



Individual variability in habitat, migration routes and niche used by Trindade petrels, *Pterodroma arminjoniana*

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Abstract

Individual variability within a population and the eventual repeatability across time and space may provide stability in a population facing environmental changes, by affecting individuals differently. Thus, the variability and repeatability of behaviours, habitats used, niches and migratory pathways could play an important role. Trindade petrels (*Pterodroma arminjoniana*) are threatened seabirds that breed year round on Trindade Island in the South Atlantic Ocean, migrate to North Atlantic Ocean in the non-breeding periods, and use wide oceanic areas. This study investigated the timing, at-sea distribution, and trophic niche throughout the annual cycle of the austral fall/winter breeding group of Trindade petrel and examined consistency in distribution and trophic niche used by the Trindade petrel at the individual level, in different breeding seasons, using geolocator tracking and stable isotope analysis. Results demonstrated that petrels breed annually, maintaining their breeding schedules. Petrels share a common, vast oligotrophic oceanic area during both breeding and non-breeding periods inside the South Atlantic and North Atlantic Subtropical Gyres, respectively. Two migratory patterns were identified and used repeatedly by individuals. Although petrels overlapped at-sea distributions in consecutive breeding seasons, consistency in parameters tested was not found. Breeding in two schedules along the year, in addition to the use of different migratory pathways and flexibility in their isotopic niche can be an advantage for Trindade petrel population to cope with environmental changes. Causes and consequences of variable niche and pathways used, and the existence of consistency and variability among birds breeding later on the year remain poorly-known.

Introduction

Intraspecific niche variation may generate distinct ecological interactions within a population and thus expose individuals to different selective pressures, which can ultimately result in ecological functional diversity and provide population resilience (Van Valen 1965; Bolnick et al. 2003). Therefore, understanding population and intrapopulation specificities

allows us to infer the ability of species to cope with environmental changes (Nussey et al. 2007). Seabirds may present differences in habitat and resource use, for example, among populations or even between sexes, ages or breeding stages within the same population (Carneiro et al. 2017; Phillips et al. 2017). Studies had historically treated all sampled individuals as identical replicates within a population or subset thereof, such as different sexes, ages and breeding stages. However, studies carried out over the last two decades have demonstrated individual consistency in characteristics such as habitat, niche, migratory pathways and resource use and have revealed that populations that were once regarded as generalists may be composed of specialist individuals (Bolnick et al. 2003), with repeated patterns of habitat use and niche exploration. In this case, individuals occupy a niche that is substantially narrower than the population niche but is unrelated to their sex, age or other subgroup categories, which is referred to as “individual specialization” by Bolnick et al. (2003).

In a recent review, consistent migratory schedules, migratory routes, staging or stopover areas, habitats and trophic

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resources used by individuals was recorded in all orders of seabirds (Phillips et al. 2017). The consistency of non-breeding areas and migratory strategies in consecutive years was first confirmed in large procellariiforms. It was demonstrated that although grey-headed (*Thalassarche chrysostoma*) and black-browed (*T. melanophris*) albatrosses may exhibit different migratory strategies, individuals may show consistent migration schedules, routes and non-breeding areas used in consecutive years (Croxall et al. 2005; Phillips et al. 2005); although the opposite has also been recorded, i.e. seabirds varying migratory pathways and stopover areas (see Dias et al. 2013).

The enhancement and miniaturisation of biologgers, specifically Global Location Sensors (geolocators), which may record individual positions daily for up to 5 years, has allowed the at-sea distribution of seabirds to be assessed during their entire annual cycle (Ramírez et al. 2016; Ramos et al. 2017) or between years (Phillips et al. 2005; McFarlane-Tranquilla et al. 2014). Similarly, the stable isotope analysis (SIA) of nitrogen and carbon ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively) provides information about assimilated food sources in consumer tissues in a larger time window in comparison with the “snapshot” provided by traditional dietary approaches based on food remains (Barrett et al. 2007). While the SIA of whole blood provides information about the 3–4 weeks before sampling, feathers reflect the food assimilated during feather growth (Hobson and Clark 1992), which coupled with a known moult schedule, can allow inferences to be made about the diet consumed long before sampling (Bearhop et al. 2002; Ramos et al. 2009). The SIA of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ may allow inferences to be made about trophic levels (Vanderklift and Ponsard 2003) and foraging areas (Cherel and Hobson 2007), respectively, acting as intrinsic markers. Thus, the sampling of different tissues of an individual at a single point in time could allow the assessment of its trophic ecology in different periods and the inference of temporal consistency over long periods or in different phases of the annual cycle in multiple years.

The Trindade petrel, *Pterodroma arminjoniana*, is a medium-sized gadfly petrel that breeds on Trindade Island in the South Atlantic Ocean and, since the mid-twentieth century, on Round Island in the Indian Ocean (Brown et al. 2010). On Trindade Island, inside the oligotrophic South Atlantic Subtropical Gyre (Peterson and Stramma 1991), ca. 1130 pairs breed year round (Luigi et al. 2009). There are two egg-laying peaks, in September–October and February–March, and the period from laying to fledging is approximately 150 days long (Fonseca-Neto 2004; Luigi et al. 2009), with an additional 2–3 months of prelaying period (Luigi et al. 2009), which results in some overlap between the breeding periods of birds that breed early or late during the year (Ramos et al. 2017). Trindade petrels utilise large oceanic areas in the southwest Atlantic Ocean during

the breeding period (Leal et al. 2017). After breeding, Trindade petrels undergo a transequatorial migration via routes associated with warmer waters over the continental ridge to reach their non-breeding area in the oligotrophic waters of the North Atlantic (from 20° N to 30° N) (Krüger et al. 2016; Ramos et al. 2017). Thus, this species has one of the most extensive ranges among gadfly petrels in the Atlantic Ocean (Ramos et al. 2017).

The aim of this study is to investigate (1) the timing, at-sea distribution, and trophic niche throughout the annual cycle of the austral fall/winter breeding Trindade petrel and (2) examine consistency in distribution and trophic niche used by the Trindade petrel at the individual level, in consecutive breeding seasons, using geocator tracking and stable isotope analysis. Gadfly petrels searching for food use efficiently the winds to travel at high speed and low cost, covering large distances, rather than return to memorised foraging grounds (Ventura et al. 2020). Furthermore, during the breeding period, due to the limitations imposed by central-place foraging and high energetic demands, seabirds are more vulnerable to fluctuations in or the depletion of food resources (Whittow 2001; Furness 2007; Elliott et al. 2009). Thus, we expect to find low individual consistency in the foraging areas used during the breeding period; low consistency in the isotopic niche in consecutive breeding seasons; and consistent departure and arrival for breeding, without switching of birds breeding early in the year to later in the year, in subsequent breeding seasons.

Methods

Study area and sample collection

One Trindade petrel per nest was captured by hand during the breeding period early during the year (January–August) on Trindade Island (20°30' S–29°19' W). Twenty adult petrels at the chick-rearing phase in 2014 and 23 petrels at the prospecting phase in 2016 received GLS (geolocators) and were subjected to blood (~0.15 mL) and P1 feather (innermost primary) sampling, when deploying as well as when recovering the GLS. The breeding stage and success during the reproductive seasons over which the loggers were deployed and recovered is unknown due to logistical constraints and to avoid excessive disturbance and eventual nest desertion. The blood samples were taken from the tarsal vein using a needle and syringe. Approximately 0.05 mL of blood was preserved in absolute ethanol or on FTA® cards for molecular sex determination using CHD genes (Fridolfsson and Ellegren 1999). For stable isotope analyses, ~0.1 mL of whole blood was placed on glass slides, dried in the sun, scraped and stored in plastic vials (Bugoni et al. 2008). During the breeding seasons of 2015, 2016, 2017 and 2018,

searches for previously sampled petrels among nests were performed for resampling, as the petrels show high nest-site fidelity.

Geolocator tracking

Geolocators were used to track the Trindade petrels at sea during the breeding and non-breeding periods. This has been shown to be possible despite the limited accuracy of geolocators (Phillips et al. 2004; Leal et al. 2017) because the foraging radius is large and the trip duration is long during breeding (Leal et al. 2017) and the migration routes of these birds cover most of the north and south subtropical and tropical Atlantic Ocean (Ramos et al. 2017). Geolocators MK3005 (2.5 g; Biotrack) were attached to a leg-mounted metal ring equivalent of ~0.75% of the mean body mass of Trindade petrels, well below the 3% recommended to avoid adverse behavioral effects in seabirds (Phillips et al. 2003).

Bird locations were estimated using the *probGLS* package in R (Merkel et al. 2016), which takes additional information from the geolocators such as salt water immersion, possible speed of the bird in flight or on water, and sea surface temperature. Data points during the equinox periods and polar day were included, as the model has an algorithm to account for missing latitude values. However, during the breeding period the *probGLS* package estimated uncertain and unrealistic positions. The memory was full for the activity and temperature data in the geolocators 004, 011 and 016, and these data was not available for the entire tracking period. Therefore, *probGLS* was used for the non-breeding/migratory period, but due to unrealistic positions for the breeding period, and lack of activity and temperature data for the entire tracking period for some birds/devices, *BASTrak* software suite (British Antarctic Survey 2008) was used to generate two positions per day (at local midday and midnight), with light data only. We estimated dawn and dusk times by inspecting each light curve integrally; latitude was derived from day length, and longitude was derived from the time of local midday in relation to Greenwich Mean Time (Afanasyev 2004). During 7 days before deployment, the devices were placed in an open area on Trindade Island for calibration at a known location, as well as the definition of the best light threshold and sun elevation angle, inferred to be 16° and -5°, respectively. Then, we applied the filter for movement compensation available at the *BASTrak* software, where the latitude is compensated for longitudinal movement assuming uniform movement. To filter unrealistic positions, we removed positions resulted from periods spent at the nest, that were obtained from light curves showing interference at dawn or dusk, the data within the 15 closest days to the equinoxes, and those that represented unrealistic flying speeds (>40 km/h⁻¹ sustained over a 48 h period) (Phillips et al. 2004).

Stable isotope analysis

Sampled feathers were washed five times with distilled water, oven-dried at 70 °C for 3 h, cut with scissors into small pieces, weighed (~0.7 mg) and placed in tin capsules (5×9 mm). Lipids in the blood samples were not extracted due to the low lipid content of this tissue (Bearhop et al. 2000), which was subsequently confirmed by SIA showing a C:N ratio < 3.5 (Post et al. 2007). Blood samples were lyophilized, ground, homogenised, and encapsulated as indicated above, and all samples were analysed with an elemental analyser (Costech ECS 4010) coupled to a continuous-flow isotope ratio mass spectrometer (Delta PlusXP, Thermo Finnigan). Variable isotopic reference materials, differing according to each lab, were interspersed with each 10–15 unknown samples for calibration. SIA was carried out in two laboratories, the Stable Isotope Core Laboratory at Washington State University (USA) and the University of New Mexico Centre for Stable Isotopes (USA). The results for samples analysed in different laboratories might not be directly comparable; thus, the δ¹³C and δ¹⁵N values of growing feathers (*n* = 10) of the yellow-nosed albatross, *Thalassarche chlororhynchos*, were analysed in both laboratories. The paired *t* test showed no significant difference between values for δ¹⁵N (*t* = 2.21; *P* = 0.05), but a significant difference was found for δ¹³C (*t* = -5.69; *P* < 0.001). Thus, the δ¹⁵N values obtained in the two laboratories could be compared directly, but the δ¹³C values were corrected through a linear regression equation (δ¹³C corrected = -0.513 + 0.936*(δ¹³C)) to make them comparable between laboratories. Stable isotope (SI) values are expressed in standard δ notation as the deviation from standards in parts per thousand (‰), as follows:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N}(\text{‰}) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1, \quad (1)$$

where R_{sample} is the ratio between the heavy and light isotopes in the sample, and R_{standard} is the ratio between the heavy and light isotopes in Vienna Pee Dee Belemnite limestone, the international standard for carbon, or atmospheric N₂, the international standard for nitrogen.

At-sea distribution and isotopic niche

The distribution of petrels was assessed through kernel density estimation of the core area and home range (50 and 95% utilisation distribution—UD) using the *kernelUD* function of the package *adehabitatHR* (Calenge 2006) setting *h* = 1.8 (corresponding to a search radius of approx. 200 km). To avoid influence of periods at the nest at UD those positions

at a distance less than 300 km ($\sim 2 \times$ position error; Phillips et al. 2004) away from the breeding site were removed. The dates of departure from the breeding site, arrival at the main non-breeding area, departure from the non-breeding area and arrival at the breeding site were determined visually from spatial data, based on birds remaining in a given area for several days (at least 3 days). The departure date was determined as the day of the first position, on a row of positions, which reached more than 300 km away from the breeding site or from the main non-breeding area, with no subsequent return. Similarly, the arrival date was the day of the first position at the breeding site or at the main non-breeding area, defined as such by UD analysis. The migratory patterns were determined visually based on the positions of petrels with at least one complete non-breeding period tracked and the important areas were assessed through kernel density estimation of the core area and home range (50% and 95% UD). The standard ellipse area corrected for small sample size (SEAc) in the *SIBER* package (Stable Isotope Bayesian Ellipses in R; metrics in *siar* package; Parnell et al. 2010) was used to compare the estimated isotopic niches. Because stable isotope ratios in feathers and whole blood cannot be directly compared, whole blood values were standardised using the Eqs. (2) and (3), after Cherel et al. (2014):

$$\delta^{13}\text{C}_{\text{feather}} = 0.972(\pm 0.020)\delta^{13}\text{C}_{\text{blood}} + 0.962(\pm 0.414), \quad (2)$$

and

$$\delta^{15}\text{N}_{\text{feather}} = 1.014(\pm 0.056)\delta^{15}\text{N}_{\text{blood}} + 0.447(\pm 0.665). \quad (3)$$

The SIA of whole blood provides information about the assimilated food sources in consumer tissues over a time window (e.g., 3–4 weeks) (Hobson and Clark 1992) and thus represents the breeding period. Previous studies in gadfly petrels, including Trindade petrels (Krüger et al. 2016; Ramírez et al. 2016), have used P1 feathers as representative of the end of the breeding season/beginning of the subsequent non-breeding season, sometimes with no information on the moulting patterns (Warham 1996; Luigi et al. 2009). However, none of the petrels sampled in our study had moulting primaries, including those examined at the end of breeding, similar to other hundred petrels sampled previously, none with primary moult (Luigi et al. 2009). In addition, we performed a paired *t*-test between the corrected SI values from the whole blood of petrels at the end of breeding and their P1 feathers sampled in the subsequent breeding season ($n = 12$), which showed significant differences between the values for $\delta^{15}\text{N}$ ($t = -2.76$; $P = 0.01$) and $\delta^{13}\text{C}$ ($t = 2.86$; $P = 0.01$). Therefore, we used the results of the stable isotope analysis of the P1 feathers, assuming that they reflect the resources used during the non-breeding period. Based on the stable isotope ratios determined in feathers and

whole blood, we compared the isotopic niches of the non-breeding versus breeding periods. Isotopic niches during the non-breeding period were compared between tracked petrels showing different migratory patterns.

Individual consistency analysis

Kernel density estimation of the centroids (5% UDs), core range (50% UD) and home range (95% UD) was performed using the *kernelUD* function of the package *adehabitatHR* (Calenge 2006), with $h = 1.8$. To measure individual consistency in resource and at-sea distribution, we considered five variables: (1) distance of centroids (5% UDs) of the breeding period to the island (km), (2) latitude of centroid of the breeding period, (3) longitude of centroid of the breeding period (both in decimal degrees), (4) $\delta^{15}\text{N}$ values of whole blood and (5) $\delta^{13}\text{C}$ values of whole blood. To calculate the repeatability (i.e., consistency) of these response variables, we fitted generalised linear mixed models (GLMMs) with Gaussian distributions. For each of these variables, a model with the individual as a random effect was built. To control for confounding effects, we included sex and year (of the first sampling) as fixed effects in the structure of the models. For the same reason, the breeding stage (prospecting, incubating and chick-rearing) was included as a fixed effect in the models built for the stable isotope levels in breeding birds, determined from blood samples. Based on the variance components of the GLMMs, we estimated the repeatability (R) of each variable using the *rptGaussian* function of the *rptR* package (Stoffel et al. 2017) as:

$$R = \frac{S_A^2}{(S_A^2 + S^2)}, \quad (4)$$

where S_A^2 is the interindividual variance, and S^2 is the global within-individual variance, defined as follows:

$$S^2 = E(X_{\text{pop}} - E(X_{\text{pop}}))^2, \quad (5)$$

where X_{pop} represents each residual value of a given variable for all individuals, and $E(X_{\text{pop}})$ is the mean of the residual values of a given variable for all individuals. The index of repeatability ranges from 0 (low repeatability, high within-individual variance) to 1 (high repeatability, low within-individual variance). The uncertainty in the estimates was quantified through parametric bootstrapping ($N = 10,000$), and the significance test was implemented through the permutation of residuals (10,000 permutations).

In addition, the areas used by each individual in each year were considered to be those within the 50% (core area)

and 95% (home range) UD_s. The individual consistency in at-sea distribution during the breeding period was assessed throughout the percent of overlap:

$$HR_{i,j} = A_{i,j}/A_i, \quad (6)$$

where $HR_{i,j}$ is the proportion of the area of first year UD_{*i*} that overlaps with the area of second year UD_{*j*}, A_i is the area of first year UD, and $A_{i,j}$ is the area of overlap between the UD_s of the 2 years. To measure the similarity between UD estimates, we used Bhattacharyya's affinity (BA; Bhattacharyya 1943). The BA index ranges from 0, when there is no overlap, to 1, when UD_s are identical (Fieberg and Kochanny 2005). All analyses were conducted in R software (R Core Team 2015).

Results

Among the 20 petrels fitted with geolocators in 2014, 12 were recaptured in the following years, while among the 23 tagged in 2016, 15 were recaptured. In total, the blood and primary feathers of 24 petrels were sampled in two consecutive years, and the other three petrels were sampled in three consecutive years. Among these individuals, 14 were females, and 13 were males according to molecular sexing conducted for other studies (e.g., Leal et al. 2019). Because we did not find differences in foraging areas and SI values among groups, the sexes were pooled for further analysis.

Some petrels had their blood sampled in February, when petrels from the first egg-laying peak were arriving on Trindade Island. Due to the time window represented by this tissue (3–4 weeks before sampling), these samples may provide information about food sources assimilated before breeding; thus, these individuals were excluded from the analysis of consistency for this period, leaving eight remaining individuals. Among the 27 recovered geolocators, two failed to download. Tracked movements were recorded during both the breeding and non-breeding periods in two consecutive years in four petrels, while 15 were tracked during breeding in two consecutive years but only in one non-breeding period, one was tracked during only one breeding and one non-breeding period and five were tracked during only one breeding and one incomplete non-breeding period.

Thus, the timing and at-sea distribution throughout the annual cycle were determined based on 20 petrels with at least one complete non-breeding period tracked and the individual consistency during the breeding was assessed through eight petrels with blood samples, and data of 19 petrels tracked in two consecutive years; and 25 feather samples were used to

compare the isotopic niches of the nonbreeding versus breeding periods.

Annual cycle

Trindade petrels arrived on the island between 16 January and 19 February and left the island between 19 June and 17 August (Table 1). The breeding period lasted 164 ± 8 (mean \pm SD) days based on data of four petrels tracked throughout a complete breeding period (from arrival at to departure from the breeding site). The petrels arrived at the core non-breeding area in the North Atlantic Ocean between 9 August and 27 November, left the non-breeding area between 3 January and 14 February (Table 1) and stayed in this area for 97 ± 26 days. The exception was petrel A25, which did not reach the main non-breeding area in the North Atlantic Ocean and both left and returned to the island earlier than the others, on 31 May and 15 December, respectively (Fig. 1).

At-sea distribution

During the breeding period, Trindade petrels used a vast oceanic area in the southwest Atlantic Ocean, from 20° S to 36° S and 42° W to 30° W. During the non-breeding period, two important areas were identified: Area 1—east of Trindade Island from 4° S to 22° S and 28° W to 4° W; Area 2—a wide area inside the North Atlantic Subtropical Gyre from 24° N to 10° N and 51° W to 38° W, which was the main non-breeding area (Fig. 2).

Two different migratory patterns were detected among the petrels tracked during a single non-breeding period, and all patterns were recorded in both males and females (Fig. S1). The patterns could be classified as follows: petrels moving eastward to area 1 after leaving the vicinity of the island and then to area 2 ($n=19$); and birds travelling across the western tropical Atlantic directly from Trindade Island to area 2 ($n=4$). One petrel (A25) exhibited anomalous behaviour, moving to area 1 without travelling to the North Atlantic Ocean and returning the breeding area earlier, as described above. Thus, area 1 was stopover site, used frequently along the pathway to reach area 2, thus regarded as the main non-breeding area (Fig. 2; Suppl. Material: Fig. S1).

Isotopic niche

The mean SI values in blood were $\delta^{13}\text{C} = -16.1 \pm 0.4\text{‰}$ and $\delta^{15}\text{N} = 12.4 \pm 0.5\text{‰}$, and those in feathers were $\delta^{13}\text{C} = -15.8 \pm 0.3\text{‰}$ and $\delta^{15}\text{N} = 14.0 \pm 1.6\text{‰}$. The isotopic niche varied between breeding and non-breeding periods (Fig. 3A). Trindade petrels exhibited isotopic niches with similar widths in the two periods, although

Table 1 Migratory schedule of Trindade petrels, *Pterodroma arminjoniana*, from Trindade Island, South Atlantic Ocean, breeding during the austral fall- winter season

ID	Sex	Deployment date	Departure from the breeding site		Arrival at the main non-breeding area		Departure from the main non-breeding area		Arrival at the breeding site		Recovery date	No. of days tracked during breeding	
			Year 1	Year 2	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2		Year 1	Year 2
002	F	18 Jun 2014	05 Aug	–	17 Oct	–	26 Jan	–	07 Feb	–	24 Mar 2015	48	26
004	F	19 Jun 2014	24 Jul	18 Jul	01 Sep	09 Aug	19 Jan	07 Jan	28 Jan	17 Jan	04 Apr 2017	35	29
005	F	19 Jun 2014	08 Aug	21 Jul	26 Nov	17 Nov	14 Feb	30 Jan	19 Feb	10 Feb	12 Feb 2016	51	152
011	M	30 Jun 2014	16 Aug	31 Jul	26 Aug	21 Aug	03 Feb	–	14 Feb	–	02 Feb 2016	47	188
012	F	30 Jun 2014	07 Aug	28 Jun	15 Nov	19 Nov	02 Feb	11 Jan	10 Feb	2 Feb	05 Feb 2016	38	138
013	F	10 Jul 2014	17 Aug	–	04 Nov	–	07 Feb	–	17 Feb	–	30 Mar 2015	38	16
016	F	10 Jul 2014	02 Aug	–	22 Oct	–	25 Jan	–	10 Feb	–	03 Apr 2017	23	125
A23	M	02 Feb 2016	11 Jul	–	08 Oct	–	16 Jan	–	26 Jan	–	25 Mar 2017	160	58
A25	F	02 Feb 2016	31 May	–	*	–	*	–	15 Dec	–	30 Jan 2017	119	46
A26	F	03 Feb 2016	10 Jul	–	03 Nov	–	30 Jan	–	14 Feb	–	12 Apr 2017	158	55
A27	F	03 Feb 2016	10 Jul	–	24 Oct	–	16 Jan	–	07 Feb	–	12 Apr 2017	158	64
A28	F	03 Feb 2016	22 Jun	–	07 Oct	–	12 Jan	–	11 Feb	–	29 Mar 2017	140	46
A30	M	05 Feb 2016	19 Jun	–	08 Oct	–	03 Jan	–	16 Jan	–	25 Mar 2017	135	48
A31	M	05 Feb 2016	04 Aug	–	09 Oct	–	26 Jan	–	11 Feb	–	29 Mar 2017	181	22
A34	M	05 Feb 2016	04 Aug	–	14 Oct	–	15 Jan	–	03 Feb	–	07 Feb 2017	181	4
A35	F	08 Feb 2016	20 Jun	–	07 Oct	–	19 Jan	–	03 Feb	–	10 Apr 2017	133	66
A36	M	08 Feb 2016	09 Aug	–	08 Oct	–	30 Jan	–	14 Feb	–	12 Apr 2017	183	19
A38	M	08 Feb 2016	16 Jul	–	13 Nov	–	30 Jan	–	10 Feb	–	29 Mar 2017	159	23
A40	M	09 Feb 2016	08 Jul	–	27 Nov	–	09 Feb	–	16 Feb	–	03 Apr 2017	150	17
A41	F	09 Feb 2016	09 Jul	–	11 Nov	–	25 Jan	–	08 Feb	–	05 Apr 2017	151	25

*The petrel A25 did not reach the main non-breeding area in the North Atlantic Ocean

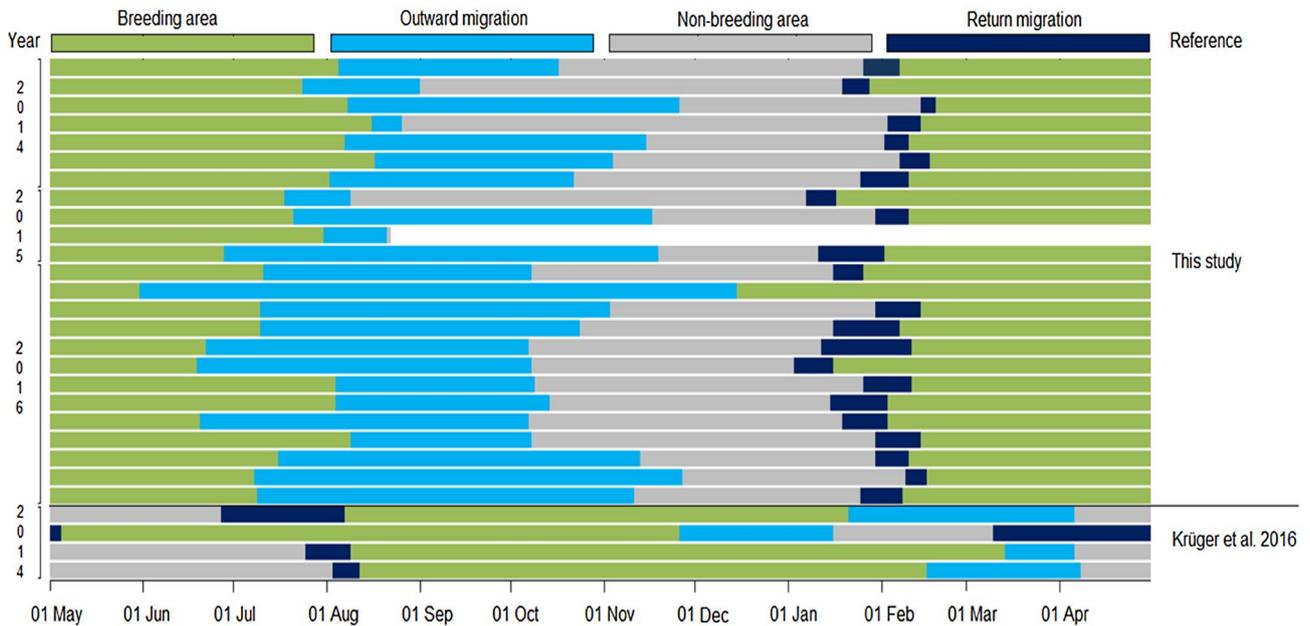


Fig. 1 Phenological schedules of Trindade petrels, *Pterodroma arminjoniana*, from Trindade Island, South Atlantic Ocean, breeding during the austral fall- winter season (this study), and those breeding

during the austral spring–summer season (Krüger et al. 2016). The outward migration includes the stopover period

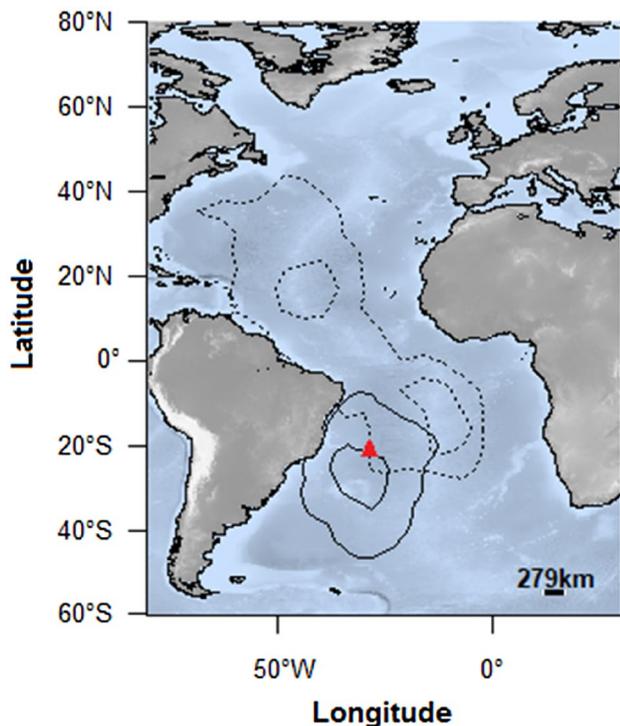


Fig. 2 Utilisation distributions (50 and 95%) of Trindade petrels, *Pterodroma arminjoniana*, tracked year-round. Trindade Island is indicated with a red triangle. Solid line = breeding; dashed line = non-breeding

the overlap was small between them (Fig. 3A). During the breeding period, $\delta^{13}\text{C}$ values were more variable, while during the non-breeding period, $\delta^{15}\text{N}$ was more variable (Fig. 3A). Petrels that exhibited different migratory patterns also showed different isotopic niches (Fig. 3B). Although the similar $\delta^{13}\text{C}$ values, Trindade petrels that travelled directly to the main non-breeding area showed lower $\delta^{15}\text{N}$ values than those petrels that used the area east of Trindade Island (Area 1), without niche overlap (Fig. 3B).

Individual consistency

Trindade petrels showed different levels of individual consistency in at-sea distribution during successive breeding periods (Fig. 4). All individuals exhibited overlap of their home ranges (95% UD) and core area (50% UD) in consecutive years. The only exception was the petrel 013 which exhibited no overlap in his core area (Table 2). The estimation of the repeatability between the parameters tested varied from ($R=0$) for $\delta^{13}\text{C}$ values and latitude to high ($R>0.3$) for longitude, although not statistically significant (Table 3). During the breeding period, the percent

of overlap (HR) ranged from 0 to 93% for the 50% UD and 29 to 90% for the 95% UD. Similarly, the BA index was highly variable (0–0.3 for the 50% UD and 0.4–0.8 for the 95% UD).

Discussion

The present study demonstrates that petrels on Trindade Island nesting during the first laying peak, maintain their breeding schedules from January to August. Throughout the annual cycle, Trindade petrels used three important areas, performed two different migratory strategies, and varied their isotopic niche. In consecutive breeding seasons, although there has been overlap of at-sea distribution, significant consistency was not found in any parameter tested. However, given the small sample size to evaluate the isotopic niche and because was not possible to compare the at-sea distribution between the two entire breeding periods, results should be evaluated carefully. Furthermore, both geolocators and stable isotopes are coarse scale techniques for habitat and niche, respectively.

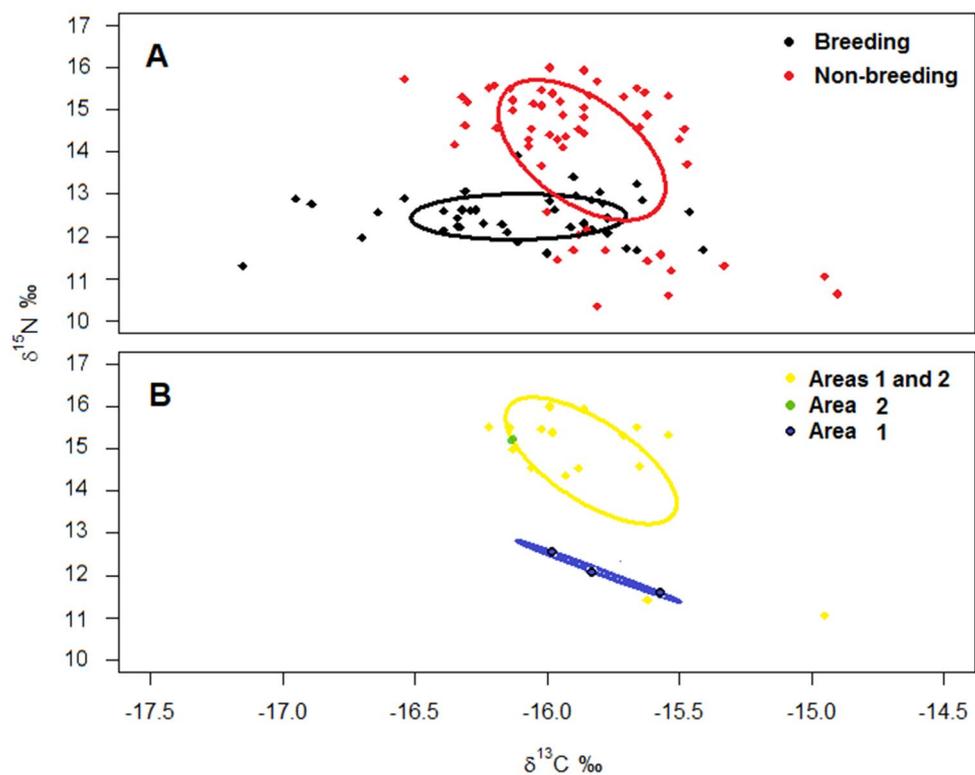
The tracking data for Trindade petrels captured while breeding in October demonstrates that they arrive on Trindade Island in August and also maintain their breeding schedules, although this is based on only four tracked individuals (Krüger et al. 2016). While austral spring–summer breeders arrive at the non-breeding area between January and April, remaining from March to August (Krüger et al. 2016), the fall–winter breeders investigated in the current study begin to arrive at non-breeding areas in August and stay until February. That way, when austral spring–summer breeders arrive on Trindade Island in August, the fall–winter breeders are at the end of their breeding, and vice versa in February, which can avoid crossing between these groups and keeps them temporally segregated during almost the entire annual cycle. Despite the absence of phenotypic and genotypic differences (Brown et al. 2010, 2011), the fall–winter and spring–summer breeders exhibit different isotopic niches, apparently as an adjustment to seasonal variations in environmental conditions (Leal et al. 2017). Temporal segregation has been demonstrated to be a factor leading to sympatric speciation in other seabirds breeding under different environmental conditions, such as *Oceanodroma/Hydrobates* storm-petrels (Smith and Friesen 2007; Bolton et al. 2008). Therefore, although the boundaries between Trindade petrel groups seem to be diffuse, it is possible that in the future this temporal segregation has evolutionary implications.

During the breeding period, Trindade petrels use a vast oceanic area bordered by the oligotrophic South Atlantic Subtropical Gyre (Peterson and Stramma 1991), where resources are expected to be scarce and patchily

Table 2 Percent of overlap (HR) and Bhattacharyya's affinity (BA) index of consecutive breeding home range and core area (95 and 50% UD), the distance between the Trindade Island and the centroid 5% UD (km), and the distance of centroids between consecutive years in repeat-tracked Trindade petrels, *Pterodroma arminjoniana*

ID	Year 1	Year 2	Distance between island and centroid (km)		Distance of centroids between years (km)	HR 50% UD (%)		BA 50%UD		HR 95% UD (%)		BA 95%UD	
			Year 1	Year 2		Year 1 on 2	Year 2 on 1	Year 1 on 2	Year 2 on 1	Year 1 on 2	Year 2 on 1		
Breeding			809 ± 188	875 ± 231	510 ± 299	36 ± 21	39 ± 15	0.2 ± 0.1	0.2 ± 0.1	54 ± 17	64 ± 16	0.6 ± 0.1	0.6 ± 0.1
002	24° S 29° W	22° S 35° W	654	412	632	2	3	0.0	0.0	42	46	0.3	0.3
004	27° S 30° W	27° S 29° W	99	750	746	72	40	0.3	0.3	87	46	0.7	0.7
005	26° S 29° W	27° S 27° W	228	635	778	64	28	0.2	0.2	77	32	0.6	0.6
011	27° S 29° W	27° S 30° W	99	746	750	93	46	0.3	0.3	90	41	0.7	0.7
012	24° S 37° W	25° S 36° W	151	904	873	40	42	0.2	0.2	54	55	0.6	0.6
013	25° S 27° W	23° S 18° W	915	569	1196	0	0	0.0	0.0	65	32	0.3	0.3
016	24° S 27° W	28° S 27° W	445	470	885	60	29	0.2	0.2	78	36	0.6	0.6
A23	23° S 35° W	30° S 33° W	804	672	1146	25	44	0.2	0.2	46	75	0.6	0.6
A25	31° S 28° W	21° S 25° W	1153	1197	443	4	8	0.0	0.0	33	60	0.4	0.4
A26	27° S 31° W	28° S 33° W	227	768	940	19	70	0.2	0.2	29	97	0.6	0.6
A27	29° S 32° W	28° S 40° W	790	1009	1392	16	34	0.1	0.1	32	79	0.5	0.5
A28	26° S 24° W	26° S 27° W	300	827	673	39	70	0.3	0.3	52	66	0.6	0.6
A30	28° S 29° W	32° S 31° W	485	857	1315	40	43	0.2	0.2	64	77	0.7	0.7
A31	25° S 32° W	24° S 32° W	111	597	504	42	25	0.2	0.2	65	64	0.7	0.7
A35	25° S 32° W	27° S 34° W	299	597	892	23	33	0.1	0.1	41	64	0.5	0.5
A36	25° S 31° W	27° S 34° W	374	555	892	55	58	0.3	0.3	59	87	0.8	0.8
A38	29° S 30° W	25° S 34° W	596	972	719	25	60	0.2	0.2	33	84	0.6	0.6
A40	30° S 28° W	25° S 31° W	630	1086	555	17	57	0.2	0.2	35	96	0.6	0.6
A41	32° S 28° W	27° S 41° W	1376	1308	1415	7	17	0.0	0.0	28	64	0.4	0.4

Fig. 3 Isotopic niches (in δ -space) of Trindade petrels, *Pterodroma arminjoniana*, based on standard ellipse areas corrected for small sample sizes (SEAc) using Stable Isotope Bayesian Ellipses in R (SIBER). **A** Breeding versus non-breeding period; **B** different migratory patterns, where area 1 = east of Trindade Island; area 2 = North Atlantic Subtropical Gyre. Whole-blood stable isotope values (in ‰) were corrected using the equation provided in Cherel et al. (2014) to allow comparison between isotopic niches during breeding and non-breeding periods using blood and feathers, respectively



distributed (Weimerskirch 2007). In line with our expectations, Trindade petrels did not presented individual consistency in foraging areas used, despite the overlap in their home and core range in consecutive breeding seasons. The same vast oceanic area is used by both sexes (Leal et al. 2017), by spring–summer breeders (Krüger et al. 2016) and was maintained even in an eight-year interval (Leal et al. 2017). During breeding, central-place foraging forces seabirds to perform foraging activity with visits to the breeding site (Orlans and Pearson 1979) on a period of high energetic demand (Whittow 2001). These requirements in an oligotrophic environment seem to require Trindade petrels to search for food over vast oceanic areas, performing long foraging trips of up to 18 days, travelling more than 10,000 km to reach areas up to 3335 km from the colony (Leal et al. 2017). Thus, it is possible that the maintenance of this same foraging area during breeding is a consequence of the central-place foraging that constrain the foraging trips in time and space, in addition to the need to explore vast areas for obtaining food for self-maintenance and offspring. Although the similar at-sea distributions, there was no consistency in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of individuals in consecutive breeding seasons. Resource availability and (un)predictability can vary over time in the same habitats, which might partly explain the variation in diet or isotopic niche (Ceia et al. 2014). This could be important for tropical species due to the oligotrophic and

ephemeral distribution of their main prey in comparison to those of temperate or polar seabirds or those that nest adjacent to fronts or upwelling areas (Phillips et al. 2018). Interannual changes in seabird diet have previously been found even in tropical environments with oceanographic stability (Le Corre et al. 2003). Thus, the absence of consistency in the isotopic niche of Trindade petrels may be a consequence of the variations in prey availability associated with the limitation at the search for food imposed by the central-place foraging.

When no longer constrained by breeding duties, Trindade petrels exhibited two migratory patterns. Most petrels ($n=19$) used stop-over sites before reaching the main non-breeding area at the centre of the North Atlantic Ocean, with a few birds ($n=4$) travelling straight to the main non-breeding area. On the other hand, all Trindade petrels breeding during spring–summer exhibited a unique migratory pattern, showing routes associated with warmer waters over the continental ridge and travelling directly to the main non-breeding area (Krüger et al. 2016), while this route was used by only four birds (16%) among the fall-winter breeders. The core non-breeding area in the centre of the North Atlantic had been characterised by intense use, i.e. 19 out of 20 petrels with complete tracking during the non-breeding period, and where birds stayed for longer. Similar to Trindade petrels, black-browed albatrosses from South Georgia are consistent in their terminal non-breeding area, although

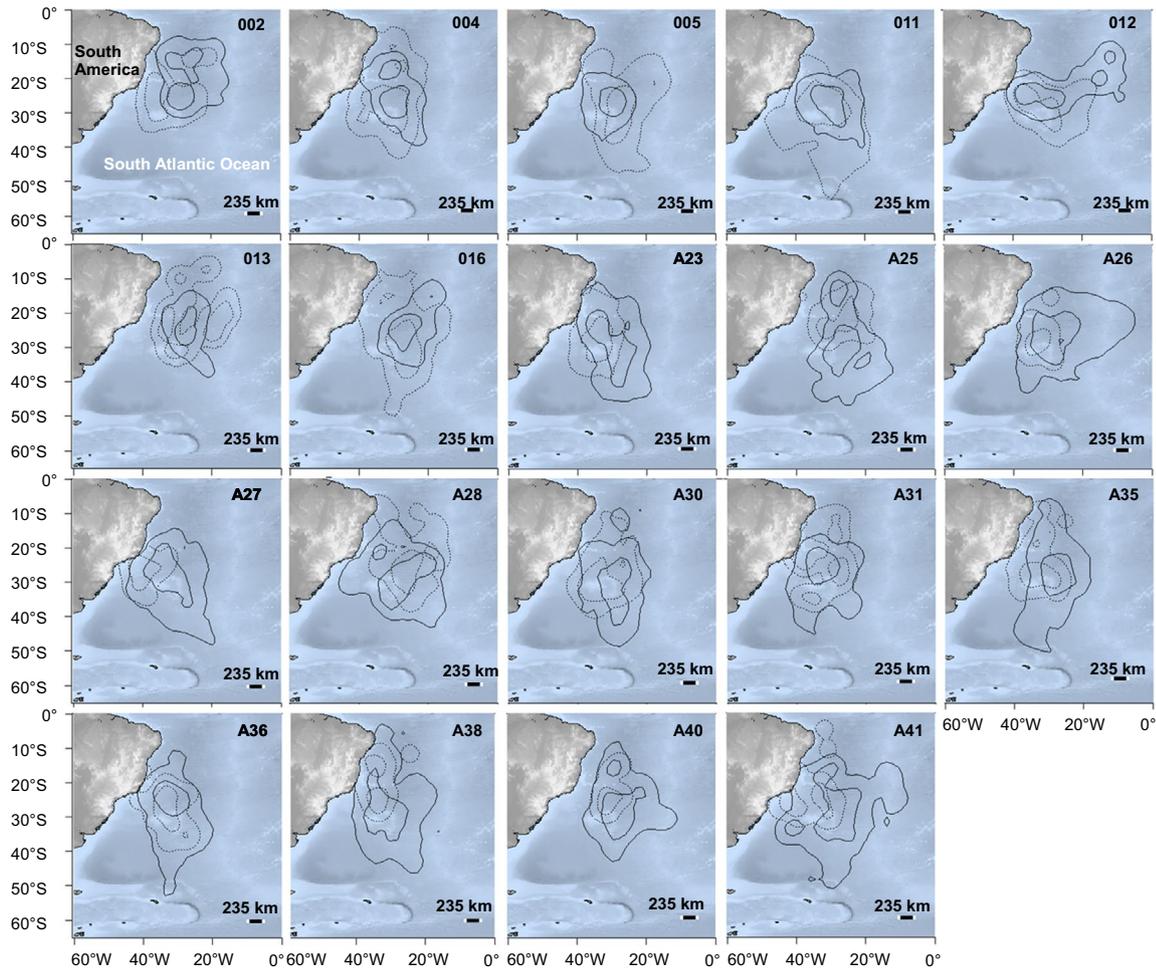


Fig. 4 Utilisation distributions (50 and 95%) of Trindade petrels, *Pterodroma arminjoniana*, tracked during two consecutive breeding periods. Solid line = year 1; dashed line = year 2

Table 3 Individual repeatability (*R*) of the variables ‘distance of centroid to the island (km)’, ‘latitude of centroid’ and ‘longitude of centroid’ (both in decimal degrees), ‘ $\delta^{15}\text{N}$ ’ and ‘ $\delta^{13}\text{C}$ ’ values, based on the variance components of the GLMMs for Trindade petrels, *Pterodroma arminjoniana*, breeding on Trindade Island, South Atlantic Ocean

Model/period	<i>n</i>	<i>R</i>	CI	<i>P</i>
Breeding				
$\delta^{13}\text{C} \sim \text{Sex} + \text{Stage} + (1 \text{ID})$	8	0.00	[0, 0.71]	0.50
$\delta^{15}\text{N} \sim \text{Sex} + \text{Stage} + (1 \text{ID})$	8	0.14	[0, 0.77]	0.39
Distance $\sim \text{Sex} + \text{Year} + (1 \text{ID})$	19	0.12	[0, 0.57]	0.4
Lat $\sim \text{Sex} + \text{Year} + (1 \text{ID})$	19	0.00	[0, 0.48]	1
Long $\sim \text{Sex} + \text{Year} + (1 \text{ID})$	19	0.41	[0, 0.74]	0.06

not in the use of staging sites (Phillips et al. 2005). For instance, long-tailed skuas, *Stercorarius longicaudus*, may show flexibility in its itineraries, apparently as an adjustment to environmental changes (van Bemmelen et al. 2017). At the same way, in response to variation in food availability and environmental conditions, Cory’s shearwater, *Calonectris borealis*, and little shearwater, *Puffinus assimilis*, seem to change their migratory routes to non-breeding areas in consecutive years (Dias et al. 2011; Zajková et al. 2017). As the South Atlantic Ocean presents seasonal patterns of sea surface temperature (Bouali et al. 2017), variations in the environmental conditions may be influencing the choice of the migratory strategy used by Trindade petrels. Moreover, it is possible that the development of individual migration patterns becomes fixed according to experience (Guilford et al. 2011; Péron and Grémillet 2013; de Grissac et al. 2016). Thus, it is not surprising that immature seabirds may

show high variability in their movement patterns (Thiers et al. 2014; de Grissac et al. 2016) and different distributions from adults (Weimerskirch et al. 2006; Péron and Grémillet 2013). The reproductive effort may also influence the migratory behaviour, e.g. failed breeders may change their migration schedules and depart earlier than successful breeders (Phillips et al. 2005; Bogdanova et al. 2011; Hedd et al. 2012; Pastor-Prieto et al. 2019), staying partially or completely segregated from active breeders (Phillips et al. 2005; González-Solís et al. 2008; Reid et al. 2014). Among the Trindade petrels tracked in this study, a single individual (A25) did not migrate to the main non-breeding area in the North Atlantic Ocean. This petrel was sampled without the presence of eggs or chicks in early February, when the birds are arriving at Trindade Island, and although it presented behaviour similar to breeding petrels returning frequently to the colony, left the island long before others, and thus it may be an immature non-breeder or have experienced breeding failure. Tracking other immature Trindade petrels is highly desirable. Overall, the variation in environmental conditions and, consequently, in food availability as well as individual experience and breeding success could contribute to the variability of the routes and strategies of Trindade petrels towards North Atlantic non-breeding grounds.

Despite travelling via different routes, except a single bird, all Trindade petrels reached the same main non-breeding area inside the North Atlantic Subtropical Gyre. Some gadfly petrels may disperse among various remote non-breeding sites and even share areas with different species (Ramos et al. 2017). However, both spring–summer (Krüger et al. 2016) and fall–winter breeders (this study) migrate to a common unique non-breeding area that is underused by other gadfly petrel species (Ramos et al. 2017, but see Ventura et al. 2020 for Desertas petrel, *Pterodroma deserta*). Direct or indirect competition for limited resources implies a cost in terms of reduced foraging efficiency, which could promote segregation in habitat use by different populations and species in time (Friesen et al. 2007), space (González-Solís et al. 2008) or diet (Wilson 2010). The environmental conditions also seem to play a relevant role in the determination of the non-breeding distribution of seabird populations (Fort et al. 2012). The main non-breeding and breeding areas have large sizes and are located within subtropical gyres, where waters are oligotrophic and conditions vary slightly (Lalli and Parsons 1997). This demonstrates the Trindade petrel ability to deal with an oligotrophic environment using the strategy of search food throughout vast oceanic areas.

Isotopic niches varied between breeding and non-breeding periods and among birds with different migratory patterns. The limited isoscapes available (McMahon et al. 2013) suggest similar baseline values among the breeding and non-breeding grounds of Trindade petrels, not using intensively areas with contrasting isotopic values. This

makes comparison between breeding and non-breeding niches reliable. Breeding Trindade petrels showed more variable $\delta^{13}\text{C}$ values than were observed during the non-breeding period. Breeding petrels also may vary their trophic niche, or even their distribution inside the vast foraging area used, what appears to be an adjustment to the different demands of this period (Leal et al. 2017). In contrast, non-breeding Trindade petrels use a common main non-breeding area, and it is possible that all birds undergo moulting in the same area, resulting in more homogeneous $\delta^{13}\text{C}$ values than when they are breeding. On the other hand, petrels during the non-breeding period showed more variable and overall higher $\delta^{15}\text{N}$ values than when breeding. After breeding, seabirds can change their diet or broaden their trophic niche since they are no longer central-place foragers and are free to select their habitat or preferred prey (Cherel et al. 2007; Karnovsky et al. 2008; Hedd et al. 2010). Thus, Trindade petrels are free to continually travel across vast oceanic areas searching for food and can select preferred prey, such as larger prey, which often increases $\delta^{15}\text{N}$ values.

In summary, our results indicate that the Trindade petrels may maintain their breeding schedules, may change their isotopic/trophic niche throughout their annual cycle and may use different routes to reach a unique non-breeding area. In addition, individual consistency could not be demonstrated with methods and parameters tested. Maybe high resolution techniques could reach different conclusions, but the species seems prone to nest desertion with deployment of larger tracking devices (authors, pers. obs.). However, further studies are needed to understand if the individuals maintain their behaviour for longer periods, as well as its causes and consequences.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-021-03938-4>.

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Availability of data and material Tracking data are available in the BirdLife Seabird Tracking database.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval This study was authorised under license number 22697-5 (SISBIO—Sistema de Autorização e Informação em Biodiversidade). This article does not contain any studies with human participants. All applicable international, national, and institutional guidelines for the care of animals found stranded alive were followed. We did not conduct experiments with animals.

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