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ORIGINAL PAPER

Post-breeding season behaviour of a threatened population of subtropical brown skuas

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Abstract
There is a wide variability in seabirds migratory strategies, not only across species, but also among populations of the same species, within populations, and even within individuals between years. Brown skuas are no exception, with an apparent latitudinal gradient in migratory distance, raising questions about the migratory behaviour of individuals in their most northerly breeding site – Amsterdam Island (southern Indian Ocean). Beyond fundamental questions, understanding the migratory behaviour of brown skuas breeding on the island is also of conservation interest – as scavengers, skuas often have high pathogen loads and could contribute to inter-colony pathogen spread, should individuals of different populations mix at their non-breeding grounds. Here, movements, activity, and diet of 21 adult brown skuas breeding at Amsterdam Island were studied during the non-breeding period using geolocation, saltwater immersion loggers, and stable isotope analysis, in order to describe the variability in migratory behaviours. Post-breeding movements of brown skuas varied considerably, ranging from residency to long-distance migrations to northern zones in the Southern Hemisphere. Most individuals remained in the Indian Ocean, targeting areas along a continuum from the subantarctic to the tropics. Similar to other colonies in the Indian Ocean, wintering grounds were generally situated in productive dynamic upwelling waters or frontal systems, with brown skuas avoiding the less productive area of the South Subtropical Gyre (Central Indian Ocean). The low $\delta^{15}N$ values of feathers grown in mixed subtropical-subantarctic waters suggest low trophic level feeding in these areas. Overall, our results provided relevant information for conservation (inter-colony mixing in the non-breeding grounds).

Keywords Post-breeding strategy · Geolocator loggers · Activity patterns · Stercorarius antarcticus hamiltonii · Stable isotopes · Southern indian ocean

Introduction

Seabirds share their time between sea and land, with a particularly marked contrast between the breeding season – during which they must regularly return on land to incubate their eggs or to feed their chicks – and the non-breeding season, during which many species of seabirds migrate far from their colony to spend the entire period at sea. However, there is a wide difference in non-breeding strategies and movements among seabird species, with a gradient ranging from non-migratory (e.g., the resident masked booby *Sula dactylatra* (Roy et al. 2021) to the longest animal migration (e.g., almost 20,000 km one-way travel of the Arctic tern *Sterna paradisaea* (Alerstam et al. 2019).

Migratory behaviours vary not only between species, but also within species. Populations of the same species

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can winter in markedly different areas (Weimerskirch et al. 2015; Merkel et al. 2021), and display very different migratory distances (Frederiksen et al. 2012). Populations with different migratory strategies are also likely to vary in their activity budgets, sometimes resulting in variation in energy expenditure and even population dynamics (Frederiksen et al. 2016; Fayet et al. 2017). Within populations, individuals can also display very different migratory behaviours – in extreme cases spreading through entire ocean basins (Franklin et al. 2022), or even different ocean basins (Davis et al. 2016) – sometimes incurring markedly different migratory distances (Dufour et al. 2021). Finally, even individuals can be flexible in their migratory behaviours (Dias et al. 2011; van Bemmelen et al. 2017). Spatially, patterns of among-population variability and resulting levels of inter-population mixing in the non-breeding grounds influence the potential for different populations to interact (and perhaps share pathogens there; Altizer et al. 2011; Boulinier et al. 2016; Gass Jr et al. 2023), as well as to be subjected to the same drivers of population change during the non-breeding season (Reynolds et al. 2011). Non-breeding season patterns of population spread affect the spatial scale at which environmental change during the non-breeding season can impact populations, as well as their ability to track environmental change (Webster et al. 2002). Among- and within-population variability in other metrics (e.g. migratory efficiency or schedule) provides information on costs of migration or other constraints on behaviour. Finally, patterns of individual flexibility inform us on the potential for individuals to exhibit plastic responses to environmental change.

Stercoraridae (jaegers or skuas) are a striking example of such variability in migratory behaviour. Species of skuas display the full diversity of migratory strategies and distance travelled from their breeding colony. Some species are long-distance transequatorial migrants, e.g. the south polar skua *Stercorarius maccormicki* (Kopp et al. 2011; Weimerskirch et al. 2015) or the long-tailed skua *S. longicaudus* (van Bemmelen et al. 2017). Others migrate shorter distances: great skuas *S. skua* remain in the Northern Hemisphere year-round (Magnusdottir et al. 2012), while brown skuas *S. antarcticus* remain in the Southern Hemisphere, exhibiting differences in strategies among populations, over a continuum from subantarctic to tropical waters (Krietsch et al. 2017; Delord et al. 2018; Schultz et al. 2018). Within brown skuas, higher latitude populations migrate longer distances than temperate ones (Delord et al. 2018; Schultz et al. 2018), and levels of population spread during the non-breeding season are also variable, with maximum levels of spread for populations of Crozet and Kerguelen spanning ca. 140° of longitude (from the Benguela Current in the Atlantic to the Tasman Sea; Delord et al. 2018). It seems therefore difficult to predict the migratory behaviour of brown skuas belonging to untracked populations.

However, having a more comprehensive view of the range of migratory behaviours of the species can be important – both to evaluate population-specific exposure to threats, and because of the species' known role in spreading pathogens (Jaeger et al. 2018). In particular, here we were interested in the migratory behaviour of brown skuas breeding on Amsterdam Island (Indian Ocean), the species' northernmost population. This population is small (~80 pairs TAAF KIORE Services 2022) and suffers from very low breeding success. The vulnerability of this population might be worsened by a recent rat eradication program on Amsterdam Island that could negatively impact the species either through lethal effects due to secondary poisoning or through a reduction in the prey base (Travers et al. 2021).

Given the latitudinal gradient in migratory distance in the species, and the status of the Amsterdam population as the species' northernmost population, we might expect individuals breeding there to migrate shorter distances – potentially staying away from the island for shorter amounts of time – than at other sites, or even remain resident year round. Should that be the case, exposure of brown skuas to secondary poisoning due to rat eradication might be particularly strong. In addition, some individuals from two other populations in the Indian Ocean (Crozet and Kerguelen) spend the non-breeding seasons in waters around Amsterdam (Delord et al. 2018). We therefore expect strong mixing between brown skuas from Amsterdam and these other populations. In a context of severe and widespread impacts of high-pathogenicity avian influenza virus (HPAIV H5N1) on wild animals (Klaassen and Wille 2023), with ongoing spread in the Southern Hemisphere (Leguia et al. 2023; Bennet et al. 2024; Bennison et al. 2024; Clessin et al. 2025) including on Crozet and Kerguelen, such mixing could have strong conservation and public health implications. Indeed, brown skuas – as scavengers – can act as reservoirs and vectors for pathogen spread (Gamble et al. 2020; Gittins et al. 2020). Given that individuals from Amsterdam have access to similar areas to those from Crozet and Kerguelen, we expect similar levels of inter-individual variability in all Indian Ocean colonies. Such inter-individual variability might promote the resilience of the species against threats faced during the non-breeding season. Given the sexual dimorphism of the species (Phillips et al. 2002) and some mild evidence of sex-based variation in migratory behaviour in other populations (King Georges Island; Krietsch et al. 2017), we expect sex to partly explain the inter-individual variability in migratory behaviour. Finally, as in other populations (Krietsch et al. 2017), we expect high levels of individual consistency across years.

Here, we therefore study the migratory behaviour of subtropical brown skuas breeding on Amsterdam Island, with a focus on how these vary (i) from other studied populations, (ii) among individuals, and when possible, (iii) within individuals across years. To get a comprehensive description of the post-breeding behaviour of individuals, we combine three approaches: location data obtained from global location sensing (GLS) loggers, activity data obtained from immersion loggers, and stable isotope analyses.

Materials and methods

Study site

Field work was conducted on Amsterdam Island (37° 50' S; 77° 33' E) in the subtropical part of the southern Indian Ocean (Belkin and Gordon 1996) in a mild, oceanic climate. The volcanic island consists of a mountainous 500–800 m plateau 'Plateau des Tourbières' with cliffs on the western edge. Non-native invasive mammal species – house mice *Mus musculus*, brown rats *Rattus norvegicus* and feral cats *Felis catus* – occur throughout the island (Micol and Jouventin 1995). Amsterdam Island has been identified as of high conservation priority due to its seabird populations (Segonzac 1972; Brooke et al. 2007, 2018; Lesage et al. 2024), including four endangered species: the Indian yellow-nosed albatross *Thalassarche carteri*, the sooty albatross *Phoebetria fusca* and the northern rockhopper penguin *Eudyptes moseleyi*, along with the endemic, Amsterdam albatross *Diomedea amsterdamensis* (due to a very small population of 300–350 individuals; Barbraud et al. Unpub. data). The central plateau provides nesting habitat for subtropical brown skuas (~80 pairs, TAAF KIORE Services 2022).

Study species and field methods

The brown skua generally breeds in loose colonies and is highly territorial during breeding, with strong breeding site tenacity and mate fidelity (Furness 1987). The brown skua is an annual breeder, usually laying two eggs in late October-early November, with hatching in late November-early December, and chick fledging ~ 50 days later in early January (Hahn & Peter 2003). The post-breeding period runs from February to November (hereafter non-breeding).

Brown skuas at Amsterdam Island were monitored occasionally (during the late 1990s') and annually since 2018, with all individuals within the monitoring colony individually marked (numbered stainless steel and plastic engraved colour bands; see Pacoureau et al. 2019). Breeding adults were captured on their nest using a running knot and global location sensing (GLS, *n* = 28) loggers were deployed in December 2018.

Molecular sexing

DNA extraction was conducted with 2 µl of blood cells using a chelex resin (Chelex 100 Molecular Biology Resin, BIO-RAD; 10%) associated with Proteinase K. Then, a PCR with amplification of the CHD gene was performed following a standard procedure (Fridolfsson and Ellegren 1999).

Tracking data analyses

GLS loggers (MK3006) weighed 2.51 g, which corresponded to ca. 0.2% of the mean adult body mass and were fixed with cable-ties to a plastic leg band. GLS loggers recorded ambient light level every 10 min, from which local sunrise and sunset hours were inferred to estimate location every 12 h (Wilson et al. 1992). GLS loggers also recorded saltwater immersion data at regular 10-min intervals, by testing for saltwater immersion every 3 s and storing the proportion of positive samples (time in seawater) at the end of each 10-min period (min: 0 – max: 200). Saltwater immersion data were used to estimate daily activity budgets, as time immersed can be interpreted as time sitting on the water, and time dry can be interpreted as time flying and/or time on land (Mackley et al. 2010). GLS also recorded sea surface temperature (SST) (sensor range: −20 to 60 °C) when the logger was immersed for at least two successive 10-min periods. Despite their high mean spatial error of location estimates (ca. 180 km; Phillips et al. 2004), GLS loggers are useful as they can track birds for prolonged periods of time. Twenty-one individuals were recaptured at the same breeding site and blood sampled (for stable isotopes and molecular sexing purposes) during consecutive seasons until 2020. The GLS recovery rate was 75%, which is in the range of previous studies on the species (Crozet: 40%, Kerguelen: 73%, Delord et al. 2018) or on similar species (Adélie Land: 80%, Weimerskirch et al. 2015). Seven of these individuals were recaptured after two years of tracking. For comparative purposes only the first year of data was used unless mentioned otherwise.

Individual locations were estimated using the probGLS package in R (Merkel et al. 2016; see Supplementary). To improve estimates, the daily median sea surface temperature SST recorded by GLS loggers was matched to satellite-derived SST (0.25° × 0.25°, NOAA OI SST V2 High- Resolution Dataset; (Merkel et al. 2016). Latitudinal data around the equinoxes (20th of March 2019 and 2020, 23rd of September 2019, 22nd of September 2020) can suffer from particularly large errors, but longitudinal data is not affected during these periods. As most individuals mostly carried out longitudinal movements, we decided to remove location data 28 days before and after the equinoxes from spatial analyses, only for birds that did not carry out longitudinal movements (see Fig. 1).

Migration timing (departure/arrival dates from/at the colony and duration of the non-breeding period) was inferred by combining visual inspection of each track (i.e., longitudinal directional movement during three consecutive days) and of activity data (i.e., periods of no saltwater immersion) (Figs. 2 & S1). Departure from the colony was inferred when rapid movement with saltwater immersions followed periods of no saltwater immersion (>24 h), while arrival back at the colony was inferred when rapid movement with saltwater immersions was followed by several days of no saltwater immersion (>24 h). The duration of the non-breeding period was calculated as the interval between colony departure and return. Note that two birds appeared to remain resident on the island year round. For those birds the study period (the *non-breeding period*) was considered as starting at the average start date across migratory individuals, and as ending at the average end date across migratory individuals. For each individual, maximum distance from the breeding colony was calculated using the trip package in R (Sumner 2018). The spatial distribution of brown skuas was visualised using Gaussian kernel analysis with a cell size of 2° x 2° and a fixed smoothing parameter (h) of 2°, using the 'adehabitatHR' package in R (Calenge 2006). Both h value and grid cell size were based on the mean accuracy of the devices (Phillips et al. 2004).

To evaluate how consistent individuals were across years, we compared the Nearest Neighbour Distance (NND; as in Votier et al. 2017) between routes of the same individual across years (first vs. second year of data), to the NND between routes of different individuals in the same year. The NND from route 1 to route 2 (NN12) was calculated as the mean distance from each location along route 1 to its nearest neighbour along route 2. The same was done from route 2 to route 1 (NND21), and the reported NND metric for the route 1 – route 2 comparison was the mean of NND12 and NND21.

Five metrics describing daily activity were calculated during the non-breeding period: (1) daily *time spent on water* (sum of time spent immersed in each 10-min block in a day, to obtain hours in the water per day), (2) daily average *wet bouts duration* (duration of uninterrupted sequences of 10-min blocks of immersion data = 200, i.e., time spent totally immersed), (3) daily average *dry bouts duration* (duration of uninterrupted sequences of 10-min blocks of immersion data = 0), (4) daily *number of wet bouts*, and (5) daily *number of dry bouts*. The loggers integrated activity within each 10-min block and so did not provide the exact timing of landings and take-offs. Although not exactly the same as we did, Phalan et al. (2007) found for comparative purposes that bouts defined as a continuous sequence of 0 values for flight (dry) and a sequence of values of 1 or greater for wet bouts, were suitable proxies for activity.

Sources of variability in phenology and activity metrics were explored. Differences between sexes in timing of non-breeding movements were tested using Wilcoxon rank tests. To assess how activity varied over time, sex and among individuals principal components analysis (PCA built with the 'PCA' function, *FactoMineR* package Lê et al. 2008) was first run over the five daily wet/dry activity metrics to circumvent collinearity issues and to avoid redundancy. The detailed results of PCA, the variables and their loadings for each axis are summarised in Table 2. As the three principal components were not normally distributed, differences between sexes and months were tested using Kruskal-Wallis tests followed by Dunn's tests (pairwise comparisons) with a Bonferroni correction for multiple testing to identify which groups were different (Tomczak and Tomczak 2014). Kruskall-Wallis effect sizes (eta2[H]) were calculated and used to report small (eta2[H] between 0,01 and 0.06), medium (eta2[H] between 0.06 and 0.14) and large effects (eta2[h] above 0.14). These analyses were performed using the *rstatix* package in R (Kassambara 2023). Only data for the months of April to August (the 5 months available for all individuals) were used in the analyses. Spatial and statistical analyses were performed using R (R Core Team 2024). Results are presented as means ± SD unless otherwise indicated.

Stable isotope analyses

Following Jaeger et al. (2009), carbon and nitrogen stable isotopes values (δ^{13}C and δ^{15}N, respectively) were measured on four fully-grown body feathers from the lower back per bird. Feathers were collected upon recapture of each individual bird. Body feathers could be collected from 20 adult skuas (out of 21 individuals) that carried a GLS. In seabirds, including skuas, feather isotope values represent the foraging habitat (δ^{13}C) and diet/trophic position (δ^{15}N) during the non-breeding period because adult birds replace their plumage at that time (Higgins and Davies 1996; Cherel et al. 2008; but see Graña Grilli and Cherel (2017). The exact dates of the moulting of brown skuas' body feathers are not known with precision. In addition, the initiation of moulting may vary depending on breeding status (i.e. individuals that fail early during the breeding period may begin moulting their body feathers earlier). In addition, a previous study (Delord et al. 2018) reported that 'most individuals did not moult all their body feathers in the wintering zone. Rather, individuals moulted over different water masses during the whole inter-nesting period, i.e. during migratory movements and

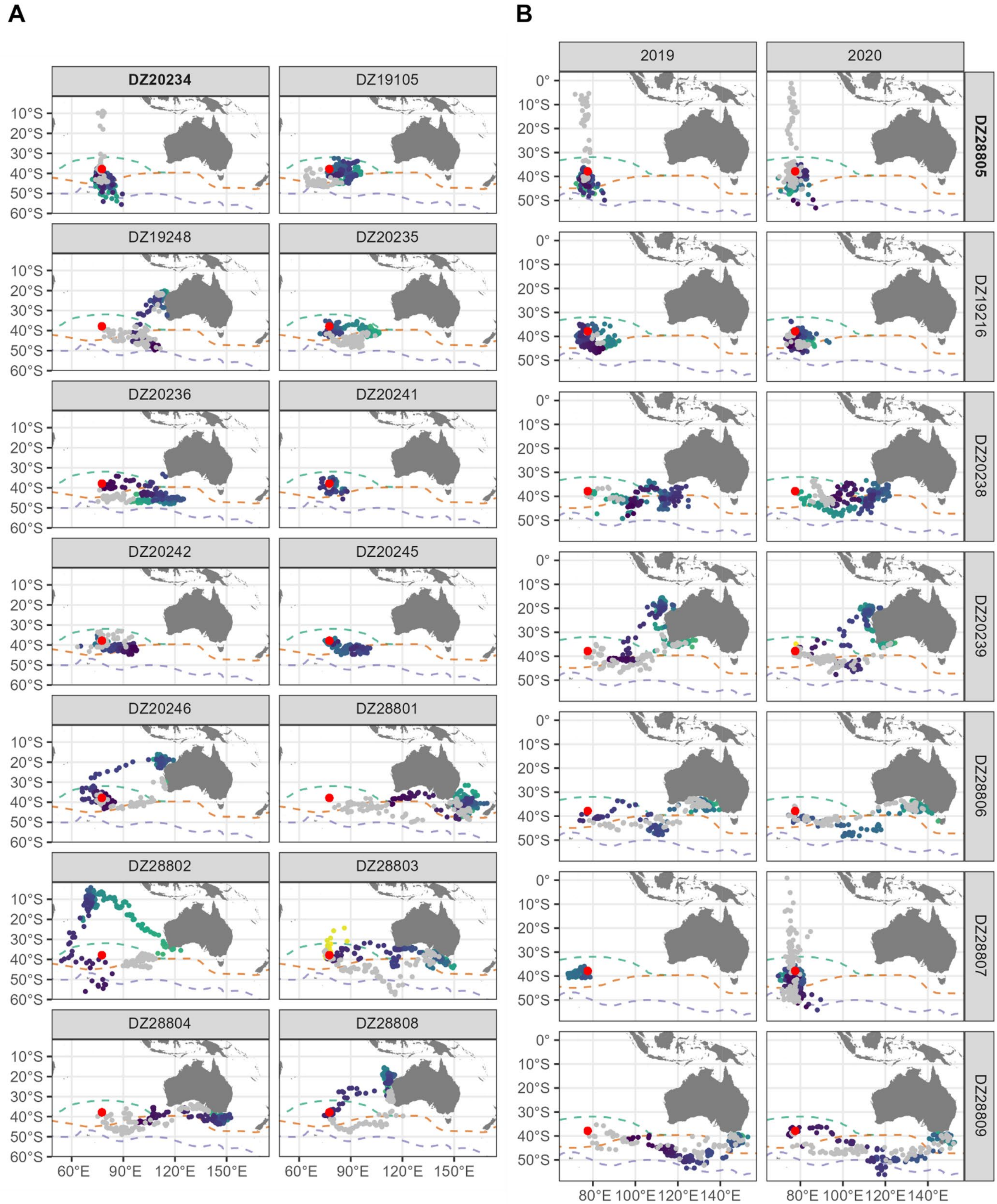

Fig. 1 Locations of individual adult brown skuas from Amsterdam Island during the post-breeding period. (**A**) Individuals with one year of tracking; (**B**) Individuals with two years of tracking. The breeding colony is indicated (red dot). Locations are coloured by day of year (from yellow to blue). Grey dots correspond to locations estimated during the equinoxes. The ID of the two resident birds in 2019 are highlighted in bold

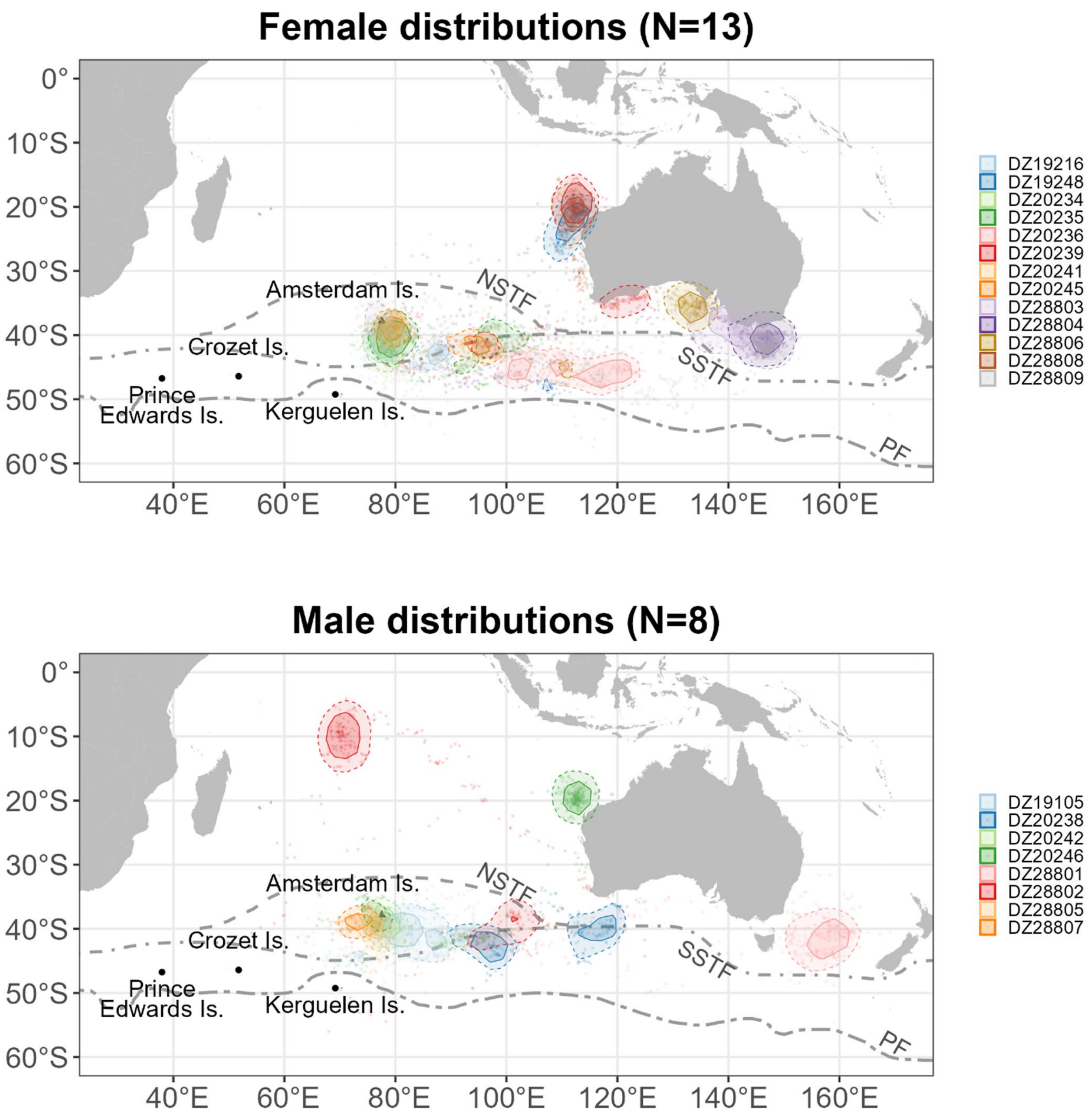

Fig. 2 Kernel densities of individual adult brown skuas from Amsterdam Island during their non-breeding period in 2019 (time between departure from the colony and arrival back at the colony for each bird, except the two residents for which we display locations between the average leaving date – 22rd March 2019 – and the average return date – 20th of August 2019 – of migratory individuals). Dots show raw location data, with a colour for each individual in a given sex panel. Semi-transparent polygons show kernel density-based utilization distributions at 25% (solid lines) and 50% (dotted lines), with the same colour code. Land shown in grey. Breeding colony (black triangle) is indicated. The main frontal structures (obtained from Belkin and Gordon 1996), the Polar Front (PF), Southern Subtropical Front (SSTF) and Northern Subtropical Front (NSTF), are shown by grey lines

before migration'. To facilitate interpretation of adult isotopic values, feathers were also collected from large chicks as control birds reflecting the skua diet during the summer breeding period. For each chick, a single body feather was used for isotopic analyzes, because chick feathers grow almost synchronously and thus present low inter-feather $\delta^{13}C$ and $\delta^{15}N$ variations (Carravieri et al. 2014). Feather preparation and isotopic analyses were detailed by Jaeger et al. (2009). In brief, feathers were cleaned using a 2:1 chloroform: methanol solution and then oven dried for 48 h at

Table 1 Feather isotopic values of brown Skuas according to individual non-breeding water masses and to feather moulting zones (see methods)

Non-breeding areas and habitats	Individuals (n)	Body feathers (n)	Feather $\delta^{13}C$ (‰)	Feather $\delta^{15}N$ (‰)	C : N mass ratio
Non-breeding water masses					
Tropical	4	15	-15.9 ± 0.2^{a}	13.0 ± 0.6^{a}	3.15 ± 0.02
Subtropical	15	52	-17.0 ± 0.6^{b}	15.1 ± 1.7^{b}	3.14 ± 0.03
Subantarctic	7	13	-19.6 ± 1.0^{c}	12.4 ± 3.0^{a}	3.15 ± 0.04
Chicks (Amsterdam)	10	10	-16.6 ± 0.4^{d}	15.8 ± 0.4^{b}	3.14 ± 0.02
Moulting zones					
North-west of Australia (tropical)	4	15	-15.9 ± 0.2^{a}	13.0 ± 0.6^{a}	3.15 ± 0.02
Amsterdam (subtropical)	3	9	$-16.9 \pm 0.6^{b, c}$	16.0 ± 1.7^{b}	3.15 ± 0.03
East of Amsterdam (subtropical)	5	19	-17.1 ± 0.4^{b}	$15.0 \pm 1.4^{b, c,d}$	3.13 ± 0.02
South of Australia (subtropical)	6	22	-17.0 ± 0.7^{b}	$15.2 \pm 1.3^{b, c}$	3.16 ± 0.03
South of Amsterdam (subantarctic)	4	7	-20.1 ± 1.1^{d}	14.0 ± 1.7^{d}	3.18 ± 0.02
Individual DZ20236 (subantarctic)	1	4	-19.1 ± 0.1^{d}	8.5 ± 0.5^{a}	3.11 ± 0.02
Unknown	4	4	–	–	-
Chicks (Amsterdam)	10	10	-16.6 ± 0.4^{c}	$15.8 \pm 0.4^{b, c}$	3.14 ± 0.02

Note that birds may winter and/or moult in several different areas, thus explaining why their total number is > 20. Within non-breeding water masses or moulting zones, values sharing the same superscript letters in the same column are not significantly different at the 0.05 level (see text). Values are means ± SD

Table 2 Results of principal components analyses (PCA) on five wet/dry metrics on brown skuas

Principal components	Total variance explained (%)	Time spent on water	Dry bouts duration	Dry bouts number	Wet bouts duration	Wet bouts number
First	42.5	+ (r = 0.91)[1]	- (r = −0.75)	- (r = −0.12)	+ (r = 0.03)	+ (r = 0.84)
Second	21.3	- (r = −0.11)	- (r = −0.33)	+ (r = 0.94)	- (r = −0.24)	- (r = −0.03)

[1] The symbol used gives the sign of the correlation (+: positive, -: negative); the number in brackets indicates the value of the correlation coefficient r

50 °C. Every single whole body feather was homogenized by cutting it with stainless steel scissors into tiny fragments and a subsample of ~0.3 mg was packed into tin containers for stable isotope analysis. The relative abundance of carbon and nitrogen isotopes were determined with a continuous flow mass spectrometer (Thermo Scientific Delta V Plus) coupled to an elemental analyzer (Thermo Scientific Flash 2000). Results are presented in the usual δ notation relative to Vienna PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively. Replicate measurements of reference materials (USGS-61 and USGS-63) indicated measurement errors < 0.10‰ for both $\delta^{13}C$ and $\delta^{15}N$ values.

For statistical analyses, feather $\delta^{13}C$ and $\delta^{15}N$ values were either grouped at the individual level (hereafter referred to as 'non-breeding water masses') or at the feather level ('moulting zone') (Table 1). First, isotopic values of the four feathers per bird were assigned to non-breeding water masses according to their $\delta^{13}C$ values (tropical, subtropical and subantarctic) and reference $\delta^{13}C$ values in (Jaeger et al. 2010). Second, each single body feather was tentatively assigned to a moulting zone (Weimerskirch et al. 2015). To do so, the GLS tracks of birds that wintered in only one marine area were used to assign feather isotope values to their wintering area, providing a match between isotopic values and moulting zones. The feather isotope values of skuas that spent the non-breeding period in more than one area were then examined to assign feathers to zones with similar isotopic values. Isotopic values could not reliably be assigned to a moulting zone for four feathers using the described 2-step protocol (see 'Unknown' in Table 1). It is important to note that different geographical moulting zones occurred within a given non-breeding water mass, due to the circumpolar annular distribution of the oceanic fronts and water masses (Table 1, Fig. 2 and Table 2).

Results

Spatial distribution and phenology

At the end of the breeding period, most birds dispersed widely, undertaking long-distance migrations, and spent the non-breeding season in the eastern part of the Indian Ocean up to the Tasman Sea (~7500 km from the breeding ground) exhibiting high inter-individual variability in area and distance reached from the colony (Figs. 1 and 2, Table S1). Some individuals remained in the area around Amsterdam year-round (Figs. 1 and 2). Among those, a small proportion (~10% of the tracked individuals, n = 2) could be considered as resident on the island ("terrestrial" individuals) throughout the year on the basis of a combination of movement and activity patterns (Table S1, Figs. 1, 2 and 3 & S1). These

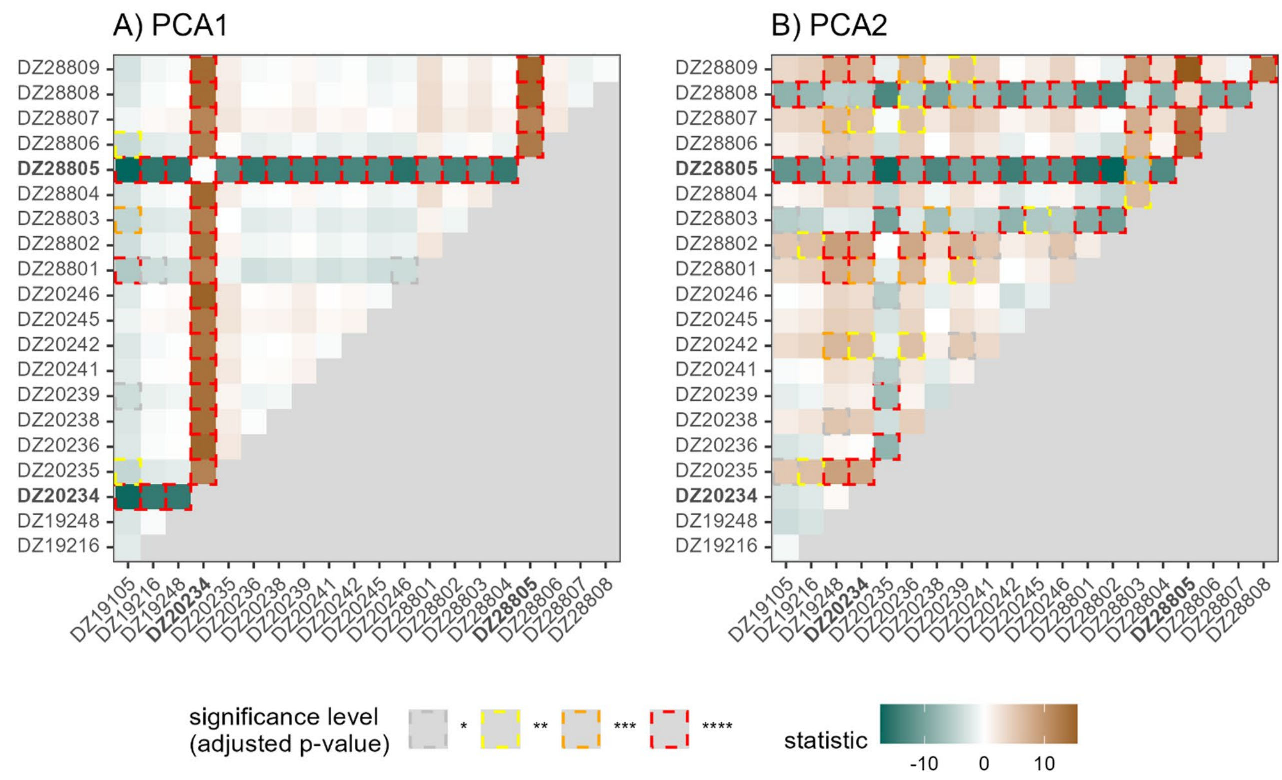

Fig. 3 Results of Dunn tests comparing values of (**A**) the 1st and (**B**) the 2nd PCA axes across individuals. Colours correspond to the test statistic (negative in green, positive in brown, null in white). Significant results are highlighted with grey to red colours. Significance levels refer to adjusted p-values (calculated using a Bonferroni correction). The ID of the two resident birds are highlighted in bold

Table 3 Timing of non-breeding movements of migratory brown skuas from Amsterdam Island, which were tracked using GLS loggers in 2018–2019

Sex	Non-breeding movements	
	Duration (days)	Maximum distance to the colony (km)
F	156 ± 36 (74–192) [a]	3973 ± 1864 (1079–6302) [b]
M	142 ± 47 (51–187) [a]	3485 ± 2290 (827–7510) [b]
All	151 ± 40	3793 ± 1982

For each parameter, values sharing the same superscript letter (a, b; Wilcoxon test) are not statistically significantly different. Mean ± SD (minimum – maximum)

two individuals were a female (DZ20234-B4100) and a male (DZ28805-B4123). Migratory individuals left the colony between late February/mid May and returned between late July/mid September (Table S1). Tracked individuals were away from the breeding colony for 151 ± 40 d, at a mean maximum distance to the colony of 3793 ± 1982 km (Table 3). Migratory females (n = 12) and males (n = 7) did not differ in non-breeding period duration (Wilcoxon rank tests: statistic = 49, p-value = 0.58), nor in distance reached during the non-breeding period (Wilcoxon rank tests: statistic = 51, p-value = 0.48) (Table 4).

The migratory skuas ranged mainly between tropical and subtropical waters and occasionally in subantarctic waters (Figs. 1 and 2, and S2). Individuals were predominantly distributed in subtropical waters (across individuals: 51.4 ± 31.8% of locations; Figs. 1 and 2), followed by subantarctic waters (24.3 ± 19.0%) and, very occasionally, Antarctic waters (0.4 ± 0.9%). 19% of individuals (n = 6) visited Antarctic waters, but only ~ 2% of their locations were within this region. The sea surface temperature recorded by geolocators varied between 18.0 ± 6.1 °C (min: 7 °C,

Table 4 Values of brown skua daily activity parameters (mean ± SD) recorded using global location sensor (GLS), separated by sex

	Females (n = 13)	Males (n = 8)	Migrants (n = 19)	All (n = 21)
Time spent on water (%)	76.4 ± 24.5	69.4 ± 29.8	81.7 ± 12.8	73.9 ± 26.7
Wet bouts (sitting on water) duration (h)	1.1 ± 9.3	0.7 ± 0.5	1.0 ± 7.8	0.9 ± 7.4
Dry bouts duration (h)	1.3 ± 4.6	2.6 ± 8.6	0.5 ± 1	1.8 ± 6.4
Wet bouts (sitting on water) number	16.3 ± 7.9	16.1 ± 8.6	17.9 ± 6.5	16.2 ± 8.1
Dry bouts number	3.4 ± 3.1	4.0 ± 3.1	3.8 ± 3.2	3.6 ± 3.1

max: 37 °C) in May to 11.0 ± 2.7 °C in August (min: 3 °C, max: 32 °C). Females and males occupied similar areas and habitats during the non-breeding period (15.8 ± 6.2 °C and 14.9 ± 4.8 °C, respectively).

Seven birds could not be recaptured the first year and were therefore tracked for two consecutive years. Only one out of these seven birds changed its migratory strategy, being resident the first year and migrating the following year (Fig. 1). All other individuals were very similar in their migratory routes and destinations (Fig. 1). The average Nearest Neighbour Distance (NND) between individuals tracked the same year was 1212 km, while the average NND between years for a given individual was 104 km (Figure S3).

The proportion of individuals that were at sea between March and August varied from 62 to 90%. The period with the fewest birds (< 15% of the tracked birds) on land was from May to July.

Only three individuals (from two breeding pairs) bred successfully during the season of deployment (failure for the other birds occurred at chick-rearing stage). The rate of breeding failure among tracked individuals seemed of the same magnitude as the high rate observed within the monitoring colony (86.7% *versus* 79.8 ± 8.0%, calculated as the percentage of nests with eggs that had one chick or more over the period 2019 to 2024, $n = 22$ nests).

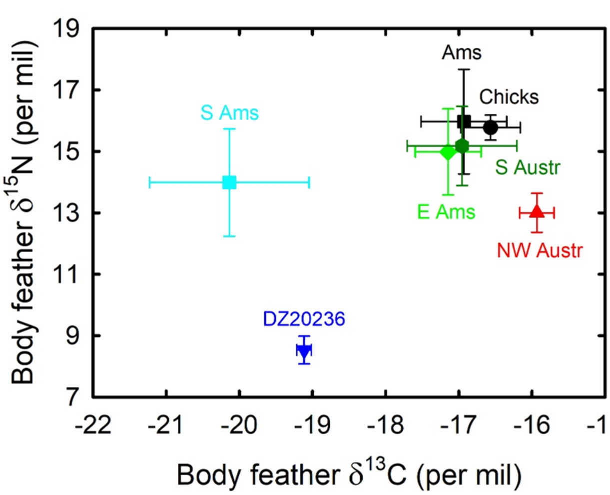

Fig. 4 Body feather $\delta^{15}N$ *versus* $\delta^{13}C$ values of adults and chicks (black circle) of brown skuas from Amsterdam Island according to their moulting zones. Values are means ± SD of all body feathers synthesized within the same habitat (see Table 1). Abbreviations: Ams, Amsterdam Island (black square); E Ams, east of Amsterdam Island (green diamond); NW Austr, north-west of Australia (red triangle up); S Ams, south of Amsterdam Island (cyan square); S Austr, south of Australia (dark green hex). DZ20236 (blue triangle down) refers to the ring number of an individual adult skua (see text)

Activity characteristics

Component loadings indicated (Table 2) that the first axis integrated the duration of dry bouts (loading = −0.75) and the percentage of time spent wet and the number of wet bouts (loading = 0.91 and 0.84, respectively). The second and third axis integrated the number of dry bouts and the duration of dry and wet bouts (Table 2 & S2).

There were inter-individual differences in PC1 and PC2 (Figs. 3 & S4-5). In particular, the two resident individuals statistically differed from all the others in their PC1 values (large effect of individual ID on PC1, eta2[H] = 0.297; Figs. 3 & S4). These two individuals (DZ20234-B4100 and DZ28805-B4123) exhibited lower PC1 values (associated with longer dry bouts). Although the values of PC2 varied significantly between individuals (large effect of individual ID on PC2, eta2[H] = 0.143), this was not as strongly linked to whether individuals were migrants or residents as for PC1 (Figs. 3 & S5).

No effect of sex was detected on PC1 (Table S3a), while sex only explained a small part of the differences between individuals in PC2 values (only small effects of sex on PC2 in May-August; Table S3b, Figure S5). Monthly variations in both PC1 and PC2 were small (small effect of the month on PC1 – eta2[H] = 0.0127 – and on PC2 – eta2[H] = 0.0135; Figures S4-5, Tables S4-5), with lower PC1 values in July and August compared with May-June for females (Table S4a, Figure S4) and with a very slight U-shape trend in PC2 across the non-breeding season (Tables S5a-b, Figure S5).

Stable isotopes

Feather isotopic values of adult brown skuas from Amsterdam Island ranged widely, from −21.0 to −15.4‰ (a 5.6‰ difference), and from 8.1 to 19.0‰ (10.9‰) for $\delta^{13}C$ and $\delta^{15}N$ values, respectively. Feather $\delta^{13}C$ values indicated wintering in the tropical ($\delta^{13}C$ >−16.0−16.4‰; $n = 15$, −15.9 ± 0.2‰), subtropical ($n = 52$, −17.0 ± 0.6‰) and subantarctic ($\delta^{13}C$ <−18.3‰; $n = 13$, −19.6 ± 1.0‰) zones, but not further South, in the Antarctic Zone ($\delta^{13}C$ <−21.2%; Jaeger et al. 2010). Some birds showed low intra-individual variations in isotopic values of their four feathers, while large SD indicated that other individuals wintered over different water masses. The bird that was resident the year preceding feather sampling (the female DZ20234-B4100) has $\delta^{13}C$ values ranging between − 18.7 and − 15.65, and $\delta^{15}N$ values between 16.75 and 19.0.

Combining GLS data and isotopic values at the feather level depicted an informative pattern (Fig. 4). Feather $\delta^{13}C$ and $\delta^{15}N$ values from different moulting zones were significantly different (Kruskal-Wallis: $H = 51.1$ and 39.7 for $\delta^{13}C$ and $\delta^{15}N$, respectively, both $p < 0.0001$). Post-hoc pairwise

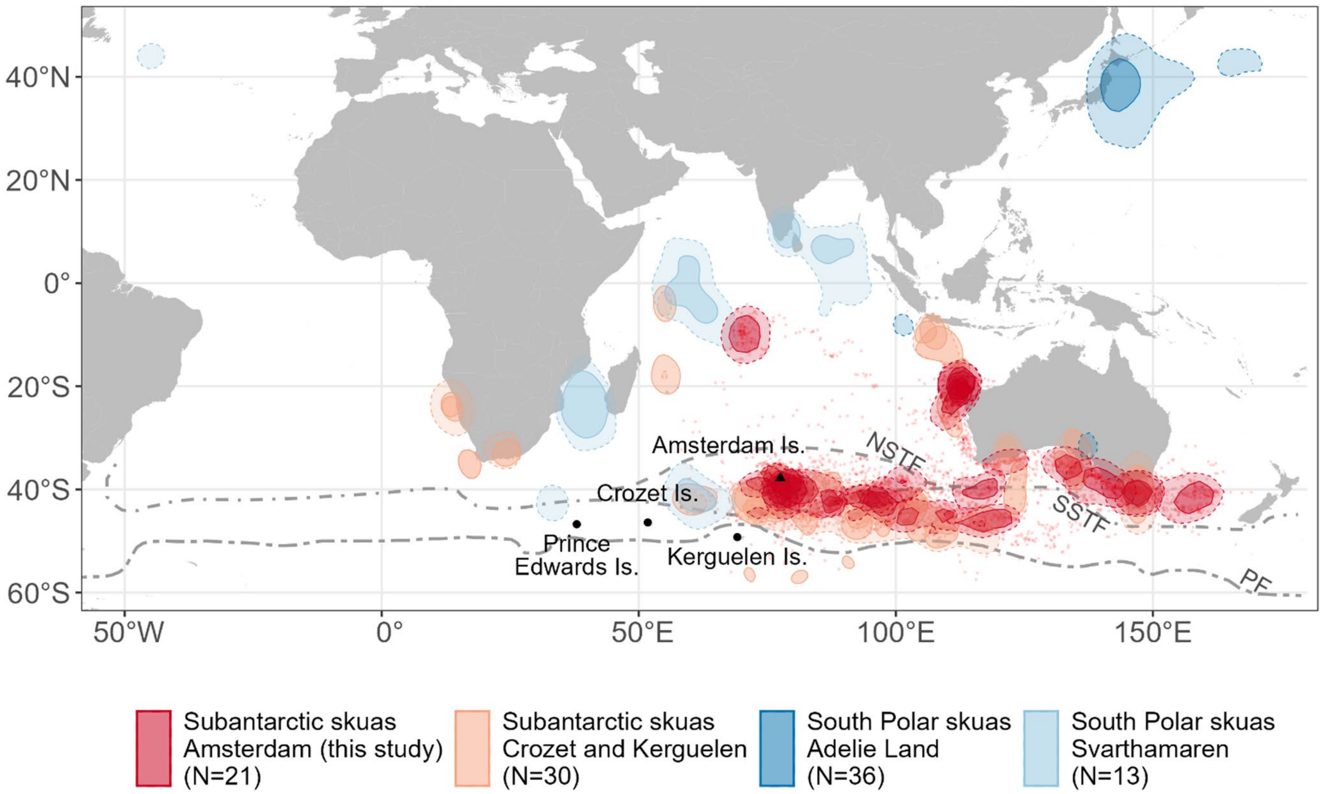

Fig. 5 Non-breeding distribution (Kernel utilization densities at 25% - solid lines - and 50% - dotted lines) of five populations of skuas (in blue South Polar skuas *Stercorarius maccormicki*, and in red brown skuas *S. antarcticus*) from subtropical to south polar breeding colonies: Amsterdam Is. (this study), Kerguelen and Crozet Is. (Delord et al. 2018), Adélie Land and Svarthamaren (Weimerskirch et al. 2015). Land shown in grey. Breeding colony (black triangle) is indicated. The main frontal structures (obtained from Belkin and Gordon 1996), the Polar Front (PF), Southern Subtropical Front (SSTF) and Northern Subtropical Front (NSTF), are shown by grey lines.

Conover-Inman tests documented three notable features (Table 1): (i) feather δ^{13}C values overall increased with decreasing latitudes, from the lower values of feathers that were moulted south of Amsterdam Island (−20.1‰) to the higher δ^{13}C values of adults that moulted in tropical waters in north-west Australia (−15.9‰); (ii) feather isotopic values were identical for chicks and adults that moulted in the subtropics, whatever the moulting grounds (Amsterdam, east of Amsterdam and south of Australia, from western Australia to the Tasman Sea); (iii) one individual (ring number DZ20236) synthesized its four body feathers in subantarctic waters (−19.1‰), where it presented remarkable low δ^{15}N values (8.5‰) that differed from all the other groups (13.0–16.0‰).

Discussion

Our study described the non-breeding movements of the most northerly breeding population of brown skuas, from the temperate Amsterdam Island in the southern Indian Ocean. Their latitudinal at-sea distribution outside of the breeding season was comparable to that of the subantarctic populations of the Crozet and Kerguelen archipelagos (Delord et al. 2018; Fig. 5) in the southern Indian Ocean, but also from subantarctic islands in the southern Atlantic Ocean (Bird Island and King George Island; Phillips et al. 2007; Carneiro et al. 2016; Krietsch et al. 2017) and from a temperate island in the southern Pacific Ocean (Chatham Island; Schultz et al. 2018). The birds targeted distant areas distributed over neritic and oceanic waters of subantarctic, subtropical and tropical biomes. These targeted habitats were consistently found in other studies in the Indian Ocean (Delord et al. 2018), but also in other ocean basins, as evidenced by stable isotopes (Mills et al. 2023). Brown skuas from Amsterdam Island showed high levels of inter-individual variability in migratory behaviour. Such inter-individual variability was previously evidenced at inter-population and intra-population levels in several species of skuas (long-tailed skua (van Bemmelen et al. 2017); Arctic skua (van Bemmelen et al. 2024); brown skua (Krietsch et al. 2017; Schultz et al. 2018); Falkland skua (Phillips et al. 2007); south polar skua (Kopp et al. 2011; Weimerskirch et al. 2015). Levels of inter-individual variability in migratory destinations were more similar to those of birds from Crozet and Kerguelen (Delord et al. 2018) than other colonies

(Phillips et al. 2007; Schultz et al. 2018). The high inter-individual variability in migratory destinations might help the Amsterdam Island population be more resilient in the face of environmental changes. However, the population from Amsterdam Island appeared to be the only one to have resident birds, albeit in small numbers. This is possibly related with the fact that Amsterdam Island hosts the most northerly population of the species in subtropical waters, where most individuals from various localities winter. The only other temperate population of brown skuas (from the Chatham Islands, located at the Subtropical Front) exhibited the smallest spatiotemporal scale in non-breeding movement (ranges away from the colony: Crozet (46°24'S) & Kerguelen (49°15'S) Islands 4000 km (Delord et al. 2018), Bird Island (52°09'S) 1500–2700 km (Carneiro et al. 2016), King George Island (62°02'S) 1700–2500 km (Krietsch et al. 2017), South East Island-Chatham (44°20'S) 1500 km (Schultz et al. 2018). But even in this latter population, all birds were migratory. Nonetheless, Swales (1965) mentions that some individuals of the Tristan skua (*Stercorarius antarcticus hamiltoni*) on Gough Is. (40°19'S) appear to reside on the island during the non-breeding season '*skua number decreased almost to nil after breeding*, *but some immature birds remained on the Is. all the winter*'. Recent tracking data does not seem to corroborate the existence of resident individuals (Steinfurth et al. 2025), but this remains to be confirmed on a larger number of individuals.

Contrary to expectations due to the reversed sexual size dimorphism (Phillips et al. 2002) and some evidence of sex differences activity elsewhere (Krietsch et al. 2017), sex could either not, or only partly explain inter-individual differences in migratory behaviour (duration, distance, activity). Sex differences in activity were swamped by differences between migrants and residents, and among the two resident birds, there was one male and one female. In general, the factors driving differences in migratory behaviour (inter-annual, inter-individual, sexual, etc.) are not entirely clear and require further study. Nevertheless, it is likely that different strategies lead to varying ecological and anthropogenic pressures across populations, which underscores the importance of considering such variability in future conservation planning and management (Carravieri et al. 2017). Differences in behaviour during the post-breeding period may have implications in terms of exposure to secondary poisoning, contaminants, plastics, interactions with fisheries, or exposure to pathogens (Carravieri et al. 2017; Clark et al. 2023; Clessin et al. 2025).

As previously found in brown skuas from the Kerguelen Islands (Delord et al. 2018), the δ^{13}C values of Amsterdam skuas correspond well to the latitudinal δ^{13}C gradient of Southern Ocean water masses (Cherel and Hobson 2007), with δ^{13}C values of feathers that were synthesized in subantarctic waters and tropical waters being lower and higher, respectively, than values of subtropical feathers. In agreement with wintering areas being primarily located in the subtropics, feather δ^{13}C values indicated that most body feathers were synthesized in subtropical waters. This precludes using δ^{13}C values to differentiate between feathers that grew on the breeding and wintering grounds, as they did not present obvious isotopic differences. Feather δ^{15}N values are difficult to interpret, because δ^{15}N baselines vary in different water masses, thus obscuring their trophic interpretation. However, the high δ^{15}N value (15.1‰) of feathers that grew in subtropical waters indicate that skuas likely fed on fishes and/or squids, because the muscle δ^{15}N values of six subtropical pelagic fishes and four pelagic squids occurring in Amsterdam waters are lower than 15.1‰ and ranged from 10.4‰ (the myctophid *Ctenoscopelus phengodes*) to 14.2‰ (the flying fish *Cheilopogon pinnatibarbatus*) (author's Unpub. data). Within that context, the low δ^{15}N values (8.1–9.0.1.0‰) of the four body feathers of the individual DZ20236 are puzzling. Such low δ^{15}N values were previously found in many feathers of brown skuas from the Kerguelen Islands (Delord et al. 2018) and in a few feathers of south polar skuas (Weimerskirch et al. 2015), when they forage at similar latitudes in the southern Indian Ocean. This could suggest that skuas fed on low trophic level prey in the area, but this remains to be confirmed. A comparison of the skua δ^{15}N values with those of other subantarctic and subtropical organisms suggests that the unknown prey were not marine mammals, seabirds, cephalopods or fish, but instead macrozooplankton, probably crustaceans (Cherel et al. 2008b, 2010; Stowasser et al. 2012); this hypothesis would need to be thoroughly investigated. More generally, the correspondence between isotopic values and broad geographic moulting zones that we established in this study paves the way to obtaining to future insights on individual migratory behaviour even in cases without logger deployments (feather sampling only).

During the non-breeding season, brown skuas from Amsterdam Island were completely segregated from populations from other ocean basins (southern Atlantic Ocean (Phillips et al. 2007; Carneiro et al. 2016; Krietsch et al. 2017); southern Pacific Ocean (Schultz et al. 2018)). In contrast, they shared non-breeding grounds with other populations of the southern Indian Ocean: the Amsterdam Island area, along the Southeast Indian Ridge in the Eastern Indian Ocean and the waters off Australia (three main sectors: Tasmania, Indian Ocean Coast/Tropic of Capricorn and Great Australian Bight (Delord et al. 2018; Fig. 5). Additionally, they shared non-breeding areas at sea with different populations of the closely-related south polar skua *Stercorarius maccormicki* (Weimerskirch et al. 2015). Knowing which populations brown skuas from Amsterdam Island can possibly mix with in their non-breeding grounds can contribute to a better understanding of epizootic pathways (Gorta et al. 2024; Clessin et al. 2025; Steinfurth et al. 2025). Indeed, as scavengers, brown skuas are potential vectors in epizooties. They have already been identified as spreaders of the pathogen of avian cholera (*Pasteurella multocida*; (Bourret et al. 2018; Jaeger et al. 2018) with conservation issues for the seabird community of the island (Brooke et al. 2007; Lamb et al. 2023). Concerning the current HPAIV H5N1 epizooty, the role of skuas warrants further investigation (Clessin et al. 2025), but should individuals mix with contaminated birds from Crozet and Kerguelen during the non-breeding season, or with other birds in coastal Australia and New Zealand, this could have dramatic consequences in terms of virus spread.

Our results can also inform other conservation issues. They helped identify the optimal period for scheduling the first phase of land operations for eradicating introduced species on Amsterdam Island. The period of lower detrimental effect on skuas based on our results (i.e. the period with the smallest proportion of the breeding population present on land) appeared to be from May to July. Based on the results of our study, the eradication of invasive non-native species campaign took place between May-July 2024, in order to have the lowest possible impact on the skua population. Nevertheless, nine skua carcasses were found post-eradication, possibly attributable to secondary poisoning (pers. obs.). The observed pre-eradication breeding failure was very high (~87%) at Amsterdam Island and very high compared to other breeding sites (e.g., ~16% (95% CI: 12%–22%) in the Kerguelen archipelago; Goutte et al. 2014), so there is hope that despite the risks of short-term impact on skua survival, the eradication might help restore higher breeding successes. Mid- and long-term post-eradication surveys will be needed to confirm the effects on brown skuas and the benefits for conservation purposes (for a review: Phillippe-Lesaffre et al. 2023).

Finally, our study also provides some insight into the intra-individual variability in migratory strategies of brown skuas from Amsterdam Island. Even though only seven individuals were tracked for two consecutive years, their strategies appeared nevertheless mostly consistent across years (Figure S1). Such inter-annual consistency was found for the species at the population level in South Georgia (Carneiro et al. 2016) and at the individual level in King George Island (Krietsch et al. 2017). However, in our study, one bird changed from being resident during the first non-breeding season to being a short-distance migrant during the next (Figure S1). Such flexibility in non-breeding movements was evidenced for long-tailed skuas (van Bemmelen et al. 2017), and reflect the potential for individuals to adjust their migratory behaviour to changing conditions. It would be interesting to develop longer longitudinal studies to understand how migratory birds might shift between resident and environmental strategies in response to environmental conditions – including to the rat eradication program (e.g. will there still be resident birds without the abundant source of food that rats might have represented in the past?).

More generally, better understanding the ecology of the Amsterdam Island population of brown skuas is important because of the uniqueness of this population. Indeed, genetic investigations are underway to elucidate the status of the Amsterdam Island population, and chances are that it is an evolutionary unit distinct from other populations in the southern Indian Ocean (i.e. Crozet Is. and Kerguelen Islands, Viricel et al. Unpub. data). With this study we both gained fundamental insight on their migratory behaviour, and applied knowledge regarding the risks of pathogen spread and secondary poisoning in the context of the rat eradication program on the island.

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Authors' contributions ASBL and KD are joint first authors. Study design: KD, CB and YC. Data analysis and processing: KD, ASBL, YC, CR, GG. KD, ASBL, CB and YC wrote the text and all authors edited and revised the manuscript, gave final approval for publication and agreed to be held accountable for the content therein.

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Data availability The data used in the present article will be provided for open access as supplementary.

Code availability The custom code used in the present article will be provided for open access as supplementary.

Declarations

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Ethics approval The Ethics Committee of French Polar Institute-IPEV and the Comité Environnement Polaire approved the field procedures for the French Southern Territories.

Consent for publication All authors have given their consent for the article to be submitted to Marine Biology.

Consent to participate All authors have agreed to participate in the study and its writing in the form of an article.

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