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

Karine Delord, Yves Cherel, Christophe Barbraud, Olivier Chastel, Henri Weimerskirch

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Corresponding Author

Family Name	Delord
Particle	
Given Name	Karine
Suffix	
Division	Centre d'Études Biologiques de Chizé
Organization	UMR 7372 du CNRS-Université de La Rochelle
Address	79360, Villiers-en-Bois, France
Phone	
Fax	
Email	karine.delord@cebc.cnrs.fr
URL	
ORCID	

Author

Family Name	Cherel
Particle	
Given Name	Yves
Suffix	
Division	Centre d'Études Biologiques de Chizé
Organization	UMR 7372 du CNRS-Université de La Rochelle
Address	79360, Villiers-en-Bois, France
Phone	
Fax	
Email	
URL	
ORCID	

Author

Family Name	Barbraud
Particle	
Given Name	Christophe
Suffix	
Division	Centre d'Études Biologiques de Chizé
Organization	UMR 7372 du CNRS-Université de La Rochelle
Address	79360, Villiers-en-Bois, France
Phone	
Fax	

Email
URL
ORCID

Author	Family Name	Chastel
	Particle	
	Given Name	Olivier
	Suffix	
	Division	Centre d'Études Biologiques de Chizé
	Organization	UMR 7372 du CNRS-Université de La Rochelle
	Address	79360, Villiers-en-Bois, France
	Phone	
	Fax	
	Email	
	URL	
	ORCID	

Author	Family Name	Weimerskirch
	Particle	
	Given Name	Henri
	Suffix	
	Division	Centre d'Études Biologiques de Chizé
	Organization	UMR 7372 du CNRS-Université de La Rochelle
	Address	79360, Villiers-en-Bois, France
	Phone	
	Fax	
	Email	
	URL	
	ORCID	

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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 nonbreeding 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 (separated by '-') Activity - Feather - Geolocator - Intraspecific strategies - Phenology - Stable isotopes

Footnote Information

Electronic supplementary material The online version of this article (doi:10.1007/s00300-017-2169-1) contains supplementary material, which is available to authorized users.

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

4 **Karine Delord¹ · Yves Cherel¹ · Christophe Barbraud¹ · Olivier Chastel¹ ·**
5 **Henri Weimerskirch¹**

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18 southern hemisphere; individuals remained in the Indian
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24 Ocean. Individuals clearly differed in migratory strategies,
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28 females leaving the breeding sites earlier and returning
29 later compared to males. The duration of migration
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requires further investigation. 38

Keywords Activity · Feather · Geocator · Intraspecific 40
strategies · Phenology · Stable isotopes 41

Introduction 42

Migration is commonly considered to be a response to 43
seasonal variation in the environment and particularly to 44
prey availability (Jessopp et al. 2013). Seabirds are central 45
place foragers during breeding but can range over much 46
larger areas in search of food outside the breeding period. 47
Migration often necessitates large-scale movements 48
beyond the breeding home range and is an essential com- 49
ponent of the life-history of flying seabirds (Shaffer et al. 50
2006; Egevang et al. 2010; Weimerskirch et al. 2014). 51
Migration strategies of seabirds can differ markedly, 52
exhibiting intraspecific variations linked to population, sex 53
or age (Guilford et al. 2009; Dias et al. 2011; Fijn et al. 54
2013). Individuals from the same breeding colony could 55
migrate using different routes, thereby reaching distant and 56
distinct wintering grounds (Yamamoto et al. 2010; 57
Weimerskirch et al. 2015a, b). Timing for the outbound or 58
the inbound movements could also differ between indi- 59
viduals and the sexes, (Yamamoto et al. 2010; Hedd et al. 60
2014; Thiebot et al. 2014). Hence, describing and under- 61
standing the individual differences in migration strategy 62
that may impact winter survival of individuals is a key 63
issue in population dynamics of long-lived species 64

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A4 ✉ Karine Delord
A5 karine.delord@cebc.cnrs.fr

A6 ¹ Centre d'Études Biologiques de Chizé, UMR 7372 du CNRS-
A7 Université de La Rochelle, 79360 Villiers-en-Bois, France

65 (Barbraud and Weimerskirch 2003; Frederiksen et al. 2008;
66 Reiertsen et al. 2014).

67 The identification of migration strategies is furthermore
68 crucial to understand how individuals are differently
69 affected by climate change (Weimerskirch et al. 2012),
70 pollution, particularly oiling (Montevecchi et al. 2012a, b),
71 interaction with fisheries including the associated incident-
72 al bycatch (Phillips et al. 2005; Watkins et al. 2008; Maree
73 et al. 2014) and exposure to contaminants (Blévin et al.
74 2013; Leat et al. 2013; Carravieri et al. 2014a). Individual
75 responses to environmental variability or to anthropogenic
76 factors can have strong implications in terms of survival
77 and population dynamics (Harris et al. 2013; Goutte et al.
78 2014). Individuals, from the same or different populations,
79 might share wintering areas and experience similar threats
80 (Gonzalez-Solis et al. 2007; Frederiksen et al. 2012;
81 Tranquilla et al. 2014), or individuals might have different
82 strategies, resulting in differences in threat exposure
83 (Rayner et al. 2011; Hedd et al. 2012; Carey et al. 2014).

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

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

phenology of the prey species, especially with migratory 118
species, to avoid a mistiming in breeding cycles (Visser 119
and Both 2005). The nonbreeding distribution of brown 120
skuas is only known for South Georgia (Phillips et al. 2007; 121
Carneiro et al. 2016) and King George Island (Krietsch 122
et al. 2017). To date, the wintering ranges for Southern 123
Indian Ocean populations have been inferred primarily 124
from at-sea sightings or recoveries of ringed birds. This 125
information suggests that during the nonbreeding period 126
some individuals stay close to their breeding range, while 127
others are migratory or dispersive (Eklund 1961; Olsen and 128
Larsson 1997). Some individuals winter around Australia, 129
with two ring recoveries of Kerguelen birds there (Higgins 130
and Davies 1996). 131

The present study focuses on the intraspecific compar- 132
ison of migration strategies, wintering ranges, activity 133
patterns and diet of two populations of brown skuas in the 134
Southern Indian Ocean by combining tracking (geoloca- 135
tors) and stable isotope analyses. Using biotelemetry data, 136
we investigated whether (1) individuals vary in their 137
migratory behaviour, (2) sexes differ in their migration 138
timing and wintering areas, and (3) individuals modify 139
their activity patterns between the breeding, migration and 140
nonbreeding period. We hypothesized that a shift might be 141
accompanied by modification of the activity pattern (i.e. 142
time spent on the water recorded by the geolocators), 143
concomitant with a change in the isotopic signature 144
between the two periods, similar to recent results for the 145
south polar skua (Weimerskirch et al. 2015a, b). 146

147 Methods

148 Brown skuas were studied on two sub-Antarctic islands in 148
the southern Indian Ocean: Possession Island (46°25'S, 149
51°45'E) in the Crozet archipelago and Mayes Island 150
(49°28'S, 69°57'E) in the Kerguelen archipelago. Tracking 151
data were used to characterise the at-sea distribution of 152
adults during their breeding and nonbreeding periods. 153
Global location sensing (GLS) loggers (British Antarctic 154
Survey, Cambridge) were deployed on adults during the 155
breeding season (2008–2009 and 2011–2012 at Kerguelen; 156
 $n = 40$ and 2010–2011 at Crozet; $n = 10$). GLS loggers 157
(Mk5, Mk15) weighed 3.6 and 2.5 g, respectively, i.e. 158
 $\approx 0.14\%$ of body mass and well below the recommended 159
threshold of 3% of body mass (Phillips et al. 2003). These 160
were mounted on plastic or metal leg bands. Adults were 161
captured on the nest during the breeding season (brooding 162
or chick rearing stage). Sex of the birds, except those from 163
Crozet, was determined using molecular methods (Blan- 164
chard et al. 2007) ($n = 29$; 13 males and 16 females). 165
Processing of the GLS daylight data was carried out as 166
described previously (Péron et al. 2010). Migration timing 167

168 was determined by combined visual examination of
169 movement and activity data; outward migration started
170 from the first directional movement (followed by several
171 consecutive days with directional flight), while the final
172 nonbreeding location was the last location in the non-
173 breeding area before a sustained period of directional
174 movement towards the breeding colony. Birds were con-
175 sidered to be wintering from the end of the outward
176 migration in February to April, to the onset of the return
177 migration in the following August. The breeding success of
178 the tracked individuals was unknown.

179 GLS data allow long-term (several years) latitude and
180 longitude estimation from daylight measurements, albeit
181 although with a lower accuracy (186 ± 114 km; Phillips
182 et al. 2004) than satellite transmitters (Wilson et al. 1992).
183 Loggers measured daylight level intensity every 60 s and
184 the maximum intensity for each 10 min is recorded. An
185 internal clock allows estimation of the latitude based on
186 day length and longitude based on the timing of local
187 midday with respect to Coordinated Universal Time
188 (Afanasyev 2004). Daylight data recorded by GLS were
189 analysed using a standardized procedure for flying seabirds
190 (Phillips et al. 2004) to provide two locations per day.
191 Thresholds ($h = 4$) in the light curves were used to
192 determine sunrise and sunset. Locations fixes were calcu-
193 lated from daylight data using BASTrak software (British
194 Antarctic Survey 2009). During a 1–2 weeks period around
195 the equinoxes (20–21 March and 22–23 September), lati-
196 tude cannot be estimated accurately (Wilson et al. 1992).
197 Spatial distribution of brown skuas during the inter-
198 breeding period was investigated by producing 25% uti-
199 lization distributions (UDs) for each individual, using
200 kernel analysis with a cell size of $2^\circ \times 2^\circ$ and a fixed
201 smoothing parameter (h) of 2° . Both h value and grid cell
202 size were based on the mean accuracy of the devices.
203 Spatial analyses were performed using the “*adehabitatHR*”
204 R package (Calenge 2006).

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

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

228 We then fitted generalized linear models (GLMs) to
229 investigate the effects of sex, wintering location (three
230 different water masses sensu Longhurst (2007): subtropi-
231 cal, tropical or sub-Antarctic) and their interaction on
232 migration schedules (date of departure, date of arrival and
233 duration) using a Poisson distribution. We selected only
234 one track for the bird tracked over two consecutive years to
235 prevent pseudo-replication. General linear mixed-effects
236 models (GLMMs), fitted in the lme4 package (Zuur et al.
237 2010), were used to model activity patterns (daily pro-
238 portion of time spent on the water during daytime or during
239 darkness). Sex, wintering location, month (independent
240 variables) and two by two interactions were included as
241 fixed effects. Individual identity was fitted as a random
242 effect to account for pseudo-replication, as the same indi-
243 vidual could contribute several values. Model assumptions
244 were visually validated based on normalized residuals,
245 following the protocol presented by Zuur et al. (2010).
246 Unsexed individuals were excluded from the dataset. Due
247 to sample size, year could not be used as a fixed factor in
248 the models. The effect of breeding colony could not be
249 included due to small sample size for the Crozet popula-
250 tion. Models were ranked using the Akaike Information
251 Criterion (AIC) and Akaike weights (Burnham and
252 Anderson 2002). The model with the lowest AIC was
253 considered the best model. When Δ AIC between models
254 was <2 , the models were considered equally good
255 descriptors of the data and we chose the most parsimonious
256 model—that with the lowest number of parameters. Spatial
257 and statistical analyses were performed using R 2.15.3 (R
258 Development Core Team 2013).

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

274 brown skuas from Mayes Island prey upon seabirds on
 275 land, mainly blue petrels (Mougeot et al. 1998), a small
 276 Procellariiforme that forages at sea in southern Antarctic
 277 waters (Cherel et al. 2014). A single chick body feather
 278 was used for isotopic analyses, because chick feathers grow
 279 almost synchronously and thus present low inter-feather
 280 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variations (Carravieri et al. 2014b). Feather
 281 preparation and isotopic analyses were detailed by (Jaeger
 282 et al. 2009). In brief, feathers were cleaned using a 2:1
 283 chloroform: methanol solution and then oven dried for 48 h
 284 at 50 °C. Each whole body feather was homogenized by
 285 cutting it with scissors into small fragments and a sub-
 286 sample of ~0.3 mg was packed into tin containers for
 287 stable isotope analysis. The relative abundances of carbon
 288 and nitrogen isotopes were determined with a continuous
 289 flow mass spectrometer (Thermo Scientific Delta V
 290 Advantage) coupled to an elemental analyzer (Thermo
 291 Scientific Flash EA 1112). Results are presented in the
 292 usual δ notation relative to Vienna PeeDee Belemnite and
 293 atmospheric N_2 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Replicate
 294 measurements of internal laboratory standards (acetanilide)
 295 indicated measurement errors <0.15‰ for both $\delta^{13}\text{C}$ and
 296 $\delta^{15}\text{N}$ values.

297 For statistical analyses, feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values
 298 were either grouped at the individual level (wintering
 299 zones) or at the feather level (mouling zone) (Table 1). In
 300 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 mouling
 zone (Weimerskirch et al. 2015a, b). 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 val-
 ues 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 ‘Un-
 known’ 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 Ker-
 guelen. The loggers provided simultaneous records of loca-
 tion 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 mouling zones (see text)

Wintering areas and habitats	Individuals (<i>n</i>)	Body feathers (<i>n</i>)	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
Mouling 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^c	3.17 ± 0.01

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

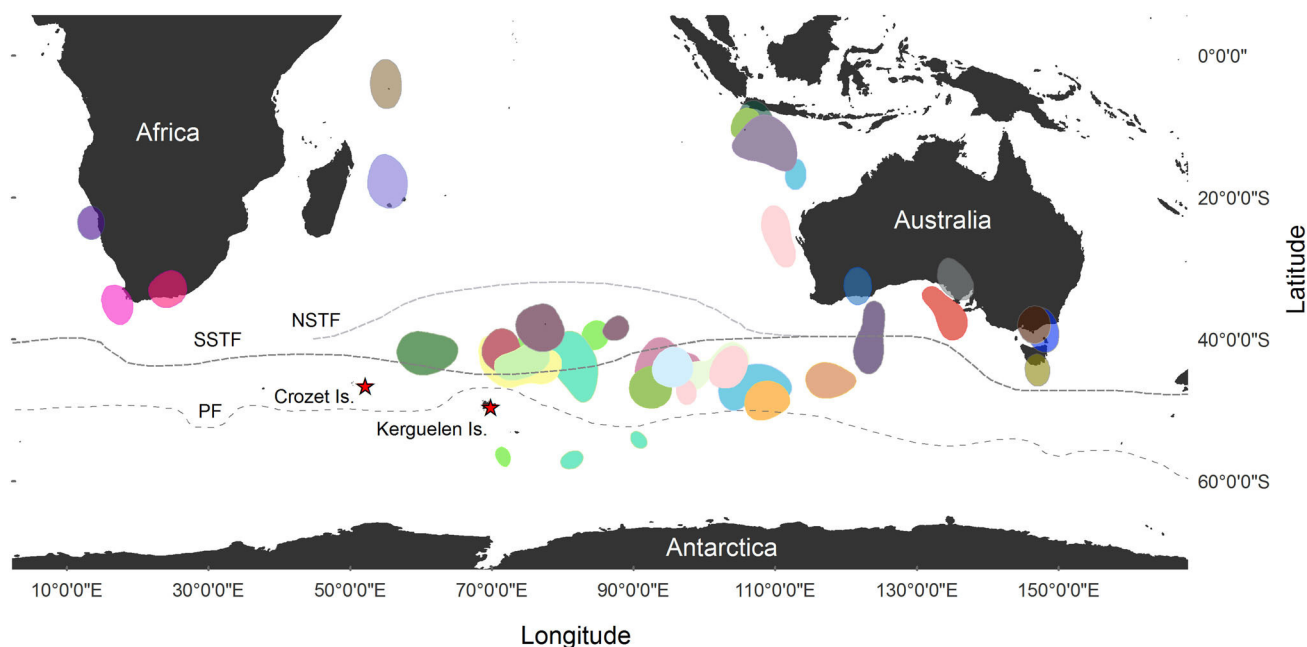


Fig. 1 Kernel densities or utilization distributions (25%) of individual adult brown skuas (*Catharacta antarctica lonnbergi*) during the inter-breeding period. Individual brown skuas from Crozet ($n = 5$,

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

325 Movements and activity

326 Brown skuas showed extensive variation in their post-
 327 breeding movements, from true long range migrations to
 328 distant wintering zones, to short movements near breeding
 329 grounds (Fig. 1). Wintering zones of brown skuas from
 330 Kerguelen and Crozet Islands (which are located
 331 ~ 1400 km apart) overlapped considerably (Fig. 1). All
 332 individuals overwintered in the southern hemisphere,
 333 remaining in the Indian Ocean (10°E – 150°E), except two
 334 individuals that overwintered in the Benguela Current
 335 (Atlantic Ocean). At the end of the breeding season adult
 336 skuas left the breeding grounds typically to move north-
 337 wards (Online Resource Fig S1). Skuas undertook their
 338 migration to wintering areas over three different water
 339 masses (*sensu* Longhurst (2007)). Each bird wintered within
 340 a single area: (i) in the tropics, in waters off Java, the
 341 Mascareignes Region and the Seychelles Archipelago (SST
 342 in July: 25.8 ± 2.2 °C), (ii) in the subtropics, in waters off
 343 Australia or in the Benguela Current System (north of the
 344 northern subtropical front, 15.4 ± 2.2 °C), or (iii) in sub-
 345 Antarctic waters of the southern Indian Ocean (between the
 346 northern subtropical front and the polar front
 347 10.3 ± 3.0 °C) (Figs. 1, 2). The population-level migra-
 348 tory strategy can be described as being one of longitudinal
 349 or dispersive migrations (individuals wintering in the sub-
 350 Antarctic area; $n = 12$) or long-distance and anticlockwise
 351 loop migrations (individuals wintering in subtropical or
 352 tropical areas; $n = 17$). Males tended to migrate more

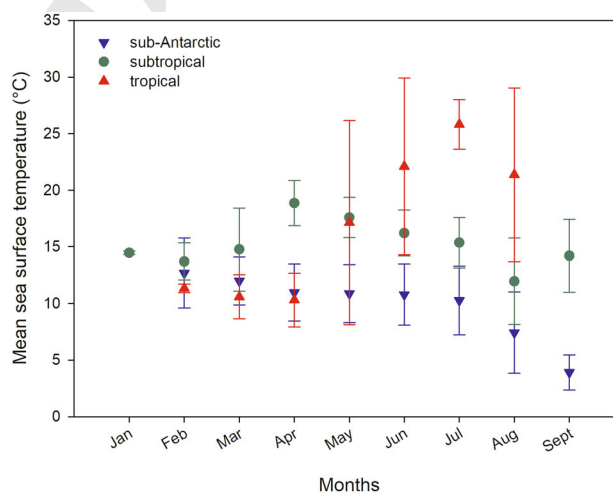


Fig. 2 Monthly sea surface temperatures (recorded by GLS loggers) during the inter-breeding period of brown skuas (*Catharacta antarctica lonnbergi*) from Crozet and Kerguelen Islands. Wintering grounds are indicated as tropical (*red triangle*), subtropical (*green dots*) or sub-Antarctic (*inverted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

towards tropical and subtropical waters (67%) than females 353
 did (47%; Fig. 3) but differences were not significant (*Chi* 354
 square test, all $p > 0.614$). While birds that wintered in 355
 subtropical waters, including coastal waters, left the colony 356
 and headed directly to their wintering zones, the birds 357
 which targeted tropical areas first moved eastward to sub- 358
 Antarctic staging zones until April–May before reaching 359
 their wintering zones (Online Resource Fig S1). In contrast, 360

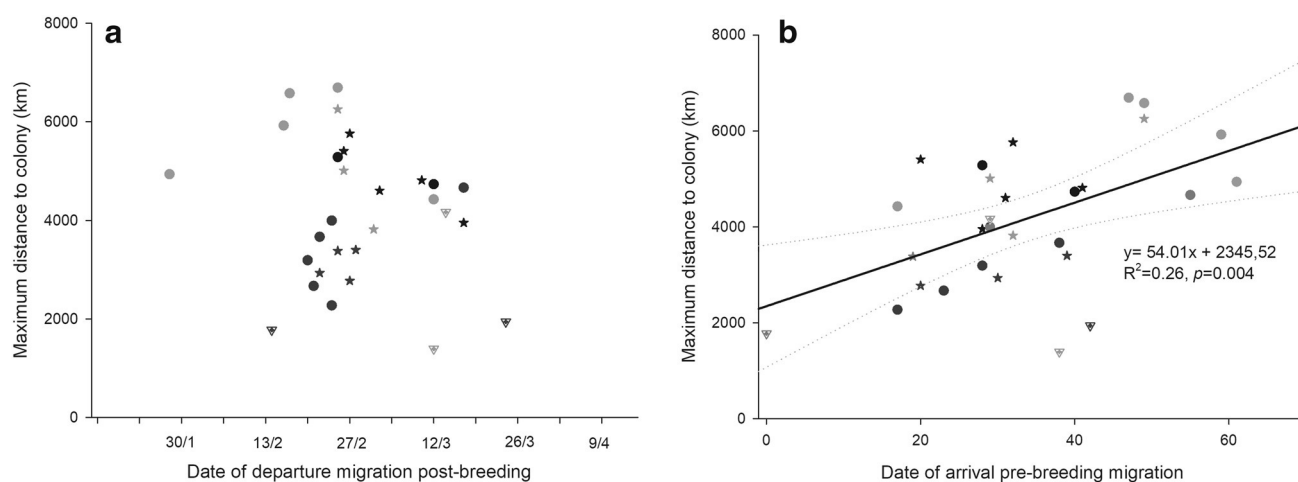


Fig. 3 Maximum distances from the breeding colony reached by individual brown skuas (*Catharacta antarctica lonnbergi*) from Crozet and Kerguelen during the inter-breeding period versus their departure (*upper panel*) and arrival (*lower panel*) dates from and to the breeding sites, respectively. *Symbols* 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

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

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

373 migration dates (outbound or inbound movements) varied
374 between sexes (Table 2; Fig. 3). Females tended to leave
375 earlier and to return later at the breeding sites compared to
376 males. Similarly, the duration of migration substantially
377 differed between the wintering areas and sexes (Table 3;
378 Fig. 3). Contrary to the inbound migration, where brown
379 skuas left their wintering grounds at the same time inde-
380 pendently of their wintering areas (21st August), the
381 average outbound migration dates occurred later for birds
382 overwintering in subtropical waters (2nd March vs. 27th
383 February) and migration lasted longer (20 ± 16 vs.
384 8 ± 13 days; Tables 2, 3) compared to those in southern-

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

385 most areas. The return migration tended to last longer for
386 birds coming from tropical and subtropical areas
387 (20.3 ± 7.3 days) compared to birds coming from sub-
388 Antarctic areas (10.5 ± 10.1 days; Tables 2, 3). Males
389 tended to migrate (outward and inward migration) during
390 shorter periods than females did (Table 2) whatever the
391 wintering area.

392 Activity (percentage of time spent on water daily) was
393 measured during the whole inter-breeding period, including
394 outward and inward migrations and the wintering zone.
395 Brown skuas spent a very high proportion of time sitting on
396 the water during the inter-breeding period (80–81%;
397 Online Resource Fig S3). The activity pattern (during
398 daytime and during night-time) varied with month and
399 wintering area (Table 4). Individuals tended to spend a
400 greater proportion of time on the water at the beginning of
401 the wintering period than at the end of the period; Online
402 **AQ1** Resource Fig S3).

403 Stable isotopes

404 Feather isotopic values of adult brown skuas from Ker-
405 guelen Islands ranged widely, from −21.3 to −15.5‰ (a
406 5.7‰ difference), and from 7.1 to 16.1‰ (9.0‰) for δ¹³C
407 and δ¹⁵N values, respectively. Only one adult body feather
408 had isotopic values similar to the chick values, thus ver-
409 ifying that adult feathers did not grow during the breeding
410 period. δ¹³C and δ¹⁵N values of feathers from individuals

that wintered in different zones were overall significantly 411
different (ANOVA: $F_{(3,80)} = 34.8$ and 24.0 for δ¹³C and 412
δ¹⁵N, respectively, both $p < 0.0001$) (Table 1). However, 413
both intra- and inter-individual isotopic variations within 414
the same group (sub-Antarctic, subtropical and tropical) 415
were high with large δ¹³C overlaps among groups (Fig. 4). 416
This indicates that most individual birds did not moult all 417
their body feathers in the wintering zone. Rather, individ- 418
uals moulted over different water masses during the whole 419
inter-nesting period, i.e. during migratory movements and 420
before migration. 421

Combining GLS data and isotopic values at the feather 422
level depicted a more informative pattern (Fig. 4). 423
Feather δ¹³C and δ¹⁵N values from different moulting 424
zones were significantly different (Kruskal–Wallis: 425
 $H = 55.0$ and 64.3 for δ¹³C and δ¹⁵N, respectively, both 426
 $p < 0.0001$). Post hoc pairwise Conover–Inman tests 427
documented three notable features (Table 1): (i) feather 428
δ¹³C values overall increased with decreasing latitudes, 429
from the lower values of chicks to the higher values of 430
adults that moulted in tropical waters (Madagascar and 431
Java); (ii) feather isotopic values were identical for birds 432
that moulted in western (Madagascar) and eastern (Java) 433
tropical waters of the Indian Ocean; (iii) Feathers of birds 434
that foraged in latitudes between ~35 and 50°S (sub- 435
tropical and sub-Antarctic) presented remarkably low 436
δ¹⁵N values (8.5‰) that differed from all the other 437
groups (11.1–14.1‰). **AQ2** 438

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

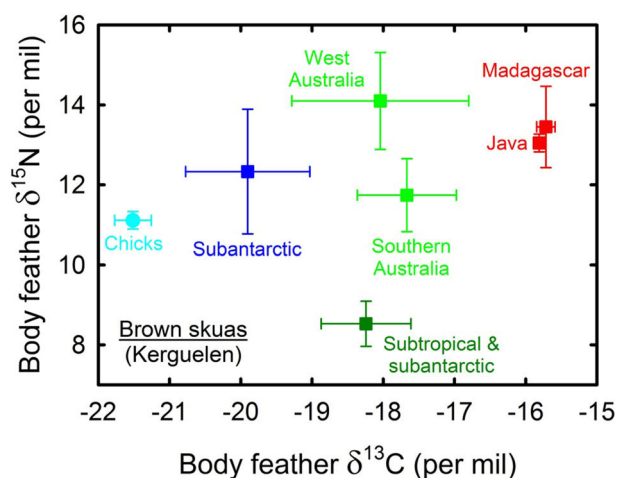


Fig. 4 Body feather $\delta^{15}\text{N}$ values versus $\delta^{13}\text{C}$ values of adult (squares) and chick (circles) brown skuas (*Catharacta antarctica lonnbergi*) from Kerguelen Islands according to their moulting zones. Values are mean \pm SD of all body feathers synthesized within the same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

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

447 Discussion

448 Using geolocation, we showed that brown skuas from two
 449 populations in the southern Indian Ocean tracked in this
 450 study migrated northward to overwinter in different areas
 451 in the southern hemisphere, remaining in the Indian Ocean
 452 (10°E – 150°E), except two individuals that overwintered in
 453 the Benguela Current (Atlantic Ocean). Inter-individual
 454 variability in migratory strategies was clear, with individ-
 455 uals targeting areas in a continuum from the sub-Antarctic
 456 to the tropics.

457 Long-distance northward migration of brown skuas was
 458 long-suspected based on coastal and at-sea resightings and
 459 observations (Furness 1987). Brown skuas had long been
 460 erroneously reported as migrants in the northern hemi-
 461 sphere until it was clearly established that these reports
 462 were misidentifications of south polar skuas (Devillers
 463 1977; Furness 1987). Both brown and south polar skuas are
 464 regularly mentioned as visitors in the Northern Indian
 465 Ocean during the southern monsoon (Sri Lanka's coastal
 466 waters; Van Den Berg et al. 1991; De Silva 2011).
 467 Unbanded and formerly misidentified *Catharacta* birds
 468 observed at sea, in large numbers off India or Sri Lanka, as

well as museum specimens from the same region, sup- 469
 470 ported the belief that they regularly migrate northward 470
 471 from sub-Antarctic and Antarctic breeding sites. Recent 471
 472 tracking studies suggest that they must be predominantly 472
 473 south polar skuas originating from Antarctic breeding 473
 474 colonies located in the southern Atlantic Ocean sector 474
 475 (Weimerskirch et al. 2015a, b). Our study indicates that 475
 476 some of these birds observed in tropical waters are brown 476
 477 skuas. Timing and migratory patterns of brown skuas 477
 478 appeared similar between the two populations from Ker- 478
 479 guelen and Crozet Islands, which concurs with typical 479
 480 return dates of untagged birds at the breeding sites (Paulian 480
 481 1953; Barré 1976; authors' unpubl. data). Adult brown 481
 482 skuas from both populations principally migrated over the 482
 483 Indian Ocean Basin to overwinter, except for a few indi- 483
 484 viduals that wintered in the very productive Benguela 484
 485 Current System in the eastern Atlantic Ocean. All indi- 485
 486 viduals remained within the southern hemisphere, thus 486
 487 contrasting with the trans-equatorial migrations performed 487
 488 by many individuals of the closely related South Polar skua 488
 489 (Kopp et al. 2011; Weimerskirch et al. 2015a, b). Previous 489
 490 studies on brown skuas from the Southern Atlantic Ocean 490
 491 showed a consistent northward migration to winter within 491
 492 the Argentine Basin, mainly in sub-Antarctic waters 492
 493 (Phillips et al. 2007; Carneiro et al. 2016; Krietsch et al. 493
 494 2017). Considering recent results (Phillips et al. 2007; 494
 495 Carneiro et al. 2016; Krietsch et al. 2017) and those from 495
 496 this study on the nonbreeding movements of individuals 496
 497 from 4 distant colonies, it appears that brown skuas might 497
 498 winter in a belt around Antarctica, as suggested by Furness 498
 499 (1987). During this period, wintering strategies differ 499
 500 among populations, although variation exists within popu- 500
 501 lations. Single individuals use only a small proportion of 501
 502 the entire nonbreeding range, a pattern that might partly 502
 503 result from competition. Our data show that there was high 503
 504 individual variability in wintering areas among popula- 504
 505 tions, and differences in migratory strategy between sexes. 505

The population-level migratory strategy of brown skuas 506
 507 can be described as longitudinal or dispersive movements 507
 508 versus long-distance and anticlockwise loop movements 508
 509 (Online Resource Fig S1). Brown skuas targeted neritic or 509
 510 oceanic waters corresponding to three biomes during the 510
 511 nonbreeding period, namely sub-Antarctic, subtropical and 511
 512 tropical waters. Brown skuas avoided the South Subtropi- 512
 513 cal Gyre in the Central Indian Ocean, which corresponds to 513
 514 less productive areas. The wintering grounds correspond to 514
 515 productive dynamic upwelling ecosystems [Benguela 515
 516 Current System or equatorial Eastern Indian Ocean (Chen 516
 517 et al. 2015)] or frontal systems [salinity front southwest of 517
 518 Sumatra (Hunt and Schneider 1987)] and to oligotrophic 518
 519 tropical waters. Some of these zones are important areas 519
 520 for several taxa, specifically seabirds (Le Corre et al. 2012; 520
 521 Delord et al. 2013, 2014). The nonbreeding distribution of 521

522 brown skuas matches areas used by other seabirds such as
 523 terns and shearwaters (De Silva 2011; Le Corre et al.
 524 2012). Individual wintering strategies and patterns of
 525 winter site fidelity are highly variables among seabird
 526 species (Kopp et al. 2011; Tranquilla et al. 2014;
 527 Weimerskirch et al. 2015a, b) as shown in great skuas
 528 (*Stercorarius skua*) and brown skuas (Magnusdottir et al.
 529 2012; Krietsch et al. 2016). Brown skuas were recently
 530 found to be consistent in their migration strategies and
 531 habitat preferences (Carneiro et al. 2016; Krietsch et al.
 532 2017). There were notable differences in migratory routes
 533 and wintering areas between individuals as found in other
 534 Stercorariidae (Phillips et al. 2007; Weimerskirch et al.
 535 2015a, b) and in other seabird species (Shaffer et al. 2006;
 536 Stenhouse et al. 2012; Fijn et al. 2013). These inter-indi-
 537 vidual differences were not sex-dependent since there was
 538 no evidence from tracking that male and female brown
 539 skuas segregated during the inter-breeding period, as
 540 reported for other Stercorariidae (Magnusdottir et al.
 541 2012). We found carry-over effects (i.e. processes affecting
 542 an individual in one season that also affect its subsequent
 543 performance) of wintering area on inward migration (du-
 544 ration and early arrival), which may be consistent with
 545 selection of early arrival breeding territory, particularly in
 546 males. It is not known whether later arrival compromises
 547 an individual's ability to re-claim its former breeding ter-
 548 ritory or reduces its survival. These individual-specific
 549 migratory strategies merit further investigation.

550 Migration and moult are usually separated in time to
 551 avoid excessive energy expenditure; the isotopic signature
 552 of brown skuas in our study clearly indicated that birds
 553 moulted partly in the wintering area, but also probably in
 554 area the visited during migration. Stable isotope values
 555 indicate that most brown skuas from Kerguelen ($n = 11$,
 556 58%) moulted their four collected body feathers in differ-
 557 ent marine habitats that differed from their breeding
 558 grounds. This suggests an extended moult of body feathers
 559 during the whole nonbreeding period, a strategy also sug-
 560 gested by the feather isotopic values of small Procellari-
 561 iformes (Cherel et al. 2016). Overall, the skuas' $\delta^{13}\text{C}$
 562 values fit well with the latitudinal $\delta^{13}\text{C}$ gradient in water
 563 masses of the Southern Ocean (Cherel and Hobson 2007).
 564 Chicks of brown skuas from Mayes, whose diet consist
 565 mainly of adult blue petrels that forage in Antarctic waters,
 566 showed accordingly low feather $\delta^{13}\text{C}$ values. The values
 567 were lower than those from adult birds, thus confirming the
 568 GLS data which showed no brown skuas wintering in the
 569 Antarctic zone. Feather $\delta^{15}\text{N}$ values are more difficult to
 570 interpret; $\delta^{15}\text{N}$ baselines vary in different water masses,
 571 obscuring the trophic interpretation of $\delta^{15}\text{N}$. However, the
 572 low $\delta^{15}\text{N}$ values of feathers that grew in mixed subtropical-
 573 sub-Antarctic waters are puzzling. Such low feather $\delta^{15}\text{N}$
 574 values were previously found in smaller numbers in brown

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

586 Migratory strategy and foraging during the nonbreeding
 587 period between members of breeding pairs is poorly doc-
 588 umented in seabirds (Anderson et al. 2009; Mueller et al.
 589 2015; Thiebot et al. 2015). Our results showed that
 590 throughout their inter-breeding period, members of the
 591 same pairs were spatially segregated (GLS data) and
 592 exhibited different foraging habitats and diets (stable iso-
 593 tope values). To the best of our knowledge, the only pre-
 594 vious studies on the foraging strategy of pairs of brown
 595 skuas focused on the breeding period (Anderson et al.
 596 2009; Carneiro et al. 2014). The results also indicated no
 597 sex-related effects on foraging time, habitat use or diet
 598 during the nonbreeding period.

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

628 polar skuas, brown skuas spent a significantly greater
629 proportion of their time in flight during darkness, indicative
630 of greater search effort in similar wintering grounds
631 (Weimerskirch et al. 2015a, b). Body size might be a factor
632 driving part of this difference in behaviour, as suggested by
633 comparing brown skuas and Falkland skuas (Phillips et al.
634 2007). Brown skuas are larger than south polar skuas
635 (Furness 1987), suggesting differences in manoeuvrability
636 which might allow different feeding behaviours. To our
637 knowledge there is no study on the foraging habits of
638 brown skuas during migration and winter. Skuas are well-
639 documented opportunistic kleptoparasites at some times
640 during their annual cycle (Furness 1987). Observations of
641 skuas attacking flocks of seabirds (terns, gulls or shear-
642 waters) and robbing them food (Furness 1987) confirm this
643 seasonal shift in feeding strategy. Brown skuas have been
644 observed attacking seabirds such as white-chinned petrels
645 (*Procellaria aequinoctialis*) or sooty albatrosses (*Phoebe-
646 tria fusca*); KD's pers. obs.) at sea.

647 The existence of such a variety of migration strategies
648 within brown skua populations is puzzling. Evaluating the
649 demographic correlates as well as the repeatability in
650 individual migratory routes and wintering locations will be
651 valuable to understand this diversity and its fitness conse-
652 quences. It would be crucial to track the ontogeny of
653 migration strategies, to evaluate heritability and conse-
654 quences for survival. Identification of carry-over effects in
655 seabird behaviour during the wintering period and identi-
656 fication of their impact on population dynamics (e.g. the
657 effect of winter conditions faced by individual on its sub-
658 sequent reproduction), should be investigated (Harris et al.
659 2013). Skuas and other seabird species are good indicators
660 of environmental contaminants (Corsolini et al. 2011;
661 Carravieri et al. 2014a; Goutte et al. 2014). Such individual
662 variability in migratory strategies should also have conse-
663 quences in terms of susceptibility to environmental stres-
664 sors such as contaminants and climate change.

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