INDIVIDUAL CONSISTENCY IN THE NON-BREEDING BEHAVIOR OF A LONG-DISTANCE MIGRANT SEABIRD, THE GREY PETREL *PROCELLARIA CINEREA*

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ABSTRACT

DELORD, K., BARBRAUD, C., PINAUD, P., RUAULT, S., PATRICK, S.C. & WEIMERSKIRCH, H. 2019. Individual consistency in the non-breeding behavior of a long-distance migrant seabird, the Grey Petrel *Procellaria cinerea*. *Marine Ornithology* 47: 93–103.

There is growing interest in the consistency of individual differences in animal behavior as it relates to life history traits and fitness. Despite the relatively large number of studies investigating repeatable behaviors, studies have only recently investigated repeatability in foraging or migratory behaviors, and this has seldom been explored between years. We examined the individual consistency in foraging behavior of the Grey Petrel *Procellaria cinerea*, a pelagic long-distance migrant seabird. We analyzed how foraging, activity, and migratory patterns were repeatable across different seasons. We used tracking data to monitor the migratory movements and behavior of individuals during the non-breeding period over five years. Despite the small sample size, we found that there was a relatively high individual consistency in wintering strategies across years, with birds displaying high fidelity to their non-breeding destinations during consecutive years. Activity parameters, date of departure of inward migration, duration of migration, and duration spent in non-breeding areas were repeatable as well. The duration of the non-breeding period was the most repeatable, reflecting consistent departure times and, to a lesser extent, consistent arrival times. A high overall repeatability was seen in the timing of return migration. With respect to sex, males tended to be more consistent in their migration strategy (i.e., timing of migration, time spent in non-breeding areas) than females. Although conditions during the Holocene have generally been stable in the Southern Ocean, species lacking variability in migratory traits are probably at a considerable disadvantage in terms of their capacity to respond to the rapid environmental changes currently underway.

Kay words: conservation implications, geolocators, migration, *Procellaria cinerea*, repeating patterns, Southern Ocean, tracking

INTRODUCTION

Consistent behavioral differences within individuals—rather than between individuals—as they relate to life history traits and fitness, have been receiving increased interest among ethologists. Indeed, there is growing evidence for consistent individual behavioral differences in a wide variety of taxa (Smith & Blumstein 2008, Bell *et al*. 2009). To date, most studies on repeatable behaviors have focused on mating, courtship, and aggression behaviors in terrestrial bird species.

There is increasing interest among seabird biologists to understand individual consistency (Phillips *et al*. 2017). Individual consistency is relevant to both seabird behavioral ecology and to the conservation of endangered species. There are now many studies that have investigated repeatability in foraging (Patrick *et al*. 2014) or migratory behaviors (e.g., Bety *et al*. 2004, Rubolini *et al*. 2007, Thorup *et al*. 2013, Vardanis *et al*. 2011, 2016); however, these behaviors were, for the most part, measured within one year, and cross-season comparisons have focused primarily on the breeding period (Wakefield *et al*. 2015, Patrick & Weimerkirch 2017). The non-breeding period is reported to be critical for adult annual survival in seabirds, and hence, understanding behavior during this time is essential to understanding

individual fitness (Barbraud & Weimerskirch 2003). However, the quantification of flexibility in migratory patterns is needed to reveal the capacity of a species to adjust its migratory strategies to environmental changes (Weimerskirch *et al*. 2014). Recent studies have begun to address these questions by examining the variability in migratory behavior (Mueller *et al*. 2015, Carneiro *et al*. 2016, Fayet *et al*. 2016), wintering area (Yamamoto *et al*. 2014, Carneiro *et al*. 2016), and site fidelity (e.g. Grist *et al*. 2014, Fifield *et al*. 2014, Perez *et al*. 2014).

The aim of this study was to examine individual consistency in foraging behavior in the Grey Petrel *Procellaria cinerea* across non-breeding seasons, using several behavioral metrics: foraging, activity, and migratory patterns. We tracked the migratory movements and behaviors of males and females using miniature geolocators over five years. Grey Petrels are medium-size seabirds that exhibit dispersive migration, traveling widely at sea (Torres *et al*. 2015). Distribution models applied to Grey Petrels indicate that this species responds to broad-scale oceanographic influences in a colony-independent manner (Torres *et al*. 2015). The habitat used by Grey Petrels from the Kerguelen Islands, Indian Ocean, indicate a preference for waters between the Subtropical and Sub-Antarctic fronts that are associated with the following dynamic features: a

mixed layer depth of 50–100 m, mean temperatures of 7–13 °C in the upper 50 m, and a moderated surface current velocity and eddy kinetic energy.

METHODS

Background

This study was carried out at Mayes Island (49°47′S, 69°94′E), Kerguelen Islands. The Kerguelen archipelago holds the largest population of Grey Petrels in the southern Indian Ocean, estimated at 1 900 to 5 600 breeding pairs (Marchant & Higgins 1990, Barbraud *et al*. 2009). Grey Petrels nest in burrows, breeding annually (Chastel 1995). Birds return to breeding colonies in the austral autumn, first appearing in early February. Eggs are laid in late March and early April, and chicks fledge in late September to early December (Weimerskirch *et al*. 1989). The non-breeding period, unless otherwise specified, includes the outward and inward migration as well as the time spent in the core wintering area, and lasts from September to January. The Grey Petrel was recently listed as 'Near Threatened' due to substantial incidental mortality as bycatch in fisheries (Barbraud *et al*. 2009, Taylor 2000, BirdLife International 2018).

Bird tracking data

Breeding adults were caught during incubation and fitted with leg-mounted geolocation loggers (GLS: Mk7, Mk9, and Mk13 models; British Antarctic Survey, Cambridge, UK) weighing 3.6 g, 2.5 g and 1.8 g, respectively, and corresponding to 0.1 % to 0.3 % of body mass (0.8 to 1.5 kg). These GLS-immersion loggers were deployed

over two consecutive years (*n* = 30, 2007 and 2008), and 17 (57 %) were recovered in subsequent breeding seasons (*n* = 5, 2008; *n* = 5,

TABLE 1
Non-breeding areas of Grey Petrels from the
Kerguelen Islands, southern Indian Ocean, tracked
with GLS during successive years (2007–2012)

Bird	Sex	Deployment period	Period	Non-breeding destinations[a]
DZ20629	M[b]	09 April 2008–10 April 2012	2008–2011	STCZ, SAZ
DZ20631	F[b]	17 April 2007–21 April 2012	2007–2011	SAZ
DZ20734	F[c]	17 April 2007–25 April 2013	2007–2012	STCZ, SAZ
DZ23338	F[b]	17 April 2007–21 April 2012	2007–2011	STCZ, SAZ
DZ23339	F[b]	17 April 2007–09 May 2009	2007–2009	SAZ
DZ23359	M[c]	24 April 2008–03 May 2013	2008–2012	STCZ, SAZ
DZ23469	F[c]	09 April 2008–30 July 2011	2008–2011	SAZ

[a] depicted according to Longhurst 2010, by STCZ (Subtropical Convergence Zone) and SAZ (Subantarctic Zone)
[b] molecular sexing
[c] sexed behaviorally; see Materials and Methods

TABLE 2
Timing of migration of Grey Petrels from the Kerguelen Islands, tracked
during the non-breeding period (including single and multiple seasons), 2007–2012

Birds	Sex	*n*	Outward migration			Inward migration			Non-breeding[c]
			Departure date	Arrival date	Duration (days)	Departure date	Arrival date	Duration (days)	Duration (days)
DZ13971	M[a]	1	12 Oct	14 Oct	2	09 Feb	13 Feb	4	118
DZ20276	M[a]	1	18 Aug	31 Oct	74	28 Feb	07 Mar	7	120
DZ20629	M[a]	4	08 Aug ± 7	12 Aug ± 9	4 ± 2	14 Feb ± 6	21 Feb ± 7	7 ± 2	186 ± 11
DZ20631	F[a]	5	07 Aug ± 15	25 Aug ± 35	18 ± 27	09 Feb ± 8	09 Feb ± 7	4 ± 1	168 ± 35
DZ20734	F[b]	6	17 Aug ± 19	25 Aug ± 22	8 ± 7	13 Feb ± 5	20 Feb ± 6	7 ± 2	184 ± 20
DZ20761	nd[d]	1	31 Jul	12 Nov	105	14 Jan	17 Feb	34	63
DZ20763	F[a]	1	21 Jul	23 Jul	2	09 Feb	13 Feb	4	201
DZ21963	F[a]	1	09 Aug	15 Aug	6	14 Feb	18 Feb	4	183
DZ23338	F[a]	5	08 Jul ± 28	09 Jul ± 29	1 ± 1	11 Feb ± 2	16 Feb ± 1	5 ± 1	217 ± 29
DZ23339	F[a]	2	2 Sep ± 64	09 Sep ± 66	4 ± 2	15 Feb ± 11	20 Feb ± 13	5 ± 2	163 ± 55
DZ23359	M[b]	5	23 Jul ± 19	25 Jul ± 18	2 ± 1	15 Feb ± 4	20 Feb ± 4	5 ± 1	205 ± 15
DZ23469	F[b]	3	25 Sep ± 27	27 Sep ± 26	2 ± 1	22 Feb ± 2	27 Feb ± 2	5 ± 1	148 ± 25
Average (all birds)			7 Aug ± 31	15 Aug ± 39	11 ± 23	13 Feb ± 8	18 Feb ± 7	6 ± 5	177 ± 39

[a] molecular sexing
[b] sexed behaviorally; see Materials and Methods
[c] apart from migration period
[d] nd: not determined

2009; *n* = 1, 2010; *n* = 3, 2012; *n* = 3, 2013). Two loggers failed before recapture, resulting in incomplete data; therefore, data from these loggers were excluded from the data set. Over the five years of the study, a total of 12 individuals were tracked—some repeatedly—corresponding to 35 annual tracks, with seven individuals carrying loggers for two or more successive winters (Tables 1, 2). The breeding status and success during the reproductive seasons over which the loggers were deployed and recovered is unknown because logistical constraints precluded bird monitoring during these times. Loggers measured daylight level intensity every 60 s and recorded the maximum for each 10-min interval. Thresholds in the light curves were used to determine sunrise and sunset. An internal clock allowed estimation of latitude based on day length and longitude based on the timing of local midday with respect to Universal Time (Afanasyev 2004). GLS light data were analyzed using BASTrak software (TransEdit2 and Locator, British Antarctic Survey, 2009), which estimated two positions per day with an average accuracy of ~ 200 km (Phillips *et al.* 2004).

Molecular sexing

The sex of each equipped bird was identified using molecular methods (*n* = 8; five females and three males), except for five birds that were not sampled and for which sex was attributed to partner differences in burrow occupancy; one individual was unsexed. Sex was determined by PCR amplification of part of two CHD genes present on the sex chromosomes (Griffiths *et al.* 1998; Supplementary Information, Appendix, available on the website).

Individual spatial distribution and migratory timing

For each year (except 2012, when data were not sufficient, *n* = 2), filtered locations were used to generate kernel utilization distribution (UD) estimates with a smoothing parameter (*h*) of two and a 2° x 2° grid cell size. UD is a mean foraging utilization distribution that is estimated using the locations recorded from individuals tracked in each year (five birds in 2007, 11 in 2008, six in 2009, six in 2010, and five in 2011). Both the *h* value and grid cell size were based on the mean accuracy of the devices. The kernel density estimation was carried out on all individuals for the period in question. Following Worton (1989) and Montevecchi *et al.* (2012), we considered the 50 % (core foraging area) and the 95 % (home range) kernel UD contours. The core areas (50 % kernel) were used to obtain mean latitude and longitude (centroid position) and to calculate individual anomalies compared to the population distribution (i.e., deviation between individual and population centroid position), hereafter referred to as anomaly. We measured the percentage overlap of the core area (50 % UD) for individuals in successive non-breeding periods to evaluate consistency. Core areas were calculated for individual birds on a yearly basis to determine consistency in the ratio between an individual's core area and that of the population. Spatial analyses were performed using the "*adehabitatHR*" R package (Calenge 2006), and the *kerneloverlap* function was used for overlap calculations.

Migration timing was determined by combining visual examination of tracks (i.e., longitudinal directional movement during three consecutive days) and determination of the index of activity (i.e., periods of no saltwater immersion). During outward migration, birds rapidly reached their destination in the non-breeding zone, after which their movements were no longer directional. On the return migration, rapid movement was followed by several days of no salt water immersion, which was indicative of individuals returning to their burrows and ending their migration. We extracted parameters that described individuals' migration journeys, timing of movements, distances and durations of travel, and the location (anomaly of centroid position) of non-breeding areas. For individuals, we determined 1) the departure date of their outward migration, 2) the arrival date at their first non-breeding area, 3) the departure date of their return migration from the last non-breeding area, and 4) the date of return to their breeding colony. We calculated the duration of the non-breeding period as the interval between departure and colony return, and the duration of outward and inward migrations as the interval between the initiation and end of migratory movements.

Activity budgets

For Mk9 and Mk13, wet/dry status was recorded every 3 s, and the sum of immersions for each 10-min bout received a score between 0 and 200. For Mk7, wet/dry status was recorded every 3 s, and the sum of wet/dry duration was stored. Mk7-scheduled data were transformed into 10-min bins so that the two schedules could be compared. We used saltwater immersion to estimate the daily budget. Because birds feed while on the water's surface, the mean percentage of time spent sitting on the water (wet; immersion data > 0) was calculated to provide information on the variation in combined resting and foraging behaviors. Conversely, when birds were not on land, the time spent dry was interpreted as flying (and thus not feeding). Daylight and darkness periods were assessed using sunset and sunrise times, and were used to estimate the time spent on the sea surface during the day and night.

Consistency

Repeatability is the proportion of variation in a behavioral trait that is due to differences between individuals (Bell *et al.* 2009). Formally, repeatability is r = $s_A^2 / (s^2 + s_A^2)$, where s_A^2 is the variance among individuals and s^2 is the variance within individuals over time (Lessells & Boag 1987). Repeatable behaviors show relatively low within-individual variance compared to high among-individual variance; the same is true for consistency (Bell *et al.* 2009). We quantified individual-level consistency for multiple individual migration trips across years, and measured the repeatability of ten behavioral parameters. First, phenological and spatial parameters for every complete migration cycle were estimated: 1) departure date (outward and inward migration), 2) arrival date (outward and inward migration), 3) migration duration (outward and inward), 4) duration of the non-breeding period, 5) 50 % kernel overlap (across years) during the non-breeding period, 6) 95 % kernel overlap during the non-breeding period, and 7) the yearly ratio between the individual and population 50 % kernel. Second, activity parameters were calculated during the non-breeding period as the percentage of time spent on water during 1) daylight, 2) darkness, and 3) 24-h periods. The repeatability (*r*) of each parameter and its associated standard error and *p*-value, testing for the null hypothesis that between-group variance equals within-group variance, were estimated using the *rptR* package (Nakagawa & Schielzeth 2010) in R (R Core Team 2016).

Data were statistically analysed using R (R Core Team 2016). Two-sample *Z*-tests were used to test for repeatability differences among migratory parameters, and to determine the impact of sex on these parameters. Mann-Whitney-Wilcoxon tests were used to compare behavior in males and females when repeatability was found to be significant. All values are presented as the mean ± SD unless otherwise stated.

RESULTS

Sample size and general movement patterns

We obtained 15 complete tracks from 12 individual Grey Petrels during their non-breeding seasons, over one to six successive years (Tables 1, 2). Seven individuals carried loggers for two or more successive non-breeding periods. Individuals consistently migrated eastward to spend the non-breeding period in the southern Indian Ocean in all years (north of the Southeast Indian Ridge), visiting different areas (Figs. 1, 2; Appendix Figs. S1, S2, available on the website). All birds followed a similar migration route, moving eastward to their non-breeding area and returning to the colony using a relatively broad longitudinal axis, mainly in the Subantarctic Zone (Fig. 2). Individuals exhibited higher variation in outward migration duration (minimum: 2 d, maximum: 105 d; Table 2) compared to inward migration duration (minimum: 4 d, maximum: 34 d). Males and females had similar non-breeding distributions (Appendix Fig. S3, available on the website.
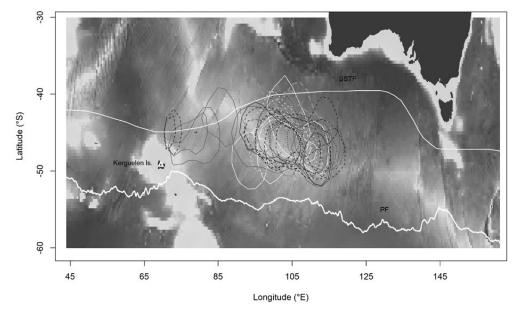

Fig. 1. Distribution of Kerguelen-breeding Grey Petrels carrying loggers for two or more successive non-breeding periods (colored by individual; seven individuals) in the southern Indian Ocean, 2007–2012. UD is the mean utilization distribution estimated using all locations recorded for each individual track in each year (50 % UD). Oceanographic frontal structures (grey lines)—the South Subtropical Front (SSTF) and Polar Front (PF) (Belkin and Gordon 1996; Sokolov and Rintoul 2009)—are shown. Bathymetry is represented in the background.
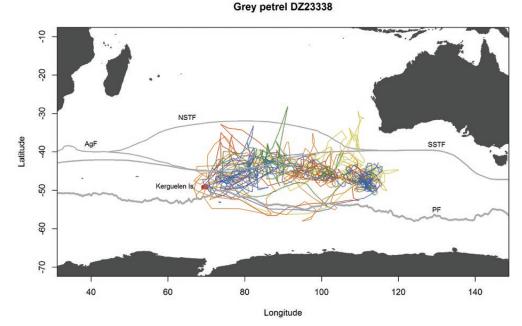

Fig. 2. Example tracks of one Grey Petrel from the Kerguelen Islands (red triangle) during the non-breeding period in five consecutive years (1st year: yellow, 2nd year: orange, 3rd: red, 4th: green, 5th: blue). Oceanographic frontal structures are depicted as in Fig. 1.

Consistency in individual migratory schedules

Grey Petrels exhibited highly directed migrations from their breeding grounds to non-breeding areas. They departed from the colony during the period extending from late July to late September, and returned to the colony during early February to early March, corresponding to a mean non-breeding season duration of 177 ± 39 d. Our results indicated a high degree of consistency in the following parameters: 1) the timing of migration, with highly repeatable dates ($r > 0.41$) and durations ($r > 0.87$; Figs. 3, 4; Table 2); 2) the annual date of departure and the duration of the inward migration, which were more repeatable compared to outward migration ($r > 0.70$; Table 3); 3) the duration of the non-breeding period, which was highly repeatable (Fig. 3); 4) the duration of migration (outward and inward), which was the most repeatable of all parameters (Appendix Table S1, S2, available on the website); and 5) the date of departure from the non-breeding area, which was highly repeatable (Fig. 4). There were also differences between sexes: 1) repeatability in migration timing was higher for males ($r = 0.22$–0.99; Appendix Table S2) than for females ($r = 0.04$–0.56; Appendix Table S1); 2) there was no significant difference between males and females in migration duration, time spent in the non-breeding area, dates of arrival/departure to/from the breeding colony, and the maximum distance during the non-breeding period ($W > 94$; $p > 0.05$, Mann-Whitney-Wilcoxon); and 3) the maximum distance

reached by females was greater (maximum: $6\,553$ km; mean: $3\,839 \pm 798$ km) than that reached by males (maximum: $4\,676$ km; mean: $3\,607 \pm 446$ km).

Non-breeding area and activity pattern consistency

During the non-breeding period, the 50 % kernel UDs overlapped ($40\ \% \pm 21\ \%$) between consecutive years among the same individuals. The degree of overlap was often higher than 32 % (1st quartile) for the core area (50 % kernel UD) and higher than 54 % for the home range (95 % kernel UD). Repeatability in the geographic extent of the core foraging area was high ($r = 0.41$; Table 3). Individuals did not show evidence of consistency in the annual anomalies of centroids ($r = 0$; longitude or latitude; Appendix Fig. S4, available on the website). The repeatability in the ratio between the surface 50 % kernel UD of individuals compared to the population—when occupying non-breeding areas across years—was high but not significant (Table 3; Fig. 5). Similarly, during the non-breeding phase, birds displayed relatively low consistency in their maximum range distance (Table 3) and spent more time on the water ($62.3\ \% \pm 11.7\ \%$ during October to January; Fig. 6) compared to the migratory phase ($27.0\ \% \pm 10.8\ \%$). Birds tended to be consistent in the percentage of time they spent on water during daylight, darkness, and over 24-h periods; however, repeatability estimates were not significant due to the large variance in the data (Table 3).
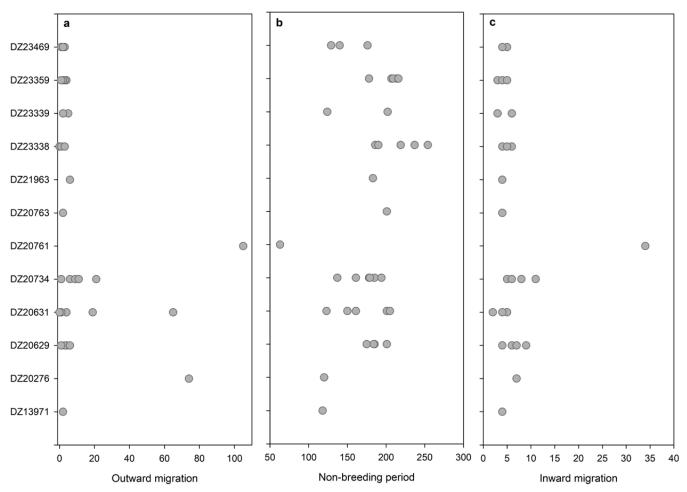

Fig. 3. Individual differences in the total number of days spent by Grey Petrels in a) outward migration, b) the non-breeding period, and c) inward migration. Codes on the y-axis correspond to ring numbers.

When the repeatability of the same parameters was evaluated in relation to sex, several differences were noteworthy. The repeatability in overlap of the core area appeared higher for males, whereas the maximum distance reached during the non-breeding phase was higher for females (Appendix Table S2). No repeatability was found in annual anomalies of centroids ($r = 0$), regardless of sex (Appendix Table S2). There was a non-significant trend that males were more repeatable in their activity parameters compared to females, suggesting that the sample size was probably insufficient to robustly assess differences in repeatability (Appendix Table S2).
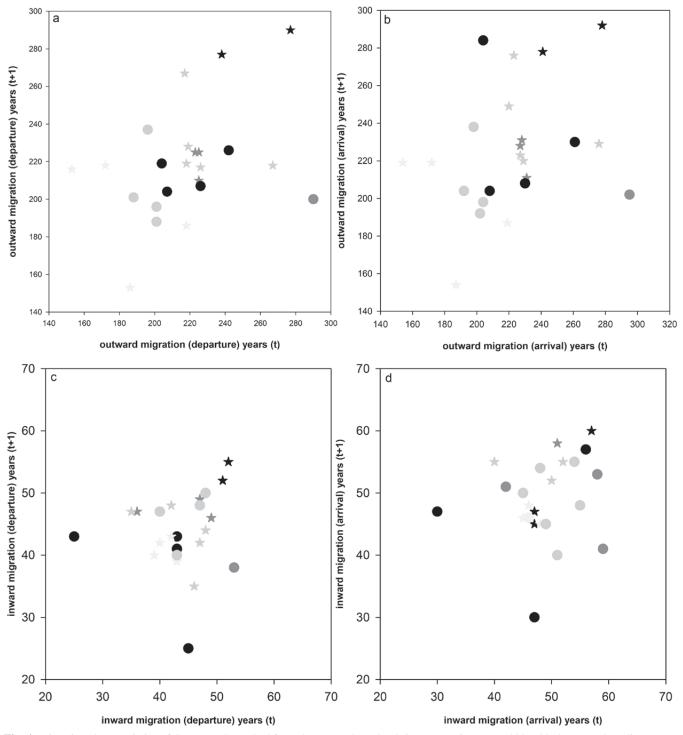

Fig. 4. Migration characteristics of Grey Petrels tracked from the Kerguelen Islands in consecutive years (2007–2012) to non-breeding areas: a) date of departure from breeding the colony (spring), b) date of arrival at the first non-breeding area, c) date of departure from the last non-breeding area, and d) date of arrival at the breeding colony (autumn). The timing of migration is shown in Julian days. Dates during year (t+1) on the y-axis are plotted in relation to dates during year (t) on the x-axis (symbols represent different individuals).

DISCUSSION

We confirmed that Grey Petrels nesting among the Kerguelen Islands are long-distance migrants that spend their non-breeding period along the Southeast Indian Ridge in the Eastern Indian Ocean (Torres *et al.* 2015). We also demonstrated that individuals exhibited a relatively high consistency in wintering strategies across years. Individuals displayed high fidelity to their non-breeding destinations, despite variation in their migration routes (e.g., Figs. 2, S2). However, given the small sample size, we cannot

generalize about consistency in destination and activity, especially for results that are not significant (Table 3).

The temporal aspects of the wintering strategy of individuals was highly repeatable (i.e., activity parameters, date of departure of inward migration, duration of migration, and duration spent in the non-breeding area). The behavior of Grey Petrels was repeatable (i.e., migratory timing), with the duration of migration (outward and inward) being the most repeatable migratory parameter. Migration schedules tended to be influenced by breeding status (e.g.,

TABLE 3
Consistency, by individual Grey Petrels (12 individuals, 35 tracks), in several migration and non-breeding parameters

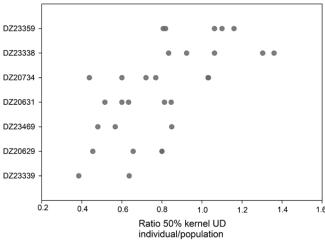|	Parameters	*r*	SE	*p*-value
Timing of travel	Date of departure from breeding colony (spring)	0.44	0.20	< 0.001
	Date of arrival at non-breeding area	0.55	0.19	< 0.001
	Date of departure from non-breeding area	0.70	0.15	< 0.01
	Date of arrival at breeding colony (autumn)	0.41	0.20	< 0.05
Duration (d)	Time spent in non-breeding areas	0.63	0.17	< 0.001
	Duration of outward migration	0.87	0.08	< 0.001
	Duration of inward migration	0.96	0.03	< 0.001
Destination	Anomaly in longitude of centroid 50 % kernel UD	0	0.11	NS[a]
	Anomaly in latitude of centroid 50 % kernel UD	0	0.11	NS[a]
	50 % kernel UD overlap for non-breeding period	0.41	0.16	< 0.001
	95 % kernel UD overlap for non-breeding period	0.13	0.10	NS[a]
	Maximum range distance during non-breeding period	0.20	0.17	< 0.001
	Ratio 50 % kernel UD individual/population	0.46	0.21	NS[a]
Activity	% of time on water during daylight during the non-breeding period	0.77	0.22	NS[a]
	% of time on water during darkness during the non-breeding period	0.75	0.23	NS[a]
	% of time on water during 24 h during the non-breeding period	0.84	0.17	NS[a]

[a] NS: Not significant

Fig. 5. Ratio between individual and population 50 % utilization distribution kernels of Grey Petrels tracked from the Kerguelen Islands during the non-breeding period in consecutive years, 2007–2012.

Fig. 6. Activity patterns of adult Grey Petrels (average daily proportion of time spent on the water with time) during the non-breeding period.

successful vs. failed breeders), with failed breeders departing from the breeding grounds earlier than successful breeders (Bogdanova *et al.* 2011, Yamamoto *et al.* 2014, Quillfeldt *et al.* 2015, Carneiro *et al.* 2016). Part of the inter-individual variation observed in the migration schedule of Grey Petrels was likely related to breeding output; however, we were not able to assess this directly.

Although previous studies have shown that activity and migration are among the least repeatable behaviors (Bell *et al.* 2009), our results are representative of activity and migration levels previously reported for several seabird species (McFarlane Tranquilla *et al.* 2014, Wakefield *et al.* 2015, Ramírez *et al.* 2016). Our results indicate that there is variation between individuals in migratory timing, and that this variation may be maintained by selection that favors repeatable migration duration in different years, irrespective of the environmental conditions between years. However, our small sample size and high level of variability (potentially due to the unknown breeding status of the tracked individuals) calls for future studies to confirm our findings.

The percentage of time spent on the water by individuals tended to be repeatable between years; however, this finding was not significant due to the large variance in the data. Birds consistently spent more time on the water during the non-breeding period compared to the migration stage. The few studies that have addressed individual repeatability in activity during the non-breeding period in seabird species (Ramírez *et al.* 2016) indicate that birds tend to behave consistently within a level of behavioral plasticity. Several species exhibit comparable temporal changes in at-sea activity patterns that reflect the energetic constraints linked to breeding, migration, molting, or non-breeding (Péron *et al.* 2010, Mackley *et al.* 2011, Cherel *et al.* 2016, Delord *et al.* 2016). The lower activity during the non-breeding period could be indicative of lower energetic needs, including the central-place foraging constraints that are in place during breeding. Alternatively, this pattern might be consistent with a change in feeding behavior, such as a dietary shift. Further investigation is needed to identify the cause of this change in at-sea activity during the non-breeding period.

Spatial consistency during the non-breeding period, with individuals using the same grounds, is a pattern shared by several seabird species (Phillips *et al.* 2005, Carneiro *et al.* 2010, Yamamoto *et al.* 2014, Orben *et al.* 2015, Ramírez *et al.* 2016). However, this pattern is not ubiquitous, and some species exhibit annual changes in their migratory routes and destinations, perhaps due to a stronger individual flexibility in their strategy (Dias *et al.* 2011, 2013; McFarlane Tranquilla *et al.* 2014). The recurrent use of areas may increase familiarity with foraging conditions, including fine-scale resource distribution. Although consistency may be related to habitat preferences associated with static features such as bathymetry (Carneiro *et al.* 2016), we found that the non-breeding area was used consistently by Kerguelen Grey Petrels, which typically select habitat based on dynamic oceanographic features (Torres *et al.* 2015). Our study area, which is located east of Kerguelen, is known to be exploited by a wide range of migratory seabirds and pinnipeds (Bost *et al.* 2009, Delord *et al.* 2013, Weimerskirch *et al.* 2015, Clay *et al.* 2016), reinforcing the idea that this area is a predictably profitable zone (Cotté *et al.* 2015, Thiebot *et al.* 2011, Torres *et al.* 2015). Further analysis of the repeatability of distribution at a lower temporal resolution (i.e., monthly) could shed light on whether Grey Petrels can change their foraging strategies in response to environmental changes.

Other species, in addition to Grey Petrels, have been reported to display sexual differences in the repeatability of their migratory strategies (Mueller *et al.* 2014). In this study, repeatability varied between males and females, the former being more consistent in their migration strategy. Compared with females, male Grey Petrels were more repeatable in the timing of their migration, in the time spent in their non-breeding area, and in the duration of their outward migration. Nevertheless, the timing and duration of migration movements, and the time spent in the non-breeding area, did not differ by gender. The competition for nesting sites (Carneiro *et al.* 2016), and the necessity for males to spend a longer time at their burrows to defend against conspecifics, is a likely explanation for the early arrival of males (Hedd *et al.* 2014) and for their consistency over time. Previous studies on seabirds found that females traveled farther or for longer periods and spent more time in transit or fewer days in non-breeding areas (Mueller *et al.* 2014, Carneiro *et al.* 2016; but see Yamamoto *et al.* 2014).

Despite growing evidence for the impact of environmental change on migratory timing in birds (Crick *et al.* 1997, Dunn *et al.* 1999, Both *et al.* 2004, Chambers *et al.* 2013), consistency as demonstrated in the Grey Petrel may be problematic. Without a high level of plasticity, strong individual consistency in the timing of migratory movements and the use of wintering/non-breeding season areas (or habitats) by Grey Petrels is likely to play an important role in its population dynamics. This has potential implications for the conservation of this species, which is at-risk of being caught by fisheries as bycatch (Barbraud *et al.* 2009). These areas have been classified as marine Important Bird Areas (Delord *et al.* 2014, Lascelles *et al.* 2014, 2016, Birdlife International 2019). Grey Petrel populations have been found to strictly segregate from each other during the non-breeding period (Torres *et al.* 2015); therefore, future environmental change could generate localized conservation issues. The region in which breeding sites are situated is managed by the Commission for the Conservation of Atlantic Marine Living Resources, which has applied and monitored mitigation measures to reduce bycatch. However, migratory and non-breeding areas overlap with other regional fisheries management organizations, namely the Indian Ocean Tuna Commission, where mitigation measures for reducing bycatch have improved very slowly (IOTC-WPEB 2012, IOTC 2015a). Unfortunately, mitigation measures cannot be applied in these areas to illegal, unreported, or unregulated fishing (IOTC 2015b). Given that Grey Petrels do not tend to change their natural history patterns, conservation of species like Grey Petrels will require humans to change their own behavior.

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