

Non-breeding distribution and activity patterns in a temperate population of brown skua

Hendrik Schultz¹, Rebecca J. Hohnhold¹, Graeme A. Taylor², Sarah J. Bury³,
Tansy Bliss⁴, Stefanie M. H. Ismar^{1,5}, Anne C. Gaskett¹, Craig D. Millar^{1,*},
Todd E. Dennis^{1,6}

¹School of Biological Sciences, The University of Auckland, Auckland 1142, New Zealand

²Department of Conservation, Wellington 6143, New Zealand

³National Institute of Water and Atmospheric Research Ltd., Wellington 6021, New Zealand

⁴Department of Conservation, Waitohi/Picton Office, Picton 7220, New Zealand

⁵GEOMAR Helmholtz-Centre for Ocean Research, 24148 Kiel, Germany

⁶College of Engineering, Science and Technology, Fiji National University, Natabua, Fiji

ABSTRACT: Brown skuas *Catharacta antarctica lonnbergi* breed across a broad latitudinal range from the Antarctic to temperate regions. While information on the non-breeding distribution and behaviour for Antarctic and subantarctic populations is known, no data exist for populations breeding at temperate latitudes. We combined geolocation sensing and stable isotope analysis of feather tissue to study the non-breeding behaviour of brown skuas from the temperate Chatham Islands, a population that was historically thought to be resident year-round. Analysis of 27 non-breeding tracks across 2 winters revealed that skuas left the colony for a mean duration of 146 d, which is 64 % of the duration reported for Antarctic and subantarctic populations from King George Island, South Shetland Islands, and Bird Island, South Georgia. Consistent with populations of brown skuas from Antarctica and the Subantarctic, the distribution was throughout mixed subtropical–subantarctic and shelf waters. Stable isotope analysis of 72 feathers suggests that moulting takes place over mixed subtropical–subantarctic and subtropical shelf waters. We conclude that brown skuas from the Chatham Islands are migratory, but the year-round mild environmental conditions may reduce the necessity to leave their territories for extended periods.

KEY WORDS: Migration · Geolocation · Sexual segregation · Seabird · Stable isotope

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INTRODUCTION

Seabirds are apex predators that feed at high trophic levels in marine ecosystems. Typically, they spend most of the year over the open ocean and come to land only for a few months to breed and raise offspring (Brooke 2004). During the non-breeding period, seabirds forage to obtain resources required for moult, often migrating large distances between breeding and non-breeding grounds (Shaffer et al. 2006, Egevang et al. 2010). The ability of seabirds to travel long distances and the accessibility of their

colonies during the breeding season make them important indicators of ecosystem health, which is critical for management of marine protected areas (Piatt et al. 2007, Einoder 2009). Investigating species-specific migratory patterns is important for understanding the natural history and demography of seabirds, including the localisation of foraging hotspots (Burger & Shaffer 2008, Lascelles et al. 2016). However, until recently, the mobility of seabirds has impeded thorough studies of their at-sea behaviour and migration routes. Advances in key technologies and the corresponding miniaturization

of tracking devices have enabled researchers to follow the movements of far-ranging seabirds (Weimerskirch et al. 1993, Phillips et al. 2004), including the trans-equatorial migrations of sooty shearwaters *Puffinus griseus* and Arctic terns *Sterna paradisaea* (Shaffer et al. 2006, Egevang et al. 2010). Seabirds offer opportunities to study intra- and inter-population differences in migratory behaviour (Kopp et al. 2011, Weimerskirch et al. 2015b). For example, Weimerskirch et al. (2017) observed variation in the non-breeding movements of great frigatebirds *Fregata minor* ranging from residency to long-distance migration. While frigatebirds were studied at similar latitudes, seabirds that breed across a wide geographic range allow investigation of migratory patterns at different latitudes.

Brown skuas *Catharacta antarctica lonnbergi* have a circumpolar breeding distribution ranging from 64° S in the Antarctic to 38° S at the subtropical Amsterdam Islands. Populations breeding at high latitudes in Antarctica and the Subantarctic migrate during the non-breeding period. Non-breeding routes of skuas from Bird Island, South Georgia, and King George Island, South Shetland Islands, have consistently showed a northwards trend towards subantarctic and subtropical waters (Phillips et al. 2007, Carneiro et al. 2016, Krietsch et al. 2017). In contrast, the non-breeding distribution of brown skuas from the subantarctic Kerguelen and Crozet archipelagos showed high inter-individual variability, ranging from subantarctic to subtropical and tropical latitudes, and their duration of migration was shorter than that of Antarctic populations (Delord et al. 2018). To date, no detailed study on brown skuas from temperate latitudes has been published, but it has been suggested that some individuals may remain at their colonies throughout the year (Hemmings 1990). Here, we investigated, for the first time, non-breeding behaviour in a temperate population of brown skuas from the Chatham Islands. The archipelago is located just north of the Subtropical Front and is characterised by a mild austral winter with mean annual air temperatures ranging from 11 to 12°C (Pearce 2016). While their breeding ecology has been well characterised, little is known about their non-breeding behaviour (but see Hemmings 1990). Brown skuas breeding on South East Island, Chatham Islands, were reported to be year-round residents (Hemmings 1990), but more recent observations indicate that skua territories were mostly deserted during winter. Only between 1 and 8 skuas were observed on South East Island during 8 separate winter visits between 3 March and 5 June, from

2013 to 2017, and some of these skuas were positively identified as juvenile birds (T. Bliss pers. comm.).

The aim of this study was to shed light on the natural history of the Chatham Island brown skua during the non-breeding period. By combining tracking data obtained via light-based geolocation devices with stable isotope analysis of feathers, we investigated their migration schedules, geographic distribution, key aspects of at-sea behaviour and diet. Given what is known about the non-breeding behaviour of other brown skua populations from Antarctica and the Subantarctic, we hypothesized that brown skuas from the Chatham Islands would leave their territories after the breeding season. Due to the reduced seasonality at this temperate breeding location, we further hypothesized that the extent of migration (i.e. duration and distance travelled) would be reduced compared to populations of brown skuas breeding at higher latitudes.

MATERIALS AND METHODS

Field methods

Fieldwork was conducted on South East Island (44° 20' S, 176° 10' W) in the Chatham Island archipelago (see Fig. 1) in 3 consecutive brown skua breeding seasons (2014 to 2016), during incubation and early chick-rearing periods (October to December). There are ca. 100 breeding individuals on South East Island, with a total of ca. 200 on the Chatham Islands, New Zealand. Breeding adults were captured within their territories using a hand net. Blood (~200 µl) was sampled from the tarsal vein using sterile syringes for molecular identification of sex (Griffiths et al. 1998) and stable isotope analysis.

Deployment, settings and retrieval of geolocators

A total of 56 global location-sensing immersion loggers (Intigeo-C250; Migrate Technology; henceforth referred to as 'geolocators') were deployed on 30 breeding skuas in 2014 and on 26 different breeding individuals in 2015. Geolocators were attached to a metal leg band using a weatherproof cable tie and a thin layer of self-amalgamating tape. The total load of the tracking device and attachment materials was 7.3 g, equating to <0.01% of mean adult body weight. Geolocators were set to mode 11, measuring light-levels at 1 min intervals, and saving the maxi-

imum recorded value every 10 min. In addition, geolocators tested for saltwater immersion every 30 s and stored the cumulative counts of 'wet' every 10 min. Devices were configured to detect only saltwater immersion.

We retrieved a total of 27 functioning geolocators containing data from 10 females and 17 males (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m603p215_supp.pdf). In October 2015, we retrieved 13 (43%) of the 30 geolocators that had been deployed in 2014. All 13 recovered geolocators were functional, enabling us to download their light and immersion data. In the following breeding season (2016), we retrieved 20 (79%) geolocators, out of which 6 had malfunctioned after deployment. The 14 remaining geolocators were included in light-level analysis. Three geolocators showed artefacts in their saltwater immersion data and were excluded from the analysis of at-sea activity patterns. Out of the 27 tracked skuas, 21 had bred successfully during the previous breeding season (Table S1).

Light-level analysis

The R package 'BASTag' (Wotherspoon et al. 2016) was used to select twilight events in light-level data from each geocator. The light intensity threshold was set to 1.5, which is the recommended value for Intigeo geolocators from Migrate Technology (Rakhimberdiev et al. 2016). Twilight periods with strong shading events were excluded from further analysis. Subsequently, light-level data were analysed in the R package 'FLightR' (Rakhimberdiev et al. 2017). The hidden Markov chain model of 'FLightR' combines a physical 'template fit' approach (Ekstrom 2007) and a movement model (uncorrelated random walk) in conjunction with a particle filter to estimate posterior locations. 'FLightR' then determines the most likely track consisting of up to 2 location estimates per day. We defined a spatial mask based on prior locations derived from simple threshold analysis, but we did not use land or behavioural masks. We used the 'rooftop' method (Lisovski et al. 2012) to create a calibration object for each geocator. Light-level analyses were restricted to the non-breeding period, including data that were collected during the equinoxes.

Characterisation of migratory patterns

Non-breeding periods for individual skuas (departure/arrival dates, and duration) were inferred

visually from saltwater immersion data using the R package 'BASTag' (Wotherspoon et al. 2016; see Text S1 in the Supplement for details). Maximum distances of individuals from the breeding colony (great-circle distances between each location and the colony) were calculated using the R package 'trip' (Sumner 2016). For each individual, total distances of non-breeding movements were calculated as summed great circle distances between consecutive locations.

Delineation of the non-breeding distribution

Individual kernel utilisation distributions (UDs) were calculated in a Lambert Equal Area projection centred on South East Island, using the R package 'adehabitatHR' (Calenge 2006). Cell size and bandwidth parameters were set to 50 and 100 km, respectively, to account for the grid resolution and approximate error of the 'FLightR' model. To calculate a pooled UD of all tracked skuas while accounting for individual differences in tracking duration, all 27 individual UD were stacked, and averaged (Clay et al. 2016). Core non-breeding areas were defined by the 25 and 50% UD contours. We followed a terminology similar to Phillips et al. (2009) to delineate the oceanic non-breeding areas: 'subtropical' for waters north of the Subtropical Front, 'mixed subtropical-subantarctic' for the oceanic region between the Subtropical Front and Subantarctic Front, 'subantarctic' for water masses between the Subantarctic Front and the Antarctic Polar Front, and 'Antarctic' for the oceanic regime south of the Antarctic Polar Front. Neritic waters in proximity of continental shelf and shelf slopes were termed 'shelf'. We used latitudinal isoscapes as proposed by Phillips et al. (2009) for the South Atlantic Ocean and by Jaeger et al. (2010) for the Indian Ocean to describe oceanic non-breeding areas based on stable carbon and nitrogen isotope ratios from feather tissue.

Stable isotope analysis

Blood and feather samples were analysed for stable carbon ($^{13}\text{C}/^{12}\text{C}$, expressed as $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$ expressed as $\delta^{15}\text{N}$) isotopes. Avian blood samples reflect diet integrated over 2 to 4 wk prior to sampling (Hobson & Bairlein 2003), and therefore when collected from nesting birds, reflect breeding season diet. In contrast, feathers are metabolically inert and hence stable isotopes indicate the latitudi-

nal origin ($\delta^{13}\text{C}$) and composition ($\delta^{15}\text{N}$) of the seabirds' diet during their non-breeding moult (Cherel et al. 2000).

The tip of the outermost right rectrix was sampled from breeding adults for analysis of stable isotopes in each of the 3 breeding seasons (2014 to 2016). Brown skuas moult primarily post-breeding, while away from the colony (Furness 1987). We did not find moulting birds during 3 breeding seasons, and signs of primary moult in this population have not been observed before mid-January (A. D. Hemmings pers. comm.). Therefore, assuming similar timings of primary and tail feather moult, the majority of the sampled rectrices were likely grown during the non-breeding period. We acknowledge, however, that since moulting in brown skuas has not been well characterised, isotope signatures from some feathers may reflect pre- or post-breeding periods (see Text S2 in the Supplement for additional details).

Rectrices from 61 individuals were analysed for stable carbon and nitrogen isotopes: 27 skuas that were successfully tracked during their non-breeding migration, and 34 individuals that had not been tracked. Feathers from 11 individuals were analysed across 2 different non-breeding periods. In addition, blood samples from 68 nesting adults were analysed to serve as a reference for breeding season diet. Sample preparation for analysis of stable isotopes was performed as described in Ismar et al. (2014). In brief, feathers were first rinsed with 70% ethanol, then dried and homogenised using sterile stainless-steel scissors. Blood samples were freeze-dried overnight and then homogenised within the sampling tube using a rounded spatula. Subsequently, 0.75 to 0.85 mg of homogenised material was transferred into tin capsules. Stable isotope analyses were carried out on a Delta V Plus continuous flow isotope ratio mass spectrometer linked to a Flash 2000 elemental analyser using a MAS200R autosampler (Thermo-Fisher Scientific) at the National Institute of Water and Atmospheric Research (NIWA) Environmental Stable Isotope Laboratory in Wellington (see Text S3 in the Supplement for details).

To identify the spatial distribution and diet of brown skuas during the non-breeding period, a hierarchical cluster analysis was performed on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values using Ward's method implemented in the R package 'cluster' (Maechler et al. 2017). To test whether individuals belonging to cluster I or II differed in their non-breeding distributions, we generated individual UD (25%) and calculated the pairwise overlaps between UD of all 27 individuals (Bhattacharyya's affinity index), using the R package

'adehabitatHR' (Calenge 2006). Subsequently, we performed an analysis of similarities (ANOSIM) implemented in the R package 'vegan' (Oksanen et al. 2017) on the pairwise Bhattacharyya distances using cluster affiliation (cluster I and II) as a grouping factor. Significant differences in the overlaps of the 2 isotopic clusters would indicate that the spatial distributions differ between the 2 groups (see Carneiro et al. 2016 for detailed method).

Analysis of activity patterns

We used the online tool 'Actave.net' (Mattern et al. 2015) to assign each data point to 1 of 3 behavioural categories ('in flight', 'on water' or 'foraging'). 'Actave.net' requires ϵ (cumulative counts of 'wet' per 10 min sampling period) to range from 0 (continuous dry) to 200 (continuous wet), which assumes sampling of 'wet' every 3 s. Since Intigeo geolocators sampled wet counts every 30 s, immersion counts in our data set ranged from $\epsilon = 0$ (continuous dry) to $\epsilon = 20$ (continuous wet). Hence, prior to loading the data into 'Actave.net', all sampling points were scaled by a factor of 10. Based on these data, 'Actave.net' categorised all data points into either in flight (immersion value $\epsilon = 0$), foraging ($0 < \epsilon < 200$) or on water ($\epsilon = 200$). While this conservative approach may categorise some non-foraging data as foraging, it is generally considered to be an appropriate choice for a range of seabird species, including the brown skua (McKnight et al. 2011, Cherel et al. 2016, Krietsch et al. 2017). The foraging category was further differentiated into 'dusk', 'night', 'dawn' and 'day', based on nautical twilight times. However, due to the accuracy of the geolocation method, and since nautical twilight times were based on location, the relatively short periods of dawn and dusk were removed from the analysis. Moreover, we used 'Actave.net' to calculate the daily frequency and duration of flight bouts, defined as a series of continuous data points that were categorised as 'in flight'. We exclusively performed the analysis of activity patterns on data obtained during the non-breeding season (as defined by departure and arrival dates).

Statistical analyses

All statistical analyses were performed using R version 3.4.1 (R Development Core Team 2017). Results are presented as means \pm SD unless otherwise indicated.

Table 1. Migration characteristics of 27 brown skuas *Catharacta antarctica lonnbergi* breeding on the Chatham Islands. Skuas were tracked using geolocators during the 2015 (n = 13) and 2016 (n = 14) non-breeding periods. Presented are general linear models testing for effects of the fixed-factors sex and breeding status on departure and arrival dates, total distance travelled, maximum distance from the colony and duration of migration. Only models with best fit according to Akaike's information criterion for small sample size (AIC_c) rankings are shown. (+) denotes parameters that were included in the best models. Breeding status and interactions among factors are not shown because they were not included in the final models. LC: lower confidence intervals; UC: upper confidence intervals

Non-breeding distribution

At-sea locations of skuas ranged between subtropical and subantarctic waters (35° to 60°S; see Fig. S1 in the Supplement). Apart from 3 exceptions, the longitudinal range of skuas was between 180 and 160°W. However, 2 females travelled as far west as New Zealand and 1 male headed more than 6000 km east towards Chile (Fig. 1). The average core area across all individuals, here defined by the 50 % UD contour, was located east along the Chatham Rise and southeast of the Chatham Islands (Fig. 1). When plotted on a monthly basis, core utilisation areas of skuas were distributed over subtropical and shelf waters in the vicinity of the Chatham Rise early (February to March) and late (June to July) in the non-breeding season. During mid-winter (April to May), skuas dispersed throughout subtropical, mixed subtropical–subantarctic and

subantarctic waters. Notably, the shelf region of the eastern Chatham Rise was utilised by skuas throughout the non-breeding period (see Fig. S2 in the Supplement). The non-breeding distribution of females and males differed temporally, with significant spatial segregation in core utilisation areas (50 %) occurring during May and June (ANOSIM: $R = 0.19$, $p = 0.011$; Fig. 2).

Stable isotopes

The mean isotope value of all sampled feathers was $-17.3 \pm 1.5\text{‰}$ (median = 17.2‰, range: -25.3 to -15.3‰) for carbon and $12.7 \pm 2.6\text{‰}$ (median = 13.4‰, range: 8.9 to 16.6‰) for nitrogen. The mean $\delta^{13}\text{C}$ value of blood that was collected during the breeding season was $-20.2 \pm 2.2\text{‰}$ (median = -19.3‰ , range: -26.9 to 17.6‰). The mean $\delta^{15}\text{N}$ value was $12.4 \pm 0.7\text{‰}$ (median = 12.4‰, range: 11.1 to 15.0‰; Figs. 3 & S4). Feather $\delta^{15}\text{N}$ values did not differ according to sex, but nitrogen data obtained from 2014 were significantly higher than those of subsequent years (2015 and 2016) (LMM; 2014 to 2015: 3.3‰, 95 % CI [1.9, 4.6], $p = 0.004$; 2014 to 2016: 3.0‰, 95 % CI [1.7, 4.3], $p = 0.004$; Table S1 in the Supplement). Feather $\delta^{13}\text{C}$ levels of females were lower than those of males (-0.9‰ , 95 % CI $[-1.6, -0.2]$, $p = 0.013$). However, this difference was not significant after removing the 5 females with low $\delta^{13}\text{C}$ levels from the analysis ($F_{1,56} = 0.38$, $p = 0.542$). The hierarchical cluster analysis revealed 3 distinct clusters in feather isotopic values (Fig. 3). Cluster I was characterised by moderate $\delta^{13}\text{C}$ ($-17.6 \pm 0.4\text{‰}$, range: -18.3 to -16.6‰) and low $\delta^{15}\text{N}$ ($9.8 \pm 0.7\text{‰}$, range: 8.9 to 11.2‰) values, representative of mixed subtropical–subantarctic waters. Cluster II showed elevated $\delta^{13}\text{C}$ ($-16.5 \pm 0.7\text{‰}$, range: -17.9 to -15.3‰) and $\delta^{15}\text{N}$ ($14.8 \pm 1.1\text{‰}$, range: 12.1 to 16.5‰) values, indicating wintering in mixed subtropical–subantarctic and shelf waters. Cluster III entailed individuals with low $\delta^{13}\text{C}$ ($-21.5 \pm 2.5\text{‰}$, range: -25.3 to -19.1‰) and elevated $\delta^{15}\text{N}$ ($14.7 \pm 1.1\text{‰}$, range: 13.8 to 16.6‰) levels (Fig. 3). Individual stable isotope signatures were not con-

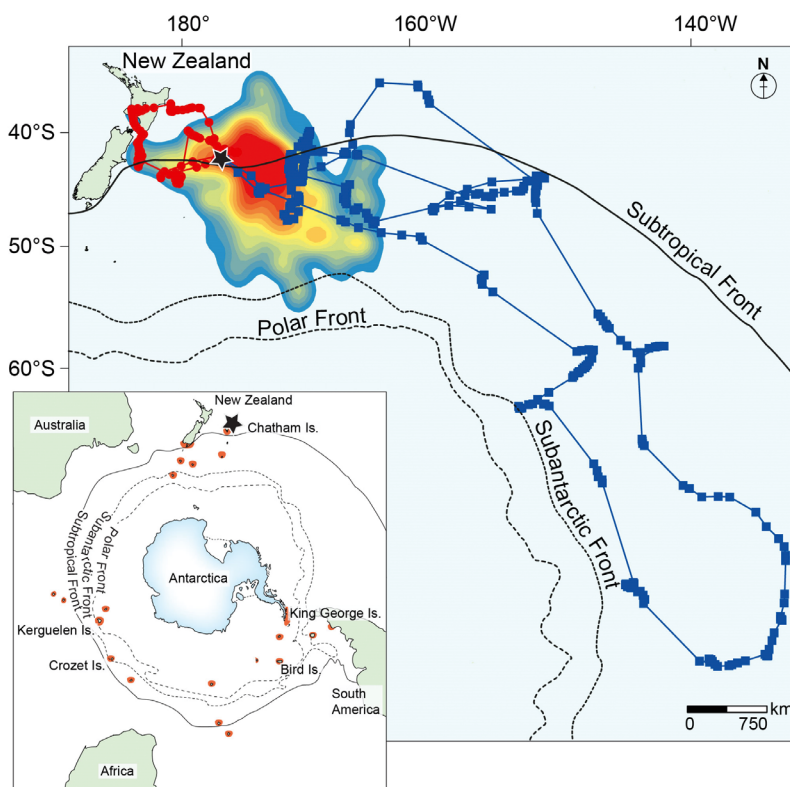


Fig. 1. Utilisation distribution (UD) based on geolocation fixes obtained from 27 brown skuas *Catharacta antarctica lonnbergi* breeding on South East Island, Chatham Islands (black star), during the 2015 and 2016 non-breeding periods. UD contours are depicted at 5% intervals ranging from 25% (red) to 90% (blue). The overlaid tracks of one female (red circles) and one male (blue squares) show the skuas' longitudinal range. Breeding colonies of *C. a. lonnbergi* and those of the related *C. a. hamiltoni* (Tristan de Cunha, Gough Island) and *C. a. antarctica* (Falkland Islands) are represented by orange buffers around islands

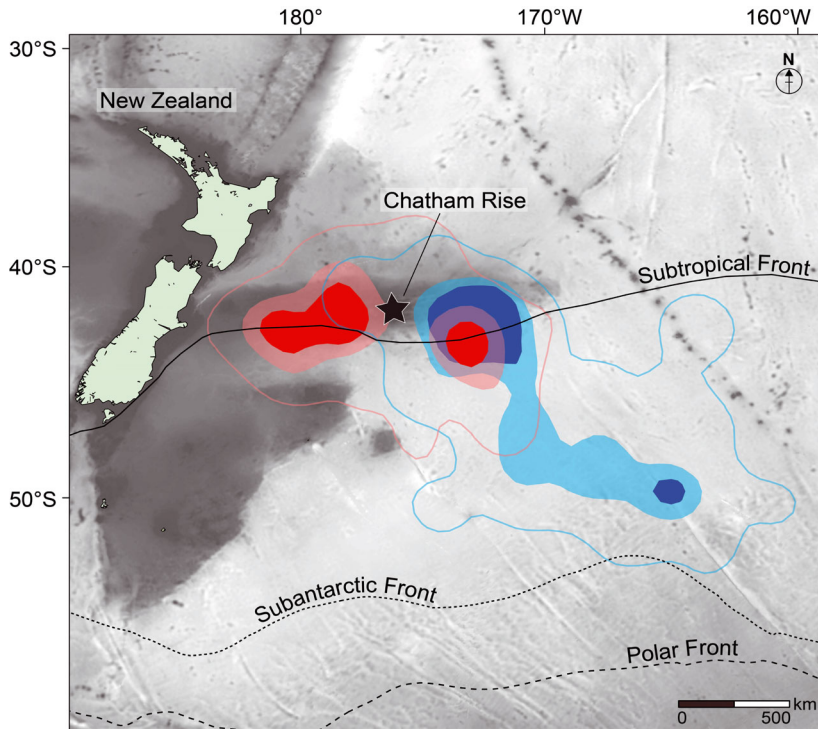


Fig. 2. Comparison of the core non-breeding utilisation distributions (25 and 50 % UD) for 10 female (red) and 17 male (blue) brown skuas *Catharacta antarctica lonnbergi* from the Chatham Islands (black star) during May and June. UD are overlaid on the bathymetric profile. The general (90 %) UD contours for females (red line) and males (blue line) are shown

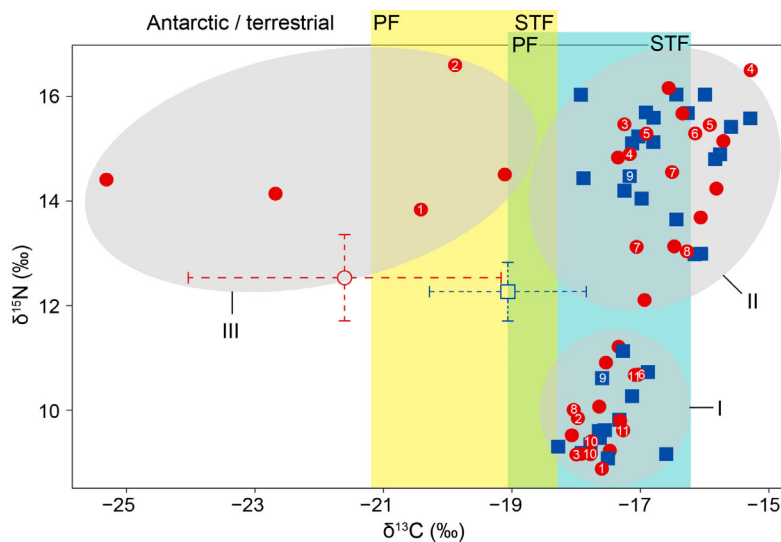


Fig. 3. Isotopic $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from tail feathers of female (red circles) and male (blue squares) brown skuas *Catharacta antarctica lonnbergi*. Numbers within circles and squares indicate the identity of individuals that were sampled in different years. Ellipses and roman numerals depict 3 distinct isotopic clusters, one with low $\delta^{15}\text{N}$ and moderate $\delta^{13}\text{C}$ (cluster I), a second with elevated $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (cluster II), and a third with moderate $\delta^{15}\text{N}$ and low $\delta^{13}\text{C}$ levels (cluster III). Blood isotopic signatures (mean \pm SD; uncorrected for differences in isotopic tissue discrimination) from females (hollow circle) and males (hollow square) during breeding are shown. The isotopic positions of the Polar Front (PF) and Subtropical Front (STF) were derived from Phillips et al. (2009; blue fill) and Jaeger et al. (2010; yellow fill)

sistent between years ($\delta^{13}\text{C}$: $r = 0.286$, 95 % CI [0.00, 0.74], $p = 0.208$; $\delta^{15}\text{N}$: $r = 0.033$, 95 % CI [0.00, 0.56], $p = 1.000$), indicating possible year-to-year variation in non-breeding behaviour. Only 5 out of 11 skuas that were sampled in 2 seasons were associated with the same isotopic cluster in both years (Fig. 3). Furthermore, the individual association with isotopic clusters (cluster I, II) was not reflected in the spatial distributions (25, 50 % UD) of the tracked skuas (ANOSIM: $R = -0.02$ to -0.04 ; $p > 0.05$). The average core areas (25, 50 % UD) of individuals associated with cluster I were distributed over mixed subtropical–subantarctic and shelf waters. Average core areas of skuas that were associated with cluster II were mainly distributed over shelf waters, but overlapped with core UD of cluster I over the Chatham Rise (see Fig. S3).

Activity patterns and behaviour

Brown skuas spent most of their daily time sitting 'on water', relatively moderate times 'foraging' and even less time 'in flight' (Table 2). Females spent more of their daily time 'in flight' and engaged in longer (but not more frequent) flight bouts than males (Table 2). Interestingly, both sexes spent a greater proportion of their daily foraging time foraging during the night (females: $60.92 \pm 2.5\%$; males: $57.54 \pm 3.10\%$) than during the day (females: $34.82 \pm 2.63\%$; males: $38.62 \pm 3.08\%$). Females spent less time foraging during daylight and more time foraging at night compared to males, even though sex-specific differences were only statistically significant during daytime foraging (Table 2).

DISCUSSION

This study is the first to describe the non-breeding distribution of brown skuas from a temperate population. Contrary to historical reports, but consistent with recent observations, all tracked skuas were migratory. We found that the ex-

Table 2. Comparison of daily activity types, flight bouts and foraging behaviours of female (n = 9) and male (n = 15) brown skuas *Catharacta antarctica lonnbergi* breeding on the Chatham Islands. Skuas were tracked using geolocators with integrated saltwater immersion sensors during the 2015 and 2016 non-breeding periods. Activity types are depicted as daily time spent 'on water', 'in flight' and 'foraging'. Flight bouts are reported as mean duration and counts d⁻¹. Foraging activities are differentiated into the categories day and night. Values are shown as mean ± SD; LC: lower confidence intervals; UC: upper confidence intervals

	Female	Male	Differences	95% LC	95% UC	p-value
Activity type (in h d ⁻¹) (%)						
On water	14.93 ± 0.83 (62.21 ± 3.46)	15.52 ± 0.56 (64.67 ± 2.32)	-0.59	-1.14	-0.04	0.048
In flight	2.99 ± 0.75 (12.45 ± 3.11)	2.32 ± 0.52 (9.67 ± 2.17)	0.67	0.16	1.18	0.017
Foraging	6.08 ± 0.25 (25.34 ± 1.02)	6.15 ± 0.48 (25.65 ± 2.00)	-0.07	-0.41	0.26	0.671
Daily flight bouts						
Duration (min)	48.89 ± 10.89	37.93 ± 5.76	1.24 ^a	1.07 ^a	1.43 ^a	0.008
Frequency (n)	4.24 ± 0.33	3.92 ± 0.50	1.09 ^a	0.99 ^a	1.19 ^a	0.079
Diel foraging activity						
Day (in h d ⁻¹) (% day)	2.08 ± 0.20 (19.55 ± 2.14)	2.33 ± 0.20 (23.04 ± 2.73)	-0.25	-0.42	-0.09	0.004
Night (in h d ⁻¹) (% night)	3.74 ± 0.17 (35.18 ± 2.29)	3.58 ± 0.39 (32.32 ± 3.77)	0.16	-0.01	0.33	0.065
^a Back-transformation of log-transformed values (i.e. ratios)						

tent of migration (i.e. both the duration and maximum distance from the colony) was shorter than for populations breeding at higher latitudes.

Non-breeding distribution

Apart from one exception, the tracked skuas did not undertake long-distance migrations, but were mainly distributed over shelf waters of the Chatham Rise and oceanic waters north of the Subantarctic Front. Notably, the shelf region east of the Chatham Rise was consistently utilised throughout the non-breeding period, indicating its importance as a wintering ground for the population. The Chatham Rise is part of the New Zealand continental shelf and constitutes an area of elevated primary productivity (Boyd et al. 2004). The significance of the Chatham Rise as a suitable habitat for seabirds has been demonstrated for grey-headed albatross *Thalasarche chrysostoma* and wandering albatross *Diomedea exulans* (Weimerskirch et al. 2015a, Clay et al. 2016). Furthermore, global analyses emphasise its ecological importance as a foraging hotspot for seabirds (Waugh et al. 2012, Lascelles et al. 2016). The Antarctic Polar Front, a region with seasonal peaks in primary productivity (Moore & Abbott 2002), consti-

tuted the southern boundary of brown skuas' non-breeding distribution. The Pacific region of the Antarctic Polar Front is of great importance for seabirds breeding in New Zealand. Sooty shearwaters *Puffinus griseus* visit the area during foraging trips (Shaffer et al. 2009) and common diving petrels *Pelecanoides urinatrix* target the region during their post-breeding migration (Rayner et al. 2017).

The latitudinal non-breeding distribution of brown skuas from the Chatham Islands was similar to populations from Bird and King George Islands (Phillips et al. 2007, Carneiro et al. 2016, Krietsch et al. 2017). Moreover, Carneiro et al. (2016) highlighted brown skuas' preference for wintering over shelf-slope regions, which is consistent with stable isotope studies (Phillips et al. 2007, 2009, Graña Grilli & Cherel 2017). Interestingly, the non-breeding distributions of brown skuas from the subantarctic Kerguelen and Crozet archipelagos were highly variable, with individuals distributing over neritic and oceanic waters of subantarctic, subtropical and tropical biomes (Delord et al. 2018). Similarly, we observed inter-individual variability in migration schedules and distances travelled. However, migration seems to occur at a smaller spatiotemporal scale than observed in Antarctic and subantarctic populations. Brown skuas from King George Island (62°S) departed from the

colony for 228 d, distributing over waters of the Patagonian Shelf and the Argentinian Basin, with core non-breeding areas being ca. 1700 and 2500 km away from the breeding colony (Krietsch et al. 2017). Similarly, skuas from Bird Island (54° S) travelled ca. 1500 to 2700 km away from their colony (Carneiro et al. 2016), and were at sea for 225 d. Interestingly, despite the relatively short duration of migration of 159 d, brown skuas from the Kerguelen (49° S) and Crozet (46° S) archipelagos undertook long-distance migrations, travelling a mean maximum distance of ca. 4000 km away from the colony (Delord et al. 2018). Brown skuas from South East Island (44° S) travelled a mean maximum distance of ca. 1500 km from the colony and returned after 146 d at sea, indicating a shorter range and duration of migration compared to populations from higher latitudes. This comparison emphasises the potential importance of both location (i.e. the proximity of the colony to suitable non-breeding grounds) and seasonality, for the spatial and temporal extent of brown skua migration. In the case of the Chatham Island brown skua, proximity of the colony to the productive waters of the Chatham Rise may reduce the need to migrate long distances, and the year-round mild climate may contribute to a reduced duration of migratory journeys.

Stable isotopes

Combining latitudinal isoscape data with the analysis of $\delta^{13}\text{C}$ from feathers allows the inference of non-breeding areas for migratory seabirds (Quillfeldt et al. 2010). Isoscapes have been determined for the southern Indian Ocean (Jaeger et al. 2010) as well as for the South Atlantic (Phillips et al. 2009), but no such data exist for South Pacific seabirds. We identified 3 discrete clusters in the isotopic signatures of feathers. Depending on which isoscape is used, the values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in cluster I indicate non-breeding distributions over either mixed subtropical–subantarctic (Phillips et al. 2009) or subtropical waters (Jaeger et al. 2010). Elevated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of cluster II have been described for wandering albatross, which forage over subtropical and shelf waters (Phillips et al. 2009) including the Chatham Rise (Weimerskirch et al. 2015a). Higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values are likely a result of the more complex food chains in shelf-slope waters (Phillips et al. 2009). Hence, considering the non-breeding distribution of tracked skuas, the elevated $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ levels suggest that moulting of rectrices occurred in shelf waters of the Chatham Rise.

Interestingly, feathers from 5 females (cluster III) showed low $\delta^{13}\text{C}$ levels. There are at least 2 possible explanations for this pattern. Moulting could have occurred in Antarctic waters or on land, since both environments are characterised by low baseline levels of $\delta^{13}\text{C}$. In the latter scenario, the 5 females may either have (1) migrated, but returned sufficiently early to moult at the colony or (2) moulted at a terrestrial site, which could have been the colony or elsewhere in their non-breeding range. Alternatively, these 5 females may have moulted over Antarctic waters south of the Polar Front. Indeed, similarly low $\delta^{13}\text{C}$ values were reported for feathers from chicks of south polar skuas *Catharacta maccormicki* and from adults that had moulted over Antarctic waters (Weimerskirch et al. 2015b).

Our results show 2 major isotopic clusters which are consistent with the findings in brown skuas breeding at high latitudes: skuas from King George Island had isotope values consistent with a non-breeding distribution over mixed subtropical–subantarctic and shelf waters (Graña Grilli & Cherel 2017). Similarly, feather isotopes of skuas from Bird Island indicated moulting over mixed subtropical–subantarctic waters, and one ‘outlier’ (elevated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) indicated that moulting occurred in shelf waters (Phillips et al. 2009). Consistent with their non-breeding distribution, brown skuas from the Kerguelen archipelago showed high variability in isotopic signatures (Delord et al. 2018). Individuals that were distributed over mixed subtropical–subantarctic waters showed low $\delta^{15}\text{N}$ values similar to those of brown skuas from Bird Island (Phillips et al. 2007) and cluster I in this study. These low $\delta^{15}\text{N}$ values likely reflect a low trophic level prey comprised of macrozooplankton, fish and squid (Phillips et al. 2007). If true, low $\delta^{15}\text{N}$ levels could result, for example, from skuas kleptoparasitising other seabirds or capturing prey of low trophic level at the sea surface. However, the interpretation of $\delta^{15}\text{N}$ from feathers is complex, especially when individuals forage across biomes that are characterised by different $\delta^{15}\text{N}$ baseline levels (Delord et al. 2018).

Interestingly, we did not find any statistical difference in the spatial distributions of individuals from cluster I or II. It is possible that the relatively low spatial resolution of the tracking data did not allow such differences to be detected. Alternatively, the mismatch between the stable isotope clusters and the spatial distributions of individuals could be the result of skuas feeding on drifting diets from other geographic regions. Consequently, our stable isotope signatures from feathers could be a blend of diets from different regions. Furthermore, the isotopic

signatures of a bird's tissue can depend on its physiological state (Hobson et al. 1993, Cherel et al. 2005). For example, it has been shown that during periods of fasting or when individuals are in a poor nutritional state, feather $\delta^{15}\text{N}$ levels were high in king penguin *Aptenodytes patagonicus* (Cherel et al. 2005). Importantly, similar isotope clusters to those reported in our study were also found in other brown skua studies (Phillips et al. 2009, Graña Grilli & Cherel 2017). This suggests that whatever factors result in differences in our study are also likely to be operating in other populations.

At-sea activity and foraging behaviour

While reports about skuas' foraging behaviour at sea are mostly anecdotal, direct observations suggest that brown skuas kleptoparasitise and attack other seabirds, scavenge on dead seabirds, fish and mammals and also feed on goose barnacles *Lepas australis* and abalone *Haliotis virginea* (Furness 1987, Hemmings 1990, Higgins & Davies 1996, Reinhardt et al. 2000). Brown skuas from the Chatham Islands foraged mainly during the night, which contrasts with the findings by Krietsch et al. (2017), who found that non-breeding brown skuas from King George Island foraged predominantly during the day. Females performed longer, but not more frequent, flight bouts than males, which is consistent with observations made in brown skuas from Antarctica and the Subantarctic (Carneiro et al. 2016, Krietsch et al. 2017). Since brown skuas display reversed sexual dimorphism (Phillips et al. 2002), sexual differences in flight behaviour may be attributed to size-dependent disparities in manoeuvrability between females and males (Carneiro et al. 2016). Moreover, non-breeding brown skuas from Bird Island spent more time in flight than the smaller Falkland skuas *Catharacta antarctica antarctica* (Phillips et al. 2007), indicating that body size may indeed play a role in shaping the activity patterns of skuas (Delord et al. 2018). It is therefore possible that size-mediated differences also contribute to the spatial segregation in the non-breeding distribution of female and male brown skuas found in this study.

CONCLUSIONS

Our findings suggest migratory behaviour in all Chatham Island brown skuas. This contradicts previous findings by Hemmings (1990), who found 82 % of

breeding brown skuas to be resident on their territories during the non-breeding period. The author's findings were based on a visit to South East Island from 7 to 14 July 1986. The discrepancy between that report and our recent findings may reflect a change in the proportions of skuas that are resident and migratory. Alternatively, since tracked skuas returned in early July (7 July \pm 19 d), the majority of brown skuas could have returned to the colony prior to Hemming's observations. Either way, both historical and contemporary findings suggest that, at the temperate Chatham Islands, migration may be less critical than it is for populations breeding at higher latitudes, where food availability is severely limited during the non-breeding period. Furthermore, the temperate conditions and food availability possibly allow skuas to reduce the duration of their migratory journeys and maximise the time at their breeding territories. Further investigation is necessary to quantify differences in migratory behaviour across the species' geographic range. A meta-comparison combining tracking data and isotopic signatures from various breeding sites is needed to evaluate whether there is a strong relationship between the duration of migration and latitude.

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