

High variability in migration and wintering strategies of brown skuas (*Catharacta antarctica lonnbergi*) in the Indian Ocean

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Abstract Movements of brown skuas (*Catharacta antarctica lonnbergi*) originating from two populations in the southern Indian Ocean were studied during the non-breeding period using geolocation. A total of 33 individuals were equipped resulting in 34 annual tracks recovered from 50 deployments. Brown skuas varied extensively in their post-breeding movements, from true long range migrations to reach distant wintering zones, to short movements in the vicinity of breeding grounds. Overall, brown skuas migrated northward to overwinter in different areas in the southern hemisphere; individuals remained in the Indian Ocean, except two that overwintered in the Benguela Current (Atlantic Ocean). Wintering grounds were generally situated in productive dynamic upwelling waters or frontal systems. Brown skuas avoided the less productive area of the South Subtropical Gyre in the Central Indian Ocean. Individuals clearly differed in migratory strategies, targeting areas in a continuum from the sub-Antarctic to the tropics. Inter-individual differences were not sex-dependent. The migration dates varied between sexes with females leaving the breeding sites earlier and returning later compared to males. The duration of migration depended on wintering area and sex. Males had shorter migrations than females, regardless of the wintering area. Isotopic signatures clearly indicated that birds moulted in the wintering area and during migration. The low $\delta^{15}\text{N}$

values of feathers that grew in mixed subtropical-sub-Antarctic waters suggest that skuas fed on low trophic level prey in these areas. The origin and consequences of such strong inter-individual variation in migratory strategies requires further investigation.

Keywords Activity · Feather · Geocator · Intraspecific strategies · Phenology · Stable isotopes

Introduction

Migration is commonly considered to be a response to seasonal variation in the environment and particularly to prey availability (Jessopp et al. 2013). Seabirds are central place foragers during breeding but can range over much larger areas in search of food outside the breeding period. Migration often necessitates large-scale movements beyond the breeding home range and is an essential component of the life-history of flying seabirds (Shaffer et al. 2006; Egevang et al. 2010; Weimerskirch et al. 2014). Migration strategies of seabirds can differ markedly, exhibiting intraspecific variations linked to population, sex or age (Guilford et al. 2009; Dias et al. 2011; Fijn et al. 2013). Individuals from the same breeding colony could migrate using different routes, thereby reaching distant and distinct wintering grounds (Yamamoto et al. 2010; Weimerskirch et al. 2015a). Timing for the outbound or the inbound movements could also differ between individuals and the sexes, (Yamamoto et al. 2010; Hedd et al. 2014; Thiebot et al. 2014). Hence, describing and understanding the individual differences in migration strategy that may impact winter survival of individuals is a key issue in population dynamics of long-lived species (Barbraud and

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Weimerskirch 2003; Frederiksen et al. 2008; Reiertsen et al. 2014).

The identification of migration strategies is furthermore crucial to understand how individuals are differently affected by climate change (Weimerskirch et al. 2012), pollution, particularly oiling (Montevecchi et al. 2012a, b), interaction with fisheries including the associated incidental bycatch (Phillips et al. 2005; Watkins et al. 2008; Maree et al. 2014) and exposure to contaminants (Blévin et al. 2013; Leat et al. 2013; Carravieri et al. 2014a). Individual responses to environmental variability or to anthropogenic factors can have strong implications in terms of survival and population dynamics (Harris et al. 2013; Goutte et al. 2014). Individuals, from the same or different populations, might share wintering areas and experience similar threats (Gonzalez-Solis et al. 2007; Frederiksen et al. 2012; Tranquilla et al. 2014), or individuals might have different strategies, resulting in differences in threat exposure (Rayner et al. 2011; Hedd et al. 2012; Carey et al. 2014).

Large skuas (Stercorariidae, *Catharacta* sp.) are colonial seabirds that breed mainly in the Southern Ocean and in Antarctica (except one Northern Atlantic species). A high degree of interspecific variation exists in migration strategies in skuas, even within species and populations (Phillips et al. 2007; Kopp et al. 2011; Weimerskirch et al. 2015b; Krietsch et al. 2017). However, few studies on migration movements of skuas have been conducted and intraspecific variations in migration patterns and in wintering areas remain poorly understood. For species that employ specialized predatory strategies (such as skuas), understanding how individuals can adjust their foraging behaviour to changing conditions to fulfil their life-history needs is a cornerstone of their ecology. The reason for such high variation is unknown, but it should clearly have different fitness consequences for individuals (because the different areas might differ in their productivity and in the experienced threats).

The aim of this study was to contribute such information for two brown skua populations (*Catharacta antarctica lonnbergi*, Mathews, 1912) breeding in the sub-Antarctic French Southern Territories. The brown skua is a long-lived seabird that mainly breeds on sub-Antarctic islands and the Antarctic Peninsula. The diet of brown skuas is relatively well documented during the breeding season, with birds feeding on local abundant resources; they often specialize as predators or scavengers of petrels and penguins (Furness 1987; Olsen and Larsson 1997). However, the diet and foraging ecology of brown skuas remain poorly known outside the breeding season (Furness 1987). Food availability usually varies throughout the year and is most likely a driver of migration and wintering strategies (Lack 1968; Alerstam et al. 2003). The timing of the migration is expected to be synchronized with the

phenology of the prey species, especially with migratory species, to avoid a mistiming in breeding cycles (Visser and Both 2005). The nonbreeding distribution of brown skuas is only known for South Georgia (Phillips et al. 2007; Carneiro et al. 2016) and King George Island (Krietsch et al. 2017). To date, the wintering ranges for Southern Indian Ocean populations have been inferred primarily from at-sea sightings or recoveries of ringed birds. This information suggests that during the nonbreeding period some individuals stay close to their breeding range, while others are migratory or dispersive (Eklund 1961; Olsen and Larsson 1997). Some individuals winter around Australia, with two ring recoveries of Kerguelen birds there (Higgins and Davies 1996).

The present study focuses on the intraspecific comparison of migration strategies, wintering ranges, activity patterns and diet of two populations of brown skuas in the Southern Indian Ocean by combining tracking (geolocators) and stable isotope analyses. Using biotelemetry data, we investigated whether (1) individuals vary in their migratory behaviour, (2) sexes differ in their migration timing and wintering areas, and (3) individuals modify their activity patterns between the breeding, migration and nonbreeding period. We hypothesized that a shift might be accompanied by modification of the activity pattern (i.e. time spent on the water recorded by the geolocators), concomitant with a change in the isotopic signature between the two periods, similar to recent results for the south polar skua (Weimerskirch et al. 2015b).

Methods

Brown skuas were studied on two sub-Antarctic islands in the southern Indian Ocean: Possession Island (46°25'S, 51°45'E) in the Crozet archipelago and Mayes Island (49°28'S, 69°57'E) in the Kerguelen archipelago. Tracking data were used to characterise the at-sea distribution of adults during their breeding and nonbreeding periods. Global location sensing (GLS) loggers (British Antarctic Survey, Cambridge) were deployed on adults during the breeding season (2008–2009 and 2011–2012 at Kerguelen; $n = 40$ and 2010–2011 at Crozet; $n = 10$). GLS loggers (Mk5, Mk15) weighed 3.6 and 2.5 g, respectively, i.e. $\approx 0.14\%$ of body mass and well below the recommended threshold of 3% of body mass (Phillips et al. 2003). These were mounted on plastic or metal leg bands. Adults were captured on the nest during the breeding season (brooding or chick rearing stage). Sex of the birds, except those from Crozet, was determined using molecular methods (Blanchard et al. 2007) ($n = 29$; 13 males and 16 females). Processing of the GLS daylight data was carried out as described previously (Péron et al. 2010). Migration timing

was determined by combined visual examination of movement and activity data; outward migration started from the first directional movement (followed by several consecutive days with directional flight), while the final nonbreeding location was the last location in the nonbreeding area before a sustained period of directional movement towards the breeding colony. Birds were considered to be wintering from the end of the outward migration in February to April, to the onset of the return migration in the following August. The breeding success of the tracked individuals was unknown.

GLS data allow long-term (several years) latitude and longitude estimation from daylight measurements, albeit although with a lower accuracy (186 ± 114 km; Phillips et al. 2004) than satellite transmitters (Wilson et al. 1992). Loggers measured daylight level intensity every 60 s and the maximum intensity for each 10 min is recorded. An internal clock allows estimation of the latitude based on day length and longitude based on the timing of local midday with respect to Coordinated Universal Time (Afanasyev 2004). Daylight data recorded by GLS were analysed using a standardized procedure for flying seabirds (Phillips et al. 2004) to provide two locations per day. Thresholds ($h = 4$) in the light curves were used to determine sunrise and sunset. Locations fixes were calculated from daylight data using BASTrak software (provided by British Antarctic Survey). During a 1–2 weeks period around the equinoxes (20–21 March and 22–23 September), latitude cannot be estimated accurately (Wilson et al. 1992). Spatial distribution of brown skuas during the interbreeding period was investigated by producing 25% utilization distributions (UDs) for each individual, using kernel analysis with a cell size of $2^\circ \times 2^\circ$ and a fixed smoothing parameter (h) of 2° . Both h value and grid cell size were based on the mean accuracy of the devices. Spatial analyses were performed using the “*adehabitatHR*” R package (Calenge 2006).

Immersion data indicated the number of 3 s periods during 10 min blocks when the sensor on the unit was immersed in saltwater and raw values ranged from 0 (no immersion) to 200 (permanently immersed). The GLS raw immersion data were processed as described previously (Péron et al. 2010) to estimate the daily percentage of time spent on the sea surface (activity) separately for diurnal and nocturnal periods (based on local sunset and sunrise times derived by analysis of the daylight curves processed using the BASTrak software package). The mean percentage of time spent on the water (wet) was calculated daily for each period (migration and wintering) to provide information on seasonal variation in foraging behaviour. Conversely, the time spent dry is generally interpreted as flight (particularly outside the breeding period), and therefore could be assumed not to be foraging. The duration of daylight and

darkness each day (consecutive light and dark period) was assessed directly from the logger daylight data. Loggers also recorded sea surface temperature (SST) when the logger was immersed for more than 10 min. The average SST recorded monthly was used as an indicator of the water masses where the birds foraged during the nonbreeding period.

We then fitted generalized linear models (GLMs) to investigate the effects of sex, wintering location (three different water masses sensu Longhurst (2007): subtropical, tropical or sub-Antarctic) and their interaction on migration schedules (date of departure, date of arrival and duration) using a Poisson distribution. We selected only one track for the bird tracked over two consecutive years to prevent pseudo-replication. General linear mixed-effects models (GLMMs), fitted in the lme4 package (Zuur et al. 2009), were used to model activity patterns (daily proportion of time spent on the water during daytime or during darkness). Sex, wintering location, month (independent variables) and two by two interactions were included as fixed effects. Individual identity was fitted as a random effect to account for pseudo-replication, as the same individual could contribute several values. Model assumptions were visually validated based on normalized residuals, following the protocol presented by Zuur et al. (2009). Unsexed individuals were excluded from the dataset. Due to sample size, year could not be used as a fixed factor in the models. The effect of breeding colony could not be included due to small sample size for the Crozet population. Models were ranked using the Akaike Information Criterion (AIC) and Akaike weights (Burnham and Anderson 2002). The model with the lowest AIC was considered the best model. When Δ AIC between models was <2 , the models were considered equally good descriptors of the data and we chose the most parsimonious model—that with the lowest number of parameters. Spatial and statistical analyses were performed using R 2.15.3 (R Core Team 2015).

Following (Jaeger et al. 2009), carbon and nitrogen stable isotopes ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) were measured on four different fully grown body feathers from the lower back. Feathers were collected upon recapture of each individual bird, thus corresponding to the previous moulting period at sea recorded by the GLS. In seabirds, including skuas, feather isotope values represent the foraging habitat ($\delta^{13}\text{C}$) and diet/trophic position ($\delta^{15}\text{N}$) during the nonbreeding period because adult birds replace their plumage at that time (Higgins and Davies 1996; Cherel et al. 2008b; but see Graña Grilli and Cherel 2017). To verify that skuas moulted body feathers outside the breeding period, ten large chicks from Kerguelen Islands were feather sampled as control birds reflecting the skua diet during the summer breeding period. At that time

brown skuas from Mayes Island prey upon seabirds on land, mainly blue petrels (*Halobaena caerulea*; Mougeot et al. 1998), a small Procellariiforme that forages at sea in southern Antarctic waters (Cherel et al. 2014). A single chick body feather was used for isotopic analyses, because chick feathers grow almost synchronously and thus present low inter-feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variations (Carravieri et al. 2014b). 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 50 °C. Each whole body feather was homogenized by cutting it with scissors into small fragments and a subsample of ~ 0.3 mg was packed into tin containers for stable isotope analysis. The relative abundances of carbon and nitrogen isotopes were determined with a continuous flow mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyzer (Thermo Scientific Flash EA 1112). Results are presented in the usual δ notation relative to Vienna PeeDee Belemnite and atmospheric N_2 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated measurement errors $< 0.15\%$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

For statistical analyses, feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were either grouped at the individual level (wintering zones) or at the feather level (moult zone) (Table 1). In the former analysis, isotopic values of the four feathers per

bird were assigned to the main wintering zone identified by the GLS data of the corresponding individual (tropical, subtropical and sub-Antarctic). In the latter analysis, each single body feather was tentatively assigned to a moult zone (Weimerskirch et al. 2015b). We first looked at the GLS tracks of birds that wintered in only one marine area to assign the corresponding feather isotope values to that area. We then carefully examined the feather isotope values of skuas that spent the nonbreeding period in more than one area to correctly assign their isotopic values. We were unable to reliably assign isotopic values to a wintering area for a few feathers using this 2-step protocol (see ‘Unknown’ in Table 1).

Results

A total of 34 successful GLS deployments (Crozet, $n = 5$; Kerguelen, $n = 29$; 1 individual from Crozet was tracked over two successive years and returned to the same area—results not presented) were made on 33 individuals. The GLS recovery rates varied from 40% at Crozet to 73% at Kerguelen. The loggers provided simultaneous records of location and immersion data during 34 annual tracks, which were mainly located within the Indian Ocean (Fig. 1). Body feathers were collected from 19 adult brown skuas (9 females and 10 males) from Kerguelen Islands only.

Table 1 Isotopic niches of brown skuas (*Catharacta antarctica lonnbergi*) according to individual wintering zones and to feather moult zones (see text)

Wintering areas and habitats	Individuals (n)	Body feathers (n)	Feather $\delta^{13}\text{C}$ (‰)	Feather $\delta^{15}\text{N}$ (‰)	C:N mass ratios
Wintering zones					
Tropical	7	28	-17.4 ± 1.5^a	11.2 ± 2.2^a	3.14 ± 0.02
Subtropical	5	19 (1 outlier)	-18.3 ± 1.2^b	12.5 ± 2.2^b	3.15 ± 0.02
Sub-Antarctic	7	27 (1 outlier)	-18.3 ± 0.6^b	8.5 ± 0.6^c	3.14 ± 0.01
Chicks (Kerguelen)	10	10	-21.5 ± 0.3^c	$11.1 \pm 0.2^{a,b}$	3.17 ± 0.01
Moult zones					
Madagascar	2	7	-15.7 ± 0.1^a	13.4 ± 1.0^a	3.14 ± 0.02
Java	2	3	-15.8 ± 0.1^a	$13.0 \pm 0.2^{a,d,f}$	3.13 ± 0.01
West Australia	2	5	-17.7 ± 0.7^b	$11.7 \pm 0.9^{b,e,f}$	3.14 ± 0.01
Southern Australia	4	9	-18.0 ± 1.2^b	14.1 ± 1.2^a	3.16 ± 0.01
Subtropical and sub-Antarctic	13	37	-18.2 ± 0.6^b	8.5 ± 0.6^c	3.14 ± 0.02
Sub-Antarctic	6	7	-19.9 ± 0.9^c	$12.3 \pm 1.6^{b,d}$	3.15 ± 0.02
Unknown	3	8	–	–	–
Chicks (Kerguelen)	10	10	-21.5 ± 0.3^c	11.1 ± 0.2^e	3.17 ± 0.01

Note that birds may moult in several different zones. Within wintering or moult zones, values sharing the same superscript letters are not significantly different at the 0.05 level. Values are mean \pm SD

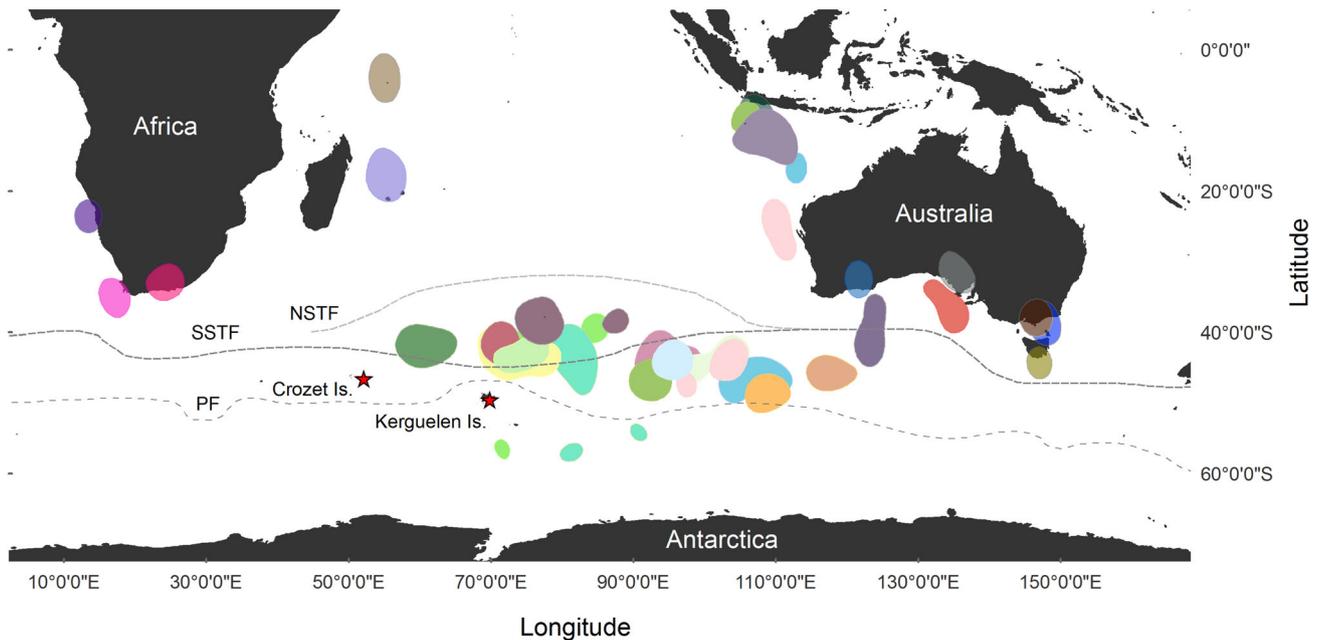


Fig. 1 Kernel densities or utilization distributions (25%) of individual adult brown skuas (*Catharacta antarctica lonnbergi*) during the inter-breeding period. Individual brown skuas from Crozet ($n = 5$,

dotted areas) and Kerguelen ($n = 25$, *undotted areas*), with breeding colonies depicted with *red stars*

Movements and activity

Brown skuas showed extensive variation in their post-breeding movements, from true long range migrations to distant wintering zones, to short movements near breeding grounds (Fig. 1). Wintering zones of brown skuas from Kerguelen and Crozet Islands (which are located ~1400 km apart) overlapped considerably (Fig. 1). All individuals overwintered in the southern hemisphere, remaining in the Indian Ocean (10°E–150°E), except two individuals that overwintered in the Benguela Current (Atlantic Ocean). At the end of the breeding season adult skuas left the breeding grounds typically to move northwards (Online Resource Fig S1). Skuas undertook their migration to wintering areas over three different water masses (*sensu* Longhurst (2007)). Each bird wintered within a single area: (i) in the tropics, in waters off Java, the Mascareignes Region and the Seychelles Archipelago (SST in July: 25.8 ± 2.2 °C), (ii) in the subtropics, in waters off Australia or in the Benguela Current System (north of the northern subtropical front, 15.4 ± 2.2 °C), or (iii) in sub-Antarctic waters of the southern Indian Ocean (between the northern subtropical front and the polar front 10.3 ± 3.0 °C) (Figs. 1, 2). The population-level migratory strategy can be described as being one of longitudinal or dispersive migrations (individuals wintering in the sub-Antarctic area; $n = 12$) or long-distance and anticlockwise loop migrations (individuals wintering in subtropical or tropical areas; $n = 17$). Males tended to migrate more

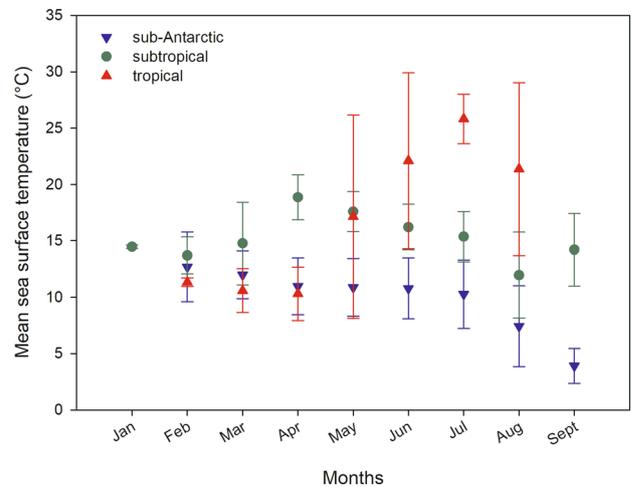


Fig. 2 Monthly sea surface temperatures (recorded by GLS loggers) during the inter-breeding period of brown skuas (*Catharacta antarctica lonnbergi*) from Crozet and Kerguelen Islands. Wintering grounds are indicated as tropical (*red triangle*), subtropical (*green dots*) or sub-Antarctic (*inverted blue triangle*). Values are mean \pm SD

towards tropical and subtropical waters (67%) than females did (47%; Fig. 3) but differences were not significant (*Chi* square test, all $p > 0.614$). While birds that wintered in subtropical waters, including coastal waters, left the colony and headed directly to their wintering zones, the birds which targeted tropical areas first moved eastward to sub-Antarctic staging zones until April–May before reaching their wintering zones (Online Resource Fig S1). In contrast,

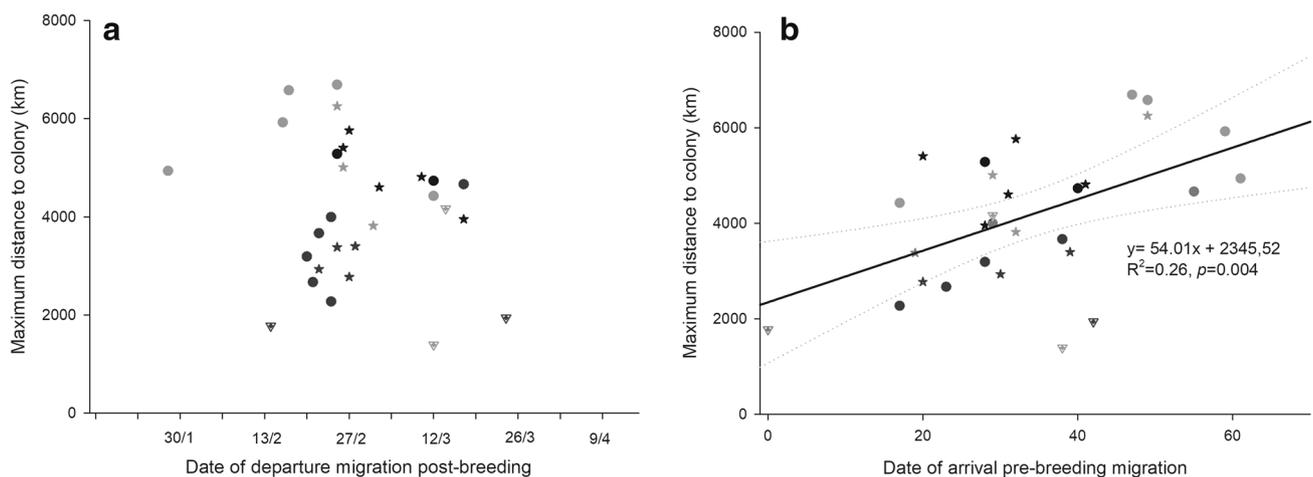


Fig. 3 Maximum distances from the breeding colony reached by individual brown skuas (*Catharacta antarctica lonnbergi*) from Crozet and Kerguelen during the inter-breeding period versus their departure (a) and arrival (b) dates from and to the breeding sites, respectively. Symbols indicate sex of individuals (dots females, stars

males, inverted triangle unknown). Colours indicate tropical (black), subtropical (grey) or sub-Antarctic (dark grey) wintering grounds. A linear regression (black line) between maximum distances reached and arrival dates at the breeding site (in reference to the earliest date: 4th August = Day 0), and its 95% CI (dotted lines) are indicated

birds that wintered in sub-Antarctic waters mainly moved eastward of the colony to pelagic areas. Irrespective of the wintering zones, it is noteworthy that individuals exhibited high variability in their wintering area (Fig. 1) even within pairs (Online Resource Fig S2a).

Individuals consistently started their post-breeding movements to reach their wintering areas in late February–early March, with a mean departure date around the 1st March (range 28th January–8th April; Table 2). Similarly, skuas consistently left their wintering area for their pre-breeding migration in late August with a mean return date around 21st August (range 30th July–24th September). The

migration dates (outbound or inbound movements) varied between sexes (Table 2; Fig. 3). Females tended to leave earlier and to return later at the breeding sites compared to males. Similarly, the duration of migration substantially differed between the wintering areas and sexes (Table 3; Fig. 3). Contrary to the inbound migration, where brown skuas left their wintering grounds at the same time independently of their wintering areas (21st August), the average outbound migration dates occurred later for birds overwintering in subtropical waters (2nd March vs. 27th February) and migration lasted longer (20 ± 16 vs. 8 ± 13 days; Tables 2, 3) compared to those in

Table 2 Inter-breeding behaviour of brown skuas (*Catharacta antarctica lonnbergi*) from Crozet and Kerguelen islands

Wintering area	Sex	n	Outward migration			Inward migration			Wintering Duration (days)
			Departure date ^a	Arrival date ^b	Duration (days)	Departure date ^c	Arrival date ^d	Duration (days)	
Subtropical	M	3	27 Feb \pm 3	2 Apr \pm 10	34 \pm 13	19 Aug \pm 13	9 Sep \pm 11	21 \pm 7	140 \pm 3
	F	5	19 Feb \pm 16	14 Mar \pm 32	24 \pm 19	27 Aug \pm 10	19 Sep \pm 18	23 \pm 9	166 \pm 38
Tropical	M	5	5 Mar \pm 8	15 Mar \pm 12	11 \pm 11	17 Aug \pm 8	3 Sep \pm 8	17 \pm 5	155 \pm 10
	F	2	4 Mar \pm 11	31 Mar \pm 4	28 \pm 15	11 Aug \pm 15	7 Sep \pm 8	27 \pm 6	133 \pm 18
Sub-Antarctic	M	4	25 Feb \pm 3	27 Feb \pm 2	3 \pm 2	24 Aug \pm 16	31 Aug \pm 9	6 \pm 9	179 \pm 18
	F	6	26 Feb \pm 10	10 Mar \pm 18	13 \pm 18	22 Aug \pm 19	4 Sep \pm 13	13 \pm 10	165 \pm 24
Total	All	29	29 Feb \pm 14	15 Mar \pm 20	15 \pm 16	21 Aug \pm 13	6 Sep \pm 14	16 \pm 10	159 \pm 24

^a Departure date from the breeding site

^b Arrival date at the wintering area

^c Departure date from the wintering area

^d Arrival date at the breeding site

Table 3 Selected generalized linear models used to test for the effects of sex and wintering area on variation of the migration patterns of brown skuas (*Catharacta antarctica lonnbergi*) from Crozet and Kerguelen islands

Independent variables		Outward migration		Inward migration	
		Departure date ^a	Duration (days)	Arrival date ^b	Duration (days)
All birds	Sex, area	~ Sex ΔAIC = 50	~ Sex + Area + Sex. Area ΔAIC = 144.5	~ Sex ΔAIC = 48.4	~ Sex + Area + Sex.Area ΔAIC = 1

Delta AIC (ΔAIC) indicates the AIC difference between the selected model and the null model

^a Departure date from the breeding site

^b Arrival date at the breeding site

southernmost areas. The return migration tended to last longer for birds coming from tropical and subtropical areas (20.3 ± 7.3 days) compared to birds coming from sub-Antarctic areas (10.5 ± 10.1 days; Tables 2, 3). Males tended to migrate (outward and inward migration) during shorter periods than females did (Table 2) whatever the wintering area.

Activity (percentage of time spent on water daily) was measured during the whole inter-breeding period, including outward and inward migrations and the wintering zone. Brown skuas spent a very high proportion of time sitting on the water during the inter-breeding period (80–81%; Online Resource Fig S3). The activity pattern (during daytime and during night-time) varied with month and wintering area (Table 4). Individuals tended to spend a greater proportion of time on the water at the beginning of the wintering period than at the end of the period; Online Resource Fig S3).

Stable isotopes

Feather isotopic values of adult brown skuas from Kerguelen Islands ranged widely, from −21.3 to −15.5‰ (a 5.7‰ difference), and from 7.1 to 16.1‰ (9.0‰) for δ¹³C and δ¹⁵N values, respectively. Only one adult body feather had isotopic values similar to the chick values, thus verifying that adult feathers did not grow during the breeding period. δ¹³C and δ¹⁵N values of feathers from individuals

that wintered in different zones were overall significantly different (ANOVA: $F_{(3,80)} = 34.8$ and 24.0 for δ¹³C and δ¹⁵N, respectively, both $p < 0.0001$) (Table 1). However, both intra- and inter-individual isotopic variations within the same group (sub-Antarctic, subtropical and tropical) were high with large δ¹³C overlaps among groups (Fig. 4). This indicates that most individual birds 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 before migration.

Combining GLS data and isotopic values at the feather level depicted a more informative pattern (Fig. 4). Feather δ¹³C and δ¹⁵N values from different moulting zones were significantly different (Kruskal–Wallis: $H = 55.0$ and 64.3 for δ¹³C and δ¹⁵N, respectively, both $p < 0.0001$). Post hoc pairwise Conover–Inman tests documented three notable features (Table 1): (i) feather δ¹³C values overall increased with decreasing latitudes, from the lower values of chicks to the higher values of adults that moulted in tropical waters (Madagascar and Java); (ii) feather isotopic values were identical for birds that moulted in western (Madagascar) and eastern (Java) tropical waters of the Indian Ocean; (iii) Feathers of birds that foraged in latitudes between ~35 and 50°S (sub-tropical and sub-Antarctic) presented remarkably low δ¹⁵N values (8.5‰) that differed from all the other groups (11.1–14.1‰).

Table 4 Selected generalized linear mixed models of the variation of the activity patterns of brown skua (*Catharacta antarctica lonnbergi*) from French Southern Territories

Independent variables		Daily proportion of time spent on the water	
		During daytime	During darkness
All birds	Sex, month, area	~ Month:Area, random = ~ 1IID ^a ΔAIC = 345.3	~ Month:Area, random = ~ 1IID ^a ΔAIC = 211

Delta AIC (ΔAIC) indicates the AIC difference between the selected model and the null model

^a Including individual as random effect

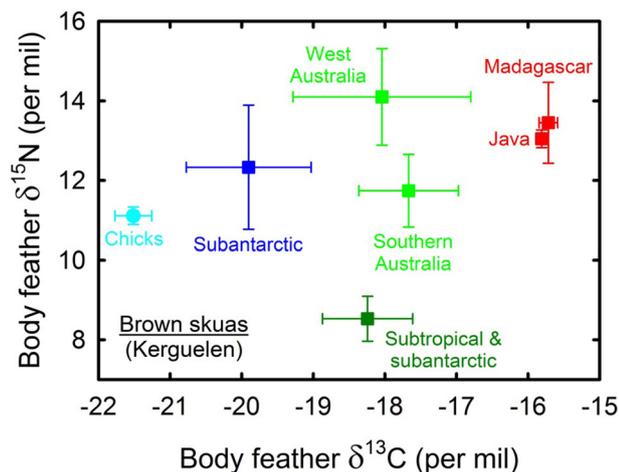


Fig. 4 Body feather $\delta^{15}\text{N}$ values versus $\delta^{13}\text{C}$ values of adult (squares) and chick (circles) brown skuas (*Catharacta antarctica lonnbergi*) from Kerguelen Islands according to their moulting zones. Values are mean \pm SD of all body feathers synthesized within the same habitat (see Table 1)

Females and males from the same pairs ($n = 4$) that were studied over the same inter-breeding period had different feather isotopic values (Mann–Whitney U tests, data not detailed). One pair (blue) differed in their feather $\delta^{13}\text{C}$ values (but not $\delta^{15}\text{N}$ values), two pairs (green and red) differed in their $\delta^{15}\text{N}$ values (but not $\delta^{13}\text{C}$ values) and one pair (grey) differed in both their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Online Resource Fig S2).

Discussion

Using geolocation, we showed that brown skuas from two populations in the southern Indian Ocean tracked in this study migrated northward to overwinter in different areas in the southern hemisphere, remaining in the Indian Ocean (10°E – 150°E), except two individuals that overwintered in the Benguela Current (Atlantic Ocean). Inter-individual variability in migratory strategies was clear, with individuals targeting areas in a continuum from the sub-Antarctic to the tropics.

Long-distance northward migration of brown skuas was long-suspected based on coastal and at-sea resightings and observations (Furness 1987). Brown skuas had long been erroneously reported as migrants in the northern hemisphere until it was clearly established that these reports were misidentifications of south polar skuas (Devillers 1977; Furness 1987). Both brown and south polar skuas are regularly mentioned as visitors in the Northern Indian Ocean during the southern monsoon (Sri Lanka's coastal waters; Van Den Berg et al. 1991; De Silva 2011). Unbanded and formerly misidentified *Catharacta* birds observed at sea, in large numbers off India or Sri Lanka, as

well as museum specimens from the same region, supported the belief that they regularly migrate northward from sub-Antarctic and Antarctic breeding sites. Recent tracking studies suggest that they must be predominantly south polar skuas originating from Antarctic breeding colonies located in the southern Atlantic Ocean sector (Weimerskirch et al. 2015b). Our study indicates that some of these birds observed in tropical waters are brown skuas. Timing and migratory patterns of brown skuas appeared similar between the two populations from Kerguelen and Crozet Islands, which concurs with typical return dates of untagged birds at the breeding sites (Paulian 1953; Barré 1976; authors' unpubl. data). Adult brown skuas from both populations principally migrated over the Indian Ocean Basin to overwinter, except for a few individuals that wintered in the very productive Benguela Current System in the eastern Atlantic Ocean. All individuals remained within the southern hemisphere, thus contrasting with the trans-equatorial migrations performed by many individuals of the closely related South Polar skua (Kopp et al. 2011; Weimerskirch et al. 2015b). Previous studies on brown skuas from the Southern Atlantic Ocean showed a consistent northward migration to winter within the Argentine Basin, mainly in sub-Antarctic waters (Phillips et al. 2007; Carneiro et al. 2016; Krietsch et al. 2017). Considering recent results (Phillips et al. 2007; Carneiro et al. 2016; Krietsch et al. 2017) and those from this study on the nonbreeding movements of individuals from 4 distant colonies, it appears that brown skuas might winter in a belt around Antarctica, as suggested by Furness (1987). During this period, wintering strategies differ among populations, although variation exists within populations. Single individuals use only a small proportion of the entire nonbreeding range, a pattern that might partly result from competition. Our data show that there was high individual variability in wintering areas among populations, and differences in migratory strategy between sexes.

The population-level migratory strategy of brown skuas can be described as longitudinal or dispersive movements versus long-distance and anticlockwise loop movements (Online Resource Fig S1). Brown skuas targeted neritic or oceanic waters corresponding to three biomes during the nonbreeding period, namely sub-Antarctic, subtropical and tropical waters. Brown skuas avoided the South Subtropical Gyre in the Central Indian Ocean, which corresponds to less productive areas. The wintering grounds correspond to productive dynamic upwelling ecosystems [Benguela Current System or equatorial Eastern Indian Ocean (Chen et al. 2015)] or frontal systems [salinity front southwest of Sumatra (Hunt and Schneider 1987)] and to oligotrophic tropical waters. Some of these zones are important areas for several taxa, specifically seabirds (Le Corre et al. 2012; Delord et al. 2013, 2014). The nonbreeding distribution of

brown skuas matches areas used by other seabirds such as terns and shearwaters (De Silva 2011; Le Corre et al. 2012). Individual wintering strategies and patterns of winter site fidelity are highly variables among seabird species (Kopp et al. 2011; Tranquilla et al. 2014; Weimerskirch et al. 2015a, b) as shown in great skuas (*Stercorarius skua*) and brown skuas (Magnusdottir et al. 2012; Krietsch et al. 2017). Brown skuas were recently found to be consistent in their migration strategies and habitat preferences (Carneiro et al. 2016; Krietsch et al. 2017). There were notable differences in migratory routes and wintering areas between individuals as found in other Stercorariidae (Phillips et al. 2007; Weimerskirch et al. 2015b) and in other seabird species (Shaffer et al. 2006; Stenhouse et al. 2012; Fijn et al. 2013). These inter-individual differences were not sex-dependent since there was no evidence from tracking that male and female brown skuas segregated during the inter-breeding period, as reported for other Stercorariidae (Magnusdottir et al. 2012). We found carry-over effects (i.e. processes affecting an individual in one season that also affect its subsequent performance) of wintering area on inward migration (duration and early arrival), which may be consistent with selection of early arrival breeding territory, particularly in males. It is not known whether later arrival compromises an individual's ability to re-claim its former breeding territory or reduces its survival. These individual-specific migratory strategies merit further investigation.

Migration and moult are usually separated in time to avoid excessive energy expenditure; the isotopic signature of brown skuas in our study clearly indicated that birds moulted partly in the wintering area, but also probably in area the visited during migration. Stable isotope values indicate that most brown skuas from Kerguelen ($n = 11$, 58%) moulted their four collected body feathers in different marine habitats that differed from their breeding grounds. This suggests an extended moult of body feathers during the whole nonbreeding period, a strategy also suggested by the feather isotopic values of small Procellariiformes (Cherel et al. 2016). Overall, the skuas' $\delta^{13}\text{C}$ values fit well with the latitudinal $\delta^{13}\text{C}$ gradient in water masses of the Southern Ocean (Cherel and Hobson 2007). Chicks of brown skuas from Mayes, whose diet consist mainly of adult blue petrels that forage in Antarctic waters, showed accordingly low feather $\delta^{13}\text{C}$ values. The values were lower than those from adult birds, thus confirming the GLS data which showed no brown skuas wintering in the Antarctic zone. Feather $\delta^{15}\text{N}$ values are more difficult to interpret; $\delta^{15}\text{N}$ baselines vary in different water masses, obscuring the trophic interpretation of $\delta^{15}\text{N}$. However, the low $\delta^{15}\text{N}$ values of feathers that grew in mixed subtropical-sub-Antarctic waters are puzzling. Such low feather $\delta^{15}\text{N}$ values were previously found in smaller numbers in brown

skuas from South Georgia (Phillips et al. 2007, 2009) and south polar skuas when they forage at similar latitudes in the southern Indian Ocean (Weimerskirch et al. 2015b). This suggests that skuas fed on low trophic level prey in the area, but this remains to be confirmed. A comparison of the skua $\delta^{15}\text{N}$ values with those of other sub-Antarctic and subtropical organisms suggests that the unknown prey was not marine mammals, seabirds, cephalopods or fish, but instead macrozooplankton, probably crustaceans (Cherel et al. 2008a, 2010; Stowasser et al. 2012); this hypothesis needs to be thoroughly investigated.

Migratory strategy and foraging during the nonbreeding period between members of breeding pairs is poorly documented in seabirds (Anderson et al. 2009; Mueller et al. 2015; Thiebot et al. 2015). Our results showed that throughout their inter-breeding period, members of the same pairs were spatially segregated (GLS data) and exhibited different foraging habitats and diets (stable isotope values). To the best of our knowledge, the only previous studies on the foraging strategy of pairs of brown skuas focused on the breeding period (Anderson et al. 2009; Carneiro et al. 2014). The results also indicated no sex-related effects on foraging time, habitat use or diet during the nonbreeding period.

Catharacta skuas have diverse feeding techniques and feed on a wide variety of prey (Le Morvan et al. 1967; Barré 1976; Hemmings 1984; Peter et al. 1990; Mougeot et al. 1998). During the breeding season, brown skuas breeding at sub-Antarctic islands show some degree of specialization related to local availability of resources. On Mayes Island at Kerguelen, brown skuas are highly dependent on burrowing petrels and feed mainly on two species, the blue petrel and the thin-billed prion (*Pachyptila belcheri*). At Possession Island, birds rely on rookeries of penguins (Barré 1976; Stahl and Mougin 1986). Migratory patterns appeared to be partly synchronized with the phenology of the skuas' prey (see Online Resource Table S6). The timing of migration of brown skuas coincided with the presence on land and the breeding cycle of their two main prey species. Brown skuas and their prey species arrive and stay at colonies until fledging. A complete shift in foraging ecology and diet between the breeding and nonbreeding period is suspected for skuas, from predation of seabirds on land during the breeding period to exclusively marine during the inter-breeding season. This specialization during the breeding season appears not to be maintained outside this period as evidenced by activity pattern and stable isotopic data. There is strong evidence that at least during moulting adult skuas do not rely on small petrels for feeding (Carravieri et al. 2014a). At South Georgia, results suggest a mixed diet of zooplankton and low trophic-level prey over the wintering grounds (Phillips et al. 2007). Compared to south polar

skuas, brown skuas spent a significantly greater proportion of their time in flight during darkness, indicative of greater search effort in similar wintering grounds (Weimerskirch et al. 2015b). Body size might be a factor driving part of this difference in behaviour, as suggested by comparing brown skuas and Falkland skuas (Phillips et al. 2007). Brown skuas are larger than south polar skuas (Furness 1987), suggesting differences in manoeuvrability which might allow different feeding behaviours. To our knowledge there is no study on the foraging habits of brown skuas during migration and winter. Skuas are well-documented opportunistic kleptoparasites at some times during their annual cycle (Furness 1987). Observations of skuas attacking flocks of seabirds (terns, gulls or shearwaters) and robbing them food (Furness 1987) confirm this seasonal shift in feeding strategy. Brown skuas have been observed attacking seabirds such as white-chinned petrels (*Procellaria aequinoctialis*) or sooty albatrosses (*Phoebastria fusca*; KD's pers. obs.) at sea.

The existence of such a variety of migration strategies within brown skua populations is puzzling. Evaluating the demographic correlates as well as the repeatability in individual migratory routes and wintering locations will be valuable to understand this diversity and its fitness consequences. It would be crucial to track the ontogeny of migration strategies, to evaluate heritability and consequences for survival. Identification of carry-over effects in seabird behaviour during the wintering period and identification of their impact on population dynamics (e.g. the effect of winter conditions faced by individual on its subsequent reproduction), should be investigated (Harris et al. 2013). Skuas and other seabird species are good indicators of environmental contaminants (Corsolini et al. 2011; Carravieri et al. 2014a; Goutte et al. 2014). Such individual variability in migratory strategies should also have consequences in terms of susceptibility to environmental stressors such as contaminants and climate change.

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