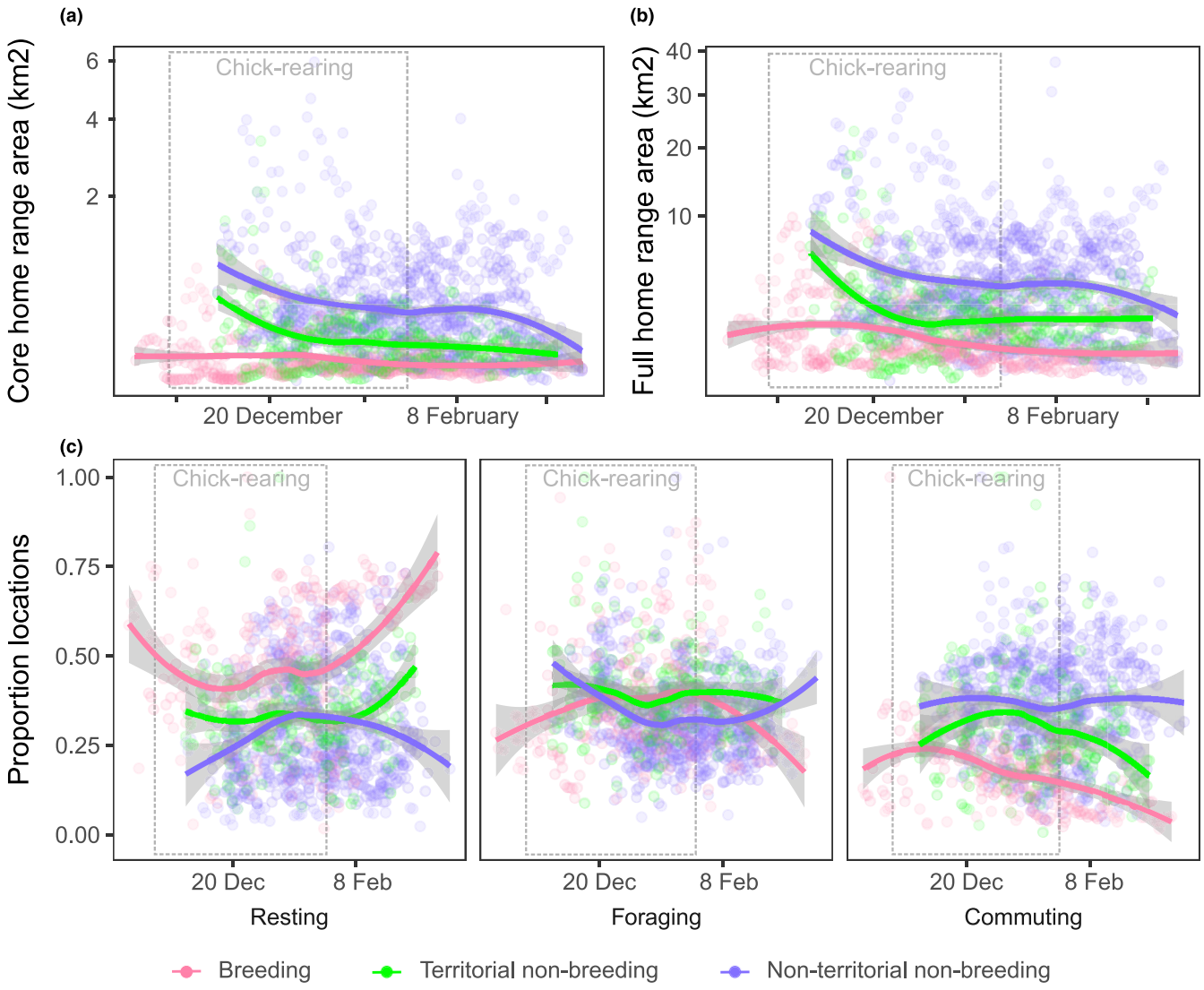

FIGURE 4 Seasonal changes in (a) core home range size (50% utilization distribution); (b) full home range size (90% utilization distribution), and (c) proportion of locations in each behavioural state for brown skuas on Amsterdam Island, 2017–2020. Shaded areas represent 95% confidence intervals. Dashed boxes represent the approximate duration of the brown skua chick-rearing period (hatching through fledging).

TABLE 2 Serological parameters for brown skuas on Amsterdam Island, 2011–2020

			Breeding status		*Pm* antibodies		*Pm* DNA
Year	Capture site	*N*	Breeder	Nonbreeder	*N* positive/tested	Titre (mean ± SD)	*N* positive/tested
2011–2012	Nest	16	16	0	16/16	6.73 ± 1.48	1/16
2015–2016	Nest	10	10	0	10/10	8.60 ± 1.11	1/10
	Club (ETX)	10	unk	unk	10/10	7.00 ± 0.89	3/10
2016–2017	Nest	10	10	0	10/10	8.30 ± 1.00	8/10
	Club (ETX)	10	unk	unk	10/10	7.40 ± 1.11	0/10
	Club (MAE)	10	unk	unk	8/10	5.10 ± 1.70	2/10
2017–2018	Club (MAE)	7	0	7	6/7	6.28 ± 2.19	2/7
2018–2019	Club (ETX)	10	0	10	10/10	8.90 ± 1.04	4/10
	Club (MAE)	9	2	7	na	na	3/9
2019–2020	Nest	6	6	0	na	na	1/6
	Club (ETX)	5	0	5	5/5	7.00 ± 1.07	0/5
	Club (MAE)	4	1	3	na	na	0/4

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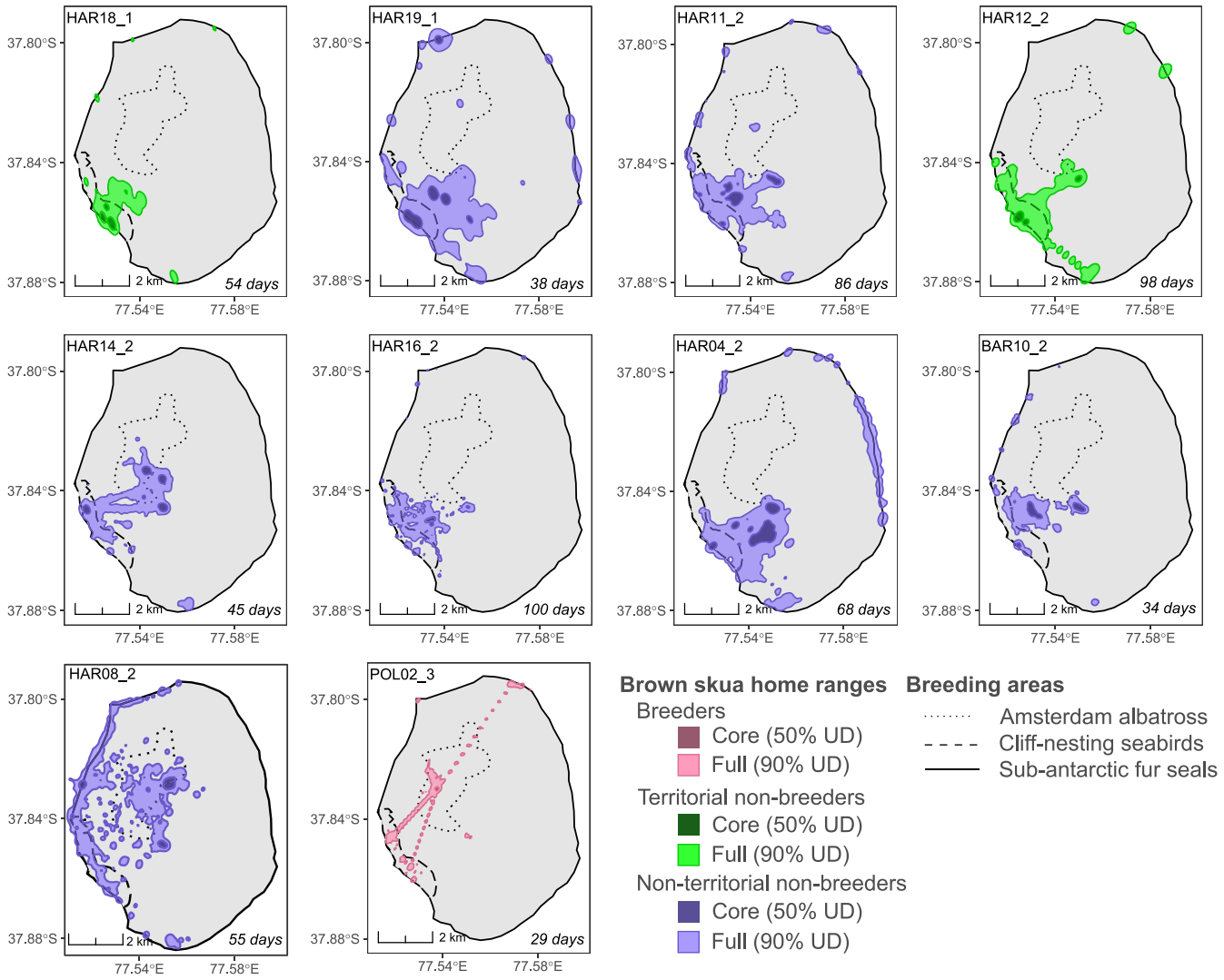

FIGURE 5 Core (90% utilization distribution) and full (50% utilization distribution) home ranges for 10 brown skuas on Amsterdam Island that tested positive for active avian cholera *Pasteurella multocida* infections at capture, 2017–2020. Each plot includes individual ID (upper left) and duration of tracking data used to calculate home range areas (lower right).

offers benefits in the form of reduced energy spent travelling among foraging patches. Differences in behaviour between groups could affect intensity of interactions between and within species and, consequently, structure spatially mediated processes such as pathogen transmission (Boulinier et al., 2016; Han et al., 2015), genetic connectivity (Cushman & Lewis, 2010), and risk exposure (Jacobson et al., 2016). For example, higher commuting rates could allow nonbreeders to transport pathogens into areas used by more individuals and species than breeders, although direct contacts may be shorter or less intense than those of more stationary breeders.

We also recorded greater inter- and intraindividual variation in space use of nonbreeders than breeders. While space use and activity patterns of breeders were relatively uniform between individuals and over time, home range sizes and time budgets of nonbreeders varied by territorial status and time of season. Such variability could be particularly important for pathogen circulation. In a simulation study, McClure et al. (2020) found that variability of home range sizes was positively associated with pathogen transmission in a mammalian system because only a few 'super-spreaders' were needed to introduce propagules into new areas. Varying degrees of territoriality in nonbreeding populations have previously been observed in territorial songbirds competing for breeding sites (Fraser & Stutchbury, 2004; Sherry & Holmes, 1989), suggesting variable strategies for territory acquisition. Ability to defend a territory is often related to social dominance, which may be a function of a variety of individual factors (Hahn & Bauer, 2008; Piper, 1997). The individual correlates we measured (sex and body size) did not explain observed variation among nonbreeders; however, we were not able to determine ages of tracked skuas, nor determine whether nonbreeders had attempted breeding and failed prior to capture. Investigating causes of nonbreeding and their relationships to behavioural heterogeneity would therefore be a useful focus for further study and could help to elucidate how specific perturbations such as widespread

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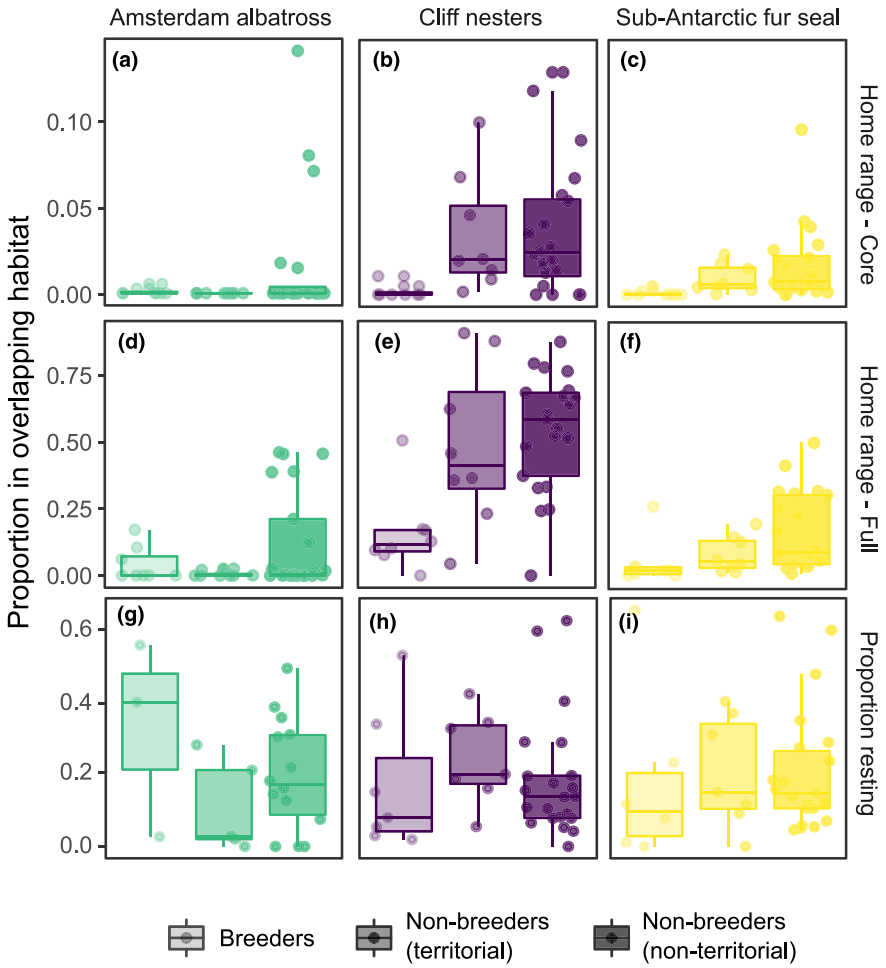

FIGURE 6 Brown skua core home range areas (50% utilization distribution; a–c); full home range areas (90% utilization distribution; d–f); and proportion of active locations overlapping Amsterdam albatross (teal: a, d, g), cliff-nesting seabird (purple: b, e, h), and sub-Antarctic fur seal breeding areas (yellow: c, f, i) on Amsterdam Island, 2017–2020.

nest failure might affect pathogen dynamics within and among species.

Building on previous work (e.g. Gamble et al., 2020; Jaeger et al., 2018), our study clarifies the role of both breeding and non-breeding brown skuas as reservoirs for avian cholera. Although only 25% of tracked skuas in this study were infected with avian cholera at the time of capture, close to 100% were seropositive to *Pm* antibodies, suggesting that nearly all skuas are exposed to the pathogen. Like Gamble et al. (2020), we found greater levels of *Pm* antibodies in skuas attending the club site closest to cliff-nesting seabird colonies than at the more distant club site; however, we also found that individuals from both club sites had similar rates of active infection and largely overlapped in their foraging areas, suggesting limited differentiation in either spatial distribution or pathogen exposure among club sites. Differences in pathogen exposure could still occur if skuas from different clubs specialized on different prey resources within shared foraging habitats. The general ubiquity of *Pm* infection in brown skuas and the ability of infected individuals to survive and behave normally suggests that they play a key role in the persistence and large-scale spread of avian cholera in this system.

Our study also reveals the potential for brown skuas to spread pathogens among discrete seabird breeding areas. Approximately half of all breeding and nonbreeding skuas in the current study (including several with active avian cholera infections) used both the breeding area of the endemic Amsterdam albatross and cliff-nesting seabird colonies where avian cholera outbreaks are recorded. Earlier tracking efforts on Amsterdam Island had failed to detect any skuas using both areas (Gamble et al., 2020); however, this study focused only on breeders from skua nesting areas outside Amsterdam albatross breeding habitat on the Plateau. The inclusion of nonbreeders in our study, as well as representation of breeders nesting both within and outside Amsterdam albatross habitat, likely accounts for this difference. Our study showed that nonbreeding and breeding skuas occupied similar proportions of Amsterdam albatross habitat. However, nonbreeders had higher rates of active foraging and commuting in these shared areas, while breeders typically travelled to island coasts to forage, consistent with Gamble et al. (2020). This suggests that nonbreeding skuas are more likely than breeders to interact directly with breeding Amsterdam albatrosses via harassment, predation, or kleptoparasitism. In seal and cliff-nesting seabird habitats, nonbreeding skuas used larger areas than did breeders, although activity patterns within these habitats were similar among groups. This implies that nonbreeding skuas could overlap and interact more frequently and/or with more individuals in seal and cliff-nesting seabird habitats compared to breeders, increasing the

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number, if not the intensity, of potential exposure or transmission events. Taken together, our movement data suggest that nonbreeders have more opportunities than breeders to spread pathogens among species, through either higher frequency or higher intensity of interspecific interactions.

Our study demonstrates that club sites offer a valuable supplement to capturing skuas on nests. Indeed, we found that individuals captured at club sites were more representative of movements of the overall skua population than individuals from nests regardless of sample size. Capturing seabirds at on-land loafing areas has several advantages over other available capture locations, in that it avoids disturbance at sensitive nesting areas (Strasser & Heath, 2013) and requires fewer specialized skills and equipment than captures at at-sea feeding areas (Zharikov et al., 2006). Although our study validates the efficacy of sampling at clubs, however, it also reveals some potential biases in the population available for capture. We captured breeding skuas at only one of two clubs, indicating that relative proportions of breeders and nonbreeders may vary among clubs as well as across the breeding season. Additionally, apparent breeders represented only 8% of skuas captured at club sites. Although there is no reliable estimate of the population-level ratio of breeders to nonbreeders, this suggests that breeders may be underrepresented when capturing at club sites alone. Many breeding skuas in this study also occupied territories at club sites during nesting; however, breeders used these secondary territories less frequently and for shorter intervals than their nest sites, likely making breeders less available for capture at clubs than nonbreeders that exclusively occupied clubs. In addition, our sample disproportionately included females across all sites. Although skuas typically display reversed sexual size dimporphism (RSD), we did not find differences in biometry between known males and females, making it difficult to infer the sex of unknown individuals. Molecular sexing results were inconclusive for a large portion of our sample, and female bias could result if females are more likely to be sexed conclusively. Captures could also have been biased toward females if females were bolder or more aggressive than males, as might be expected in species with RSD (Schoenjahn et al., 2020); however, Catry et al. (1999) did not detect higher levels of aggression in female great skuas *Stercorarius skua* during most of the breeding season. The small number of individuals conclusively sexed in our study, particularly for males ($N = 11$), likely inhibited detection of sex-specific differences.

Understanding space use of nonbreeding seabirds could be particularly important to predicting effects of interannual environmental variation and long-term change. When food resources or territories are limited, nonbreeders at or near breeding sites can represent a pool of potential recruits to offset mortality affecting the breeding population (Klomp & Furness, 1992; Porter & Coulson, 1987). Thus, while breeding numbers may remain relatively stable over time, numbers of nonbreeders are likely to fluctuate as interannual changes in resource availability affect adult survival and recruitment (Kokko & Sutherland, 1998; Robles & Ciudad, 2017). Our study suggests that environmental changes that increase the number of nonbreeding skuas would also increase interspecific interactions, with potentially deleterious effects on other seabird species of conservation concern. For example, ongoing or planned eradications of introduced rodents in mixed-species seabird colonies such as Amsterdam Island could reduce supplemental food availability and limit the number of nonbreeding skuas the island can support; however, it could also increase predation pressure on other seabirds (Travers et al., 2021), with potentially conflicting effects on pathogen circulation.

Beyond this study system, incorporating nonbreeders into tracking studies is an important component of understanding population-wide movement patterns and predicting spatially heterogeneous processes. Our work indicates that nonbreeders move more extensively than breeders during the breeding season, and similar differences have also been observed in other avian and nonavian species (e.g. Cooper & Marra, 2020; Francioli et al., 2020). Nonbreeders may therefore play particularly important roles in spatial connectivity, including by transmitting pathogens among breeding populations (Boulinier et al., 2016). For example, recent outbreaks of highly pathogenic avian influenza in seabirds in Europe and North America have involved mortality events occurring at spatially disjunct breeding colonies (Banyard et al., 2022). Tracking movements of nonbreeders among colonies could help to better understand and predict spatial patterns of transmission of avian influenza and other pathogens of concern, as well as identify colony sites or age classes with particularly high frequencies of among-colony movements that could be targeted for management interventions (e.g. vaccination) to help manage future outbreaks.

AUTHOR CONTRIBUTIONS

Jeremy Tornos, Jeremy Tornos, Amandine Gamble, Hubert Gantelet and Nicolas Keck conceived ideas and designed methodology; Amandine Gamble, Jeremy Tornos, Marine Bely, Augustin Clessin and Aline Flechet collected data; Amandine Gamble, Jeremy Tornos, Romain Dedet and Juliette Baron conducted laboratory analyses; Juliet Lamb analysed the data and led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

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Animal Experimentation Ethical Committee (French Ministry of Research permit #10257-2018011712301381v6) and by the Comité de l'Environnement Polaire (A-2017-97, A-2017-111, A-2018-123, A 2018-139, A-2019-69, 2019-121, A-2019-132 and A-2019-135).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data used in this manuscript are archived in Zenodo 10.5281/zenodo.7362496 (Lamb et al., 2022).

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REFERENCES

Aebischer, N. J., Robertson, P. A., & Kenward, R. E. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology*, *74*, 1313–1325. https://doi.org/10.2307/1940062

Amstrup, S. C., McDonald, T. L., & Durner, G. M. (2004). Using satellite radiotelemetry data to delineate and manage wildlife populations. *Wildlife Society Bulletin*, *32*, 661–679. https://doi.org/10.2193/0091-7648(2004)032[0661:USRDTD]2.0.CO;2

Banyard, A. C., Lean, F. Z. X., Robinson, C., Howie, F., Tyler, G., Nisbet, C., Seekings, J., Meyer, S., Whittard, E., Ashpitel, H. F., Bas, M., Byrne, A. M. P., Lewis, T., James, J., Stephan, L., Lewis, N. S., Brown, I. H., Hansen, R. D. E., & Reid, S. M. (2022). Detection of highly pathogenic avian influenza virus H5N1 clade 2.3.4.4b in great Skuas: A species of conservation concern in Great Britain. *Viruses*, *14*, 212. https://doi.org/10.3390/v14020212

Borghello, P., Torres, D. S., Montalti, D., & Ibañez, A. E. (2019). Diet of the Brown Skua (*Stercorarius antarcticus lonnbergi*) at Hope Bay, Antarctic peninsula: Differences between breeders and non-breeders. *Polar Biology*, *42*, 385–394. https://doi.org/10.1007/s00300-018-2429-8

Boulinier, T., Kada, S., Ponchon, A., Dupraz, M., Dietrich, M., Gamble, A., Bourret, V., Duriez, O., Bazire, R., Tornos, J., Tveraa, T., Chambert, T., Garnier, R., & McCoy, K. D. (2016). Migration, prospecting, dispersal? What host movement matters for infectious agent circulation? *Integrative and Comparative Biology*, *56*, 330–342. https://doi.org/10.1093/icb/icw015

Bourret, V., Gamble, A., Tornos, J., Jaeger, A., Delord, K., Barbraud, C., Tortosa, P., Kada, S., Thiebot, J.-B., Thibault, E., Gantelet, H., Weimerskirch, H., Garnier, R., & Boulinier, T. (2018). Vaccination protects endangered albatross chicks against avian cholera. *Conservation Letters*, *11*, e12443. https://doi.org/10.1111/conl.12443

Branconi, R., Barbasch, T. A., Francis, R. K., Srinivasan, M., Jones, G. P., & Buston, P. M. (2020). Ecological and social constraints combine to promote evolution of non-breeding strategies in clownfish. *Communications Biology*, *3*, 1–7. https://doi.org/10.1038/s42003-020-01380-8

Bretagnolle, V., Mougeot, F., & Thibault, J. C. (2008). Density dependence in a recovering osprey population: Demographic and behavioural processes. *Journal of Animal Ecology*, *77*, 998–1007. https://doi.org/10.1111/j.1365-2656.2008.01418.x

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research*, *33*, 261–304. https://doi.org/10.1177/0049124104268644

Calenge, C. (2006). The package adehabitat for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*, 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Carneiro, A. P. B., Manica, A., Trivelpiece, W. Z., & Phillips, R. A. (2015). Flexibility in foraging strategies of Brown Skuas in response to local and seasonal dietary constraints. *Journal of Ornithology*, *156*, 625–633. https://doi.org/10.1007/s10336-015-1156-y

Catry, P., Phillips, R. A., & Furness, R. W. (1999). Evolution of reversed sexual size dimorphism in skuas and jaegers. *The Auk*, *116*, 158–168. https://doi.org/10.2307/4089462

Clay, T. A., Manica, A., Ryan, P. G., Silk, J. R., Croxall, J. P., Ireland, L., & Phillips, R. A. (2016). Proximate drivers of spatial segregation in non-breeding albatrosses. *Scientific Reports*, *6*, 1–13. https://doi.org/10.1038/srep29932

Cooper, N. W., & Marra, P. P. (2020). Hidden long-distance movements by a migratory bird. *Current Biology*, *30*, 4056–4062. https://doi.org/10.1016/j.cub.2020.07.056

Cushman, S. A., & Lewis, J. S. (2010). Movement behavior explains genetic differentiation in American black bears. *Landscape Ecology*, *25*, 1613–1625. https://doi.org/10.1007/s10980-010-9534-6

Duong, T. (2020). *Ks: Kernel smoothing*. R package version 1.11.7. https://CRAN.R-project.org/package=ks

Dwyer, J. F., Fraser, J. D., & Morrison, J. L. (2013). Range sizes and habitat use of non-breeding crested caracaras in Florida. *Journal of Field Ornithology*, *84*, 223–233. https://doi.org/10.1111/jofo.12022

Francioli, Y., Thorley, J., Finn, K., Clutton-Brock, T., & Zöttl, M. (2020). Breeders are less active foragers than non-breeders in wild Damaraland mole-rats. *Biology Letters*, *16*, 20200475. https://doi.org/10.1098/rsbl.2020.0475

Fraser, G. S., & Stutchbury, B. J. (2004). Area-sensitive forest birds move extensively among forest patches. *Biological Conservation*, *118*, 377–387. https://doi.org/10.1016/j.biocon.2003.06.006

Fridolfsson, A. K., & Ellegren, H. (1999). A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology*, *30*, 116–121. https://doi.org/10.2307/3677252

Furness, R. W. (2015). Density dependence in seabirds: Great Skuas *Stercorarius skua* start to breed at a younger age when conditions are better. *Ringing & Migration*, *30*, 43–50. https://doi.org/10.1080/03078698.2015.1059631

Furness, R. W., Boesman, P. F. D., & Garcia, E. (2020). Brown skua (*Stercorarius antarcticus*). In J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. de Juana (Eds.), *Birds of the world*. Cornell Lab of Ornithology. https://doi.org/10.2173/bow.brnsku3.01

Gamble, A., Bazire, R., Delord, K., Barbraud, C., Jaeger, A., Gantelet, H., Thibault, E., Lebarbenchon, C., Lagadec, E., Tortosa, P., Weimerskirch, H., Thiebot, J.-B., Garnier, R., Tornos, J., & Boulinier, T. (2019). ECOPATH: Brown skua *Pasteurella multocida* epidemiological data and GPS tracking data (Amsterdam Island, 2015–2017). *OSU OREME (Dataset)*. https://doi.org/10.15148/b4b4a2e1-3d00-45b7-b3b2-2ca05d054346

Gamble, A., Bazire, R., Delord, K., Barbraud, C., Jaeger, A., Gantelet, H., Thibault, E., Lebarbenchon, C., Lagadec, E., Tortosa, P., Weimerskirch, H., Thiebot, J.-B., Garnier, R., Tornos, J., & Boulinier, T. (2020). Predator and scavenger movements among and within endangered seabird colonies: Opportunities for pathogen spread. *Journal of Applied Ecology*, *57*, 367–378. https://doi.org/10.1111/1365-2664.13531

Guinet, C., Jouventin, P., & Georges, J.-Y. (1994). Long term population changes of fur seals Arctocephalus gazella and Arctocephalus tropicalis on sub-Antarctic (Crozet) and subtropical (St-Paul and Amsterdam) islands and their possible relationship to El Niño

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southern oscillation. *Antarctic Science*, *6*, 473–478. https://doi.org/10.1017/S0954102094000714

Hahn, S., & Bauer, S. (2008). Dominance in feeding territories relates to foraging success and offspring growth in brown skuas *Catharacta Antarctica lonnbergi*. *Behavioral Ecology and Sociobiology*, *62*, 1149–1157. https://doi.org/10.1007/s00265-007-0543-7

Han, B. A., Park, A. W., Jolles, A. E., & Altizer, S. (2015). Infectious disease transmission and behavioural allometry in wild mammals. *Journal of Animal Ecology*, *84*, 637–646. https://doi.org/10.1111/1365-2656.12336

Hays, G. C., Bailey, H., Bograd, S. J., Bowen, W. D., Campagna, C., Carmichael, R. H., Casale, P., Chiaradia, A., Costa, D. P., Cuevas, E., Nico de Bruyn, P. J., Dias, M. P., Duarte, C. M., Dunn, D. C., Dutton, P. H., Esteban, N., Friedlaender, A., Goetz, K. T., Godley, B. J., … Sequeira, A. M. M. (2019). Translating marine animal tracking data into conservation policy and management. *Trends in Ecology & Evolution*, *34*, 459–473. https://doi.org/10.1016/j.tree.2019.01.009

Heerah, K., Dias, M. P., Delord, K., Oppel, S., Barbraud, C., Weimerskirch, H., & Bost, C. A. (2019). Important areas and conservation sites for a community of globally threatened marine predators of the southern Indian Ocean. *Biological Conservation*, *234*, 192–201. https://doi.org/10.1016/j.biocon.2019.03.037

Hemmings, A. D. (1990). Human impacts and ecological constraints on Skuas. In K. R. Kerry & G. Hempel (Eds.), *Antarctic ecosystems* (pp. 224–230). Springer. https://doi.org/10.1007/978-3-642-84074-6_24

Hinam, H. L., & St. Clair, C. C. (2008). High levels of habitat loss and fragmentation limit reproductive success by reducing home range size and provisioning rates of northern saw-whet owls. *Biological Conservation*, *141*, 524–535. https://doi.org/10.1016/j.biocon.2007.11.011

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*, 346–363. https://doi.org/10.1002/bimj.200810425

Jacobson, S. L., Bliss-Ketchum, L. L., de Rivera, C. E., & Smith, W. P. (2016). A behavior-based framework for assessing barrier effects to wildlife from vehicle traffic volume. *Ecosphere*, *7*, e01345. https://doi.org/10.1002/ecs2.1345

Jaeger, A., Lebarbenchon, C., Bourret, V., Bastien, M., Lagadec, E., Thiebot, J. B., Boulinier, T., Delord, K., Barbraud, C., Marteau, C., Dellagi, K., Tortosa, P., & Weimerskirch, H. (2018). Avian cholera outbreaks threaten seabird species on Amsterdam Island. *PLoS ONE*, *13*, e0197291. https://doi.org/10.1371/journal.pone.0197291

Klomp, N. I., & Furness, R. W. (1992). Non-breeders as a buffer against environmental stress: Declines in numbers of great skuas on Foula, Shetland, and prediction of future recruitment. *Journal of Applied Ecology*, *29*, 341–348. https://doi.org/10.2307/2404503

Kokko, H., & Sutherland, W. J. (1998). Optimal floating and queuing strategies: Consequences for density dependence and habitat loss. *The American Naturalist*, *152*, 354–366. https://doi.org/10.1086/286174

Lamb, J. S., Tornos, J., Dedet, R., Gantelet, H., Keck, N., Baron, J., Bely, M., Clessin, A., Flechet, A., Gamble, A., & Boulinier, T. (2022). Data from: Hanging out at the club: Breeding status and territoriality affect individual space use, multi-species overlap, and pathogen transmission risk at a seabird colony. *Zenodo*, https://doi.org/10.5281/zenodo.7362496

Lascelles, B. G., Taylor, P. R., Miller, M. G. R., Dias, M. P., Oppel, S., Torres, L., Hedd, A., Le Corre, M., Phillips, R. A., Shaffer, S. A., Weimerskirch, H., & Small, C. (2016). Applying global criteria to tracking data to define important areas for marine conservation. *Diversity and Distributions*, *22*, 422–431. https://doi.org/10.1111/ddi.12411

Laundré, J. W., Hernández, L., & Ripple, W. J. (2010). The landscape of fear: Ecological implications of being afraid. *The Open Ecology Journal*, *3*, 1–7. https://doi.org/10.2174/1874213001003030001

Longmire, J. L., Lewis, A. K., Brown, N. C., Buckingham, J. M., Clark, L. M., Jones, M. D., Meincke, L. J., Meyne, J., Ratliff, R. L., & Ray, F. A. (1988). Isolation and molecular characterization of a highly polymorphic centromeric tandem repeat in the family Falconidae. *Genomics*, *2*, 14–24. https://doi.org/10.1016/0888-7543(88)90104-8

Mayer, M., Zedrosser, A., & Rosell, F. (2017). Extra-territorial movements differ between territory holders and subordinates in a large, monogamous rodent. *Scientific Reports*, *7*, 1–10. https://doi.org/10.1038/s41598-017-15540-0

McClure, K. M., Gilbert, A. T., Chipman, R. B., Rees, E. E., & Pepin, K. M. (2020). Variation in host home range size decreases rabies vaccination effectiveness by increasing the spatial spread of rabies virus. *Journal of Animal Ecology*, *89*, 1375–1386. https://doi.org/10.1111/1365-2656.13176

McFarlane Tranquilla, L. A., Bradley, R. W., Lank, D. B., Williams, T. D., Lougheed, L. W., & Cooke, F. (2003). The reliability of brood patches in assessing reproductive status in the marbled Murrelet: Words of caution. *Waterbirds*, *26*, 108–118. https://doi.org/10.1675/1524-4695(2003)026[0108:TROBPI]2.0.CO;2

McInnes, J. C., Emmerson, L., Southwell, C., Faux, C., & Jarman, S. N. (2016). Simultaneous DNA-based diet analysis of breeding, non-breeding and chick Adélie penguins. *Royal Society Open Science*, *3*, 150443. https://doi.org/10.1098/rsos.150443

Michelot, T., Langrock, R., & Patterson, T. A. (2016). moveHMM: An R package for the statistical modelling of animal movement data using hidden Markov models. *Methods in Ecology and Evolution*, *7*, 1308–1315. https://doi.org/10.1111/2041-210X.12578

Micol, T., & Jouventin, P. (1995). Restoration of Amsterdam Island, South Indian Ocean, following control of feral cattle. *Biological Conservation*, *73*, 199–206. https://doi.org/10.1016/0006-3207(94)00109-4

Miller, G. D., Watts, J. M., & Shellam, G. R. (2008). Viral antibodies in south polar skuas around Davis Station, Antarctica. *Antarctic Science*, *20*, 455–461. https://doi.org/10.1017/S0954102008001259

Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., Merrill, E. H., & Haydon, D. T. (2010). Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 2289–2301. https://doi.org/10.1098/rstb.2010.0082

Pardo, D., Weimerskirch, H., & Barbraud, C. (2013). When celibacy matters: Incorporating non-breeders improves demographic parameter estimates. *PLoS ONE*, *8*, e60389. https://doi.org/10.1371/journal.pone.0060389

Penteriani, V., Ferrer, M., & Delgado, M. D. M. (2011). Floater strategies and dynamics in birds, and their importance in conservation biology: Towards an understanding of nonbreeders in avian populations. *Animal Conservation*, *14*, 233–241. https://doi.org/10.1111/j.1469-1795.2010.00433.x

Picardi, S., Smith, B., Boone, M., & Basille, M. (2020). *nestR: Estimation of bird nesting from tracking data*. R package version 1.1.0. https://rdrr.io/github/picardis/nestR/

Pinheiro, J., Bates, D., & R Core Team. (2022). *Nlme: Linear and nonlinear mixed effects models*. R package version 3.1-158. https://CRAN.R-project.org/package=nlme

Piper, W. H. (1997). Social dominance in birds. In V. Nolan, E. D. Ketterson, & C. F. Thompson (Eds.), *Current ornithology* (Vol. *14*, pp. 125–187). Springer. https://doi.org/10.1007/978-1-4757-9915-6_4

Ponchon, A., Chambert, T., Lobato, E., Tveraa, T., Gremillet, D., & Boulinier, T. (2015). Breeding failure induces large scale prospecting movements in the black-legged kittiwake. *Journal of Experimental Marine Biology and Ecology*, *473*, 138–145. https://doi.org/10.1016/j.jembe.2015.08.013

Ponchon, A., Grémillet, D., Doligez, B., Chambert, T., Tveraa, T., González-Solís, J., & Boulinier, T. (2013). Tracking prospecting movements involved in breeding habitat selection: Insights, pitfalls

13652435, 2023, 3, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.14240 by Bib Montpellier, Wiley Online Library on [09/06/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

and perspectives. *Methods in Ecology and Evolution*, *4*, 143–150. https://doi.org/10.1111/j.2041-210x.2012.00259.x

Porter, J. M., & Coulson, J. C. (1987). Long-term changes in recruitment to the breeding group, and the quality of recruits at a kittiwake *Rissa tridactyla* colony. *Journal of Animal Ecology*, *56*, 675–689. https://doi.org/10.2307/5076

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Robles, H., & Ciudad, C. (2017). Floaters may buffer the extinction risk of small populations: An empirical assessment. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20170074. https://doi.org/10.1098/rspb.2017.0074

Schoenjahn, J., Pavey, C. R., & Walter, G. H. (2020). Why female birds of prey are larger than males. *Biological Journal of the Linnean Society*, *129*, 532–542. https://doi.org/10.1093/biolinnean/blz201

Schofield, G., Hobson, V. J., Lilley, M. K., Katselidis, K. A., Bishop, C. M., Brown, P., & Hays, G. C. (2010). Inter-annual variability in the home range of breeding turtles: Implications for current and future conservation management. *Biological Conservation*, *143*, 722–730. https://doi.org/10.1016/j.biocon.2009.12.011

Schultz, H., Chang, K., Bury, S. J., Gaskett, A. C., Dennis, T. E., Ismar-Rebitz, S. M. H., Southey, I., Hohnhold, R. J., & Millar, C. D. (2021). Sex-specific foraging of an apex predator puts females at risk of human–wildlife conflict. *Journal of Animal Ecology*, *90*, 1776–1786. https://doi.org/10.1111/1365-2656.13496

Sherry, T. W., & Holmes, R. T. (1989). Age-specific social dominance affects habitat use by breeding American redstarts (*Setophaga ruticilla*): A removal experiment. *Behavioral Ecology and Sociobiology*, *25*, 327–333. https://doi.org/10.1007/BF00302990

Strasser, E. H., & Heath, J. A. (2013). Reproductive failure of a human-tolerant species, the American kestrel, is associated with stress and human disturbance. *Journal of Applied Ecology*, *50*, 912–919. https://doi.org/10.1111/1365-2664.12103

Tanferna, A., López-Jiménez, L., Blas, J., Hiraldo, F., & Sergio, F. (2013). Habitat selection by black kite breeders and floaters: Implications for conservation management of raptor floaters. *Biological Conservation*, *160*, 1–9. https://doi.org/10.1016/j.biocon.2012.12.031

Townsend, K. M., Frost, A. J., Lee, C. W., Papadimitriou, J. M., & Dawkins, H. J. (1998). Development of PCR assays for species-and type-specific identification of *Pasteurella multocida* isolates. *Journal of Clinical Microbiology*, *36*, 1096–1100. https://doi.org/10.1128/JCM.36.4.1096-1100.1998

Travers, T., Lea, M. A., Alderman, R., Terauds, A., & Shaw, J. (2021). Bottom-up effect of eradications: The unintended consequences for top-order predators when eradicating invasive prey. *Journal of Applied Ecology*, *58*, 801–811. https://doi.org/10.1111/1365-2664.13828

van Bemmelen, R. S. A., Clarke, R. H., Pyle, P., & Camphuysen, C. J. (2018). Timing and duration of primary molt in northern hemisphere skuas and jaegers. *The Auk*, *135*, 1043–1054. https://doi.org/10.1642/AUK-17-232.1

Vicente, J., & VerCauteren, K. (2019). The role of scavenging in disease dynamics. In P. Olea, P. Mateo-Tomás, & J. Sánchez-Zapata (Eds.), *Carrion ecology and management* (pp. 161–182). Wildlife Research Monographs, Vol. 2. Springer. https://doi.org/10.1007/978-3-030-16501-7_7

Votier, S. C., Grecian, W. J., Patrick, S., & Newton, J. (2011). Inter-colony movements, at-sea behaviour and foraging in an immature seabird: Results from GPS-PPT tracking, radio-tracking and stable isotope analysis. *Marine Biology*, *158*, 355–362. https://doi.org/10.1007/s00227-010-1563-9

Webb, W. C., Marzluff, J. M., & Hepinstall-Cymerman, J. (2011). Linking resource use with demography in a synanthropic population of common ravens. *Biological Conservation*, *144*, 2264–2273. https://doi.org/10.1016/j.biocon.2011.06.001

White, L. A., Forester, J. D., & Craft, M. E. (2018). Dynamic, spatial models of parasite transmission in wildlife: Their structure, applications and remaining challenges. *Journal of Animal Ecology*, *87*, 559–580. https://doi.org/10.1111/1365-2656.12761

Wille, M., McBurney, S., Robertson, G. J., Wilhelm, S. I., Blehert, D. S., Soos, C., Dunphy, R., & Whitney, H. (2016). A pelagic outbreak of avian cholera in north American gulls: Scavenging as a primary mechanism for transmission? *Journal of Wildlife Diseases*, *52*, 793–802. https://doi.org/10.7589/2015-12-342

Zharikov, Y., Lank, D., Huettmann, F., Bradley, R., Parker, N., Yen, P. P. W., Mcfarlane-Tranquilla, L. A., & Cooke, F. (2006). Habitat selection and breeding success in a forest-nesting Alcid, the marbled murrelet, in two landscapes with different degrees of forest fragmentation. *Landscape Ecology*, *21*, 107–120. https://doi.org/10.1007/s10980-005-1438-5

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