

Short- and long-term consistency in the foraging niche of wandering albatrosses

Filipe R. Ceia · Richard A. Phillips · Jaime A. Ramos · Yves Cherel · Rui P. Vieira · Pierre Richard · José C. Xavier

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Abstract The wandering albatross (*Diomedea exulans*) is regarded as a generalist predator, but can it be consistent in its foraging niche at an individual level? This study tested short- and long-term consistency in the foraging niche in terms of habitat use, trophic level and, by inference, prey selection. Fieldwork was carried out at Bird Island, South Georgia, in May–October 2009, during the chick-rearing period. Blood (plasma and cells) and feathers for stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were sampled from 35 adults on their return from a foraging trip during which they carried stomach temperature, activity and global positioning system loggers. Results suggest short-term consistency in foraging niche in relation to both oceanic water mass and trophic level, and long-term consistency in use of habitat. Consistent differences between individuals partly reflected sex-specific habitat preferences. The

proportion of consistent individuals (i.e., with a narrow foraging niche) was estimated at c. 40 % for short-term habitat and trophic level (prey) preferences and 29 % for longer-term habitat preference, suggesting this is an important characteristic of this population and potentially of pelagic seabirds in general. Foraging consistency was not related to body condition or level of breeding experience; instead, it may reduce intraspecific competition.

Introduction

According to optimal foraging theory, animals should distribute themselves to maximize their foraging efficiency, which, during breeding, is dependent upon the ability to find food within the range of accessible habitat (MacArthur and Pianka 1966; Schoener 1971). Foraging strategies of individual birds can differ substantially (Fritz et al. 2003; Weimerskirch 2007) and vary according to factors such as sex, age, morphology and individual specialization (Bolnick et al. 2003), resulting in the exploitation of different niches by individuals, which could be consistent over time. The degree of variation among individuals in these characteristics has implications for susceptibility to anthropogenic threats, for example from fisheries, and other environmental changes and hence for the persistence of populations and species (Phillips et al. 2009; Dias et al. 2010).

Many populations of generalist predators are now known to include individual specialists, reflecting the often extensive intrapopulation variation in foraging niche (Bolnick et al. 2003; Woo et al. 2008; Matich et al. 2010). However, few studies have quantified the proportion of specialists in a population and whether this is constant over time. Typically, individual specialization is

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F. R. Ceia (✉) · J. A. Ramos · R. P. Vieira · J. C. Xavier
Department of Life Sciences, Faculty of Sciences and
Technology, IMAR-CMA-Institute of Marine Research,
University of Coimbra, 3004-517 Coimbra, Portugal
e-mail: ceiafilipe@zoo.uc.pt

R. A. Phillips · J. C. Xavier
British Antarctic Survey, Natural Environment Research
Council, High Cross Madingley Road, Cambridge CB3 0ET, UK

Y. Cherel
Centre d'Etudes Biologiques de Chizé, UPR 1934 du CNRS,
BP 14, 79360 Villiers-en-Bois, France

P. Richard
Laboratoire Littoral, Environnement et Sociétés, UMR 6250 du
CNRS-Université de La Rochelle, 2 Rue Olympe de Gouges,
17000 La Rochelle, France

calculated from a “snapshot” analysis of diet or gut contents and suffers from stochastic sampling effects. This reflects the logistical and other constraints involved in obtaining repeated diet samples, especially when working with seabirds. However, with the development of new approaches, including the use of data-logging devices and stable isotope analysis (SIA), there has been a recent increase in studies of consistency in habitat use and diet (Bearhop et al. 2006; Weimerskirch 2007; Votier et al. 2010). This represents an important development, as an improved understanding of variation in foraging patterns within and among individuals is crucial for determining the major factors contributing to population change (see Bolnick et al. 2003 for a review). Niche variation among individuals, and hence the degree of intraspecific competition, has major ecological and evolutionary implications (Araújo et al. 2007). For example, Weimerskirch et al. (1997) and Jaeger et al. (2009) found differences in habitat use between sexes of wandering albatrosses *Diomedea exulans* (Linnaeus, 1758) during the chick-rearing period and the non-breeding season, respectively. Differences in behaviour between age classes were also found for the wandering albatross (Weimerskirch et al. 2007; Lecomte et al. 2010), suggesting that sex, age and body mass are important factors to take into account when evaluating niche consistency.

During the breeding season, wandering albatrosses are central-place foragers, travelling great distances (up to 15,000 km) in a single foraging trip (Xavier et al. 2004; Weimerskirch et al. 2007). Given their wide foraging range, they are ideal indicator species for defining resource hotspots, which could be incorporated into networks of marine protected areas (Louzao et al. 2010). Wandering albatrosses are top marine predators, feeding mainly on fish and cephalopods and, to a lesser extent, on carrion (Xavier et al. 2004; Weimerskirch et al. 2005). However, nothing is known about short- or long-term consistency in the foraging niche of individuals. Here, we evaluate individual consistency in feeding habitat and diet during the breeding season in a wild population of wandering albatrosses of known sex and age. Specifically, we used SIA of multiple tissues with different turnover rates, together with the deployment of logger devices and conventional diet samples, to test for short- and long-term consistency in habitat use ($\delta^{13}\text{C}$) and trophic level ($\delta^{15}\text{N}$) within and among individuals. Using this combination of methods, we addressed the following questions: (1) Are individuals consistent in trophic level and foraging habitat over short- and long-term periods? (2) What is the degree of individual foraging consistency within the population? (3) Can foraging consistency be related to age or body mass index? (4) Is there sexual variation in the consistency of the foraging niche?

Materials and methods

Fieldwork was carried out on wandering albatrosses rearing chicks at Bird Island, South Georgia (54°S 38°W), in May–October 2009, during the austral winter. A total of 35 breeding adults (18 males and 17 females) were sampled in May (six), June (six), July (six), August (eight), September (six) and October (three). The age was known for 28 individuals ringed as chicks, and birds were sexed from plumage and morphology (Tickell 1968). Three types of devices—GPS, activity recorders and, when possible, a stomach temperature probe—were deployed on birds attending chicks and were removed at the end of the subsequent foraging trip (details of the devices below). Blood samples (1 ml blood from the tarsal vein) and 6–8 randomly selected breast feathers were collected from each bird on recapture, for later SIA. Stomach contents were also sampled by water-offloading, following Xavier et al. (2004). Bill length and width were measured, and birds were weighed before the foraging trip. The procedure of capture, deployment or retrieval of devices, collection of samples and release took 10–15 min. No birds were sampled more than once, nor a sample taken from the partner of a previously sampled bird. The blood samples were separated into plasma and red blood cells (RBC) using a centrifuge (15 min at 3,000 rpm), stored frozen and later freeze-dried and homogenized prior to SIA.

Diet sampling and analysis

Food samples collected from each individual reflected recent prey ingestions. Following Xavier et al. (2004), regurgitates were separated into oil and solid mass. Each component (cephalopod, fish, crustacean and carrion) was weighed separately, and individual prey items were identified to species where possible. Identification of cephalopod beaks followed Xavier and Cherel (2009) and that of fish otoliths followed Hecht (1987), Williams and McEldowney (1990) and Smale et al. (1995). Fresh squid and fish (with beaks and otoliths attached, respectively) were stored frozen for SIA.

Stable isotope analysis (SIA)

Stable isotope analyses of carbon and nitrogen can provide useful insights into seabird diet, and they are a natural and crucial tool in contemporary studies of the ecological niche (Newsome et al. 2006). Carbon stable isotope value ($\delta^{13}\text{C}$) mainly reflects the consumers’ foraging habitat, while nitrogen stable isotope value ($\delta^{15}\text{N}$) is mainly used to define consumers’ trophic position. Moreover, different tissues have different turnover rates and therefore can reflect temporal changes in trophic position and foraging

habitat (i.e., a change in isotopic niche; reviewed in Rubenstein and Hobson 2004; Bond and Jones 2009). We analysed $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) in plasma, RBC and breast feathers from each adult and in prey items obtained from stomach contents. Plasma and RBC retain information on diet (carbon source and trophic level) from a few days prior to sample collection to the previous 3–4 weeks, respectively (Hobson and Clark 1993; Votier et al. 2010). Hence, the isotopic signature of plasma is the representative of the food and feeding ecology of the birds during their single tracking trip (Jaeger et al. 2010b). Breast feathers represent diet during the moult, since feather keratin is metabolically inert after synthesis, which in wandering albatrosses occurs during the non-breeding period (Jaeger et al. 2009). Therefore, based on SIA of different tissues from the same bird, we are able to test for short- and long-term consistency in individual foraging niche.

Lipids are depleted in ^{13}C relative to whole tissues and are removed from plasma using successive rinses in a 2:1 chloroform/methanol solution (Cherel et al. 2005b). The low lipid content of whole blood (or RBC) does not typically require lipid extraction (Cherel et al. 2005a). Prior to SIA, feathers were cleaned of surface contaminants using successive rinses in a 2:1 chloroform/ether solution, air-dried and then ground to fine powder in a freezer mill operating at liquid nitrogen temperature. Flesh samples from regurgitates were stored frozen, then freeze-dried and ground to fine powder before SIA. Lipids were extracted from flesh using a 2:1 chloroform/methanol solution.

Nitrogen and carbon isotope ratios were determined by a continuous-flow isotope ratio mass spectrometer (Delta V Advantage, Thermo Scientific) coupled to an elemental analyser (Flash EA1112, Thermo Scientific). Approximately 0.3 mg of each sample was combusted in a tin cup for the simultaneous determination of nitrogen and carbon isotope ratios. Results are presented in the usual δ notation based on the PeeDee Belemnite (PDB) for carbon and atmospheric N_2 (AIR) for nitrogen. Replicate measurements of internal laboratory standards (acetanilide) indicate measurement errors <0.1 ‰ both for $\delta^{13}\text{C}$ and for $\delta^{15}\text{N}$.

Tracking data collection and analysis

In total, 35 breeding adults of both sexes were fitted concurrently with a GPS (19.5 g, $46.5 \times 32 \times 18.5$ mm, Earth and Ocean, Kiel, Germany) and activity recorder (MK 7, 3.6 g, $18 \times 18 \times 6.5$ mm, British Antarctic Survey, Cambridge) before they departed for a single foraging trip at sea. The GPS loggers have an accuracy of 10 m; they were attached to feathers in the mantle region with Tesa tape and recorded the position of the albatross every 20 min. GPS data were obtained from 30 of the 35 loggers

deployed and were used to determine latitude and longitude at the point of inflection, which was the location furthest from the colony and assumed to represent the point at which the bird began its return, maximum distance from colony (km), and trip duration (days). The activity recorders check for saltwater immersion every 3 s, record every change of state from ‘wet’ (indicating sitting on the sea surface) to ‘dry’ (indicating flying or on land) that lasts ≥ 6 s and were used to determine the percentage of time spent flying in each trip and by daylight and darkness (civil twilight). Additionally, 26 of these birds were also equipped with a stomach temperature logger (51.5 g in total including the spring, Earth and Ocean, Kiel, Germany), of which 22 were retrieved and downloaded successfully. These incorporated a temperature sensor with a relative resolution of 0.1 °C, inside a cylindrical titanium housing of $150 \text{ mm} \times 19 \text{ mm}$ in diameter. The anchoring spring hinders the regurgitation of the probe while the bird is at sea. Loggers record temperature changes in the proventriculus, with sudden drops in temperature indicating ingestion of cold prey (Wilson et al. 1992). Housings were specifically designed to be large enough to sample temperature for most of the stomach volume and not become covered by food after ingestion of only a few prey items (Wilson et al. 1995). Temperature was logged every 20 s and was used to estimate the number of prey ingestions. Changes in temperature were bimodal; those of the first peak (<4 °C) usually reflect ingestion of water or very small prey (Weimerskirch et al. 2007) and were excluded from the analyses. The total mass of the three devices was below 3 % of adult mass (0.6–1.0 %), as recommended by Phillips et al. (2003; but see Passos et al. 2010).

Data analysis

We regressed stable isotope ratios in plasma on those in RBC to obtain an index of consistency in carbon source (water mass) and trophic level. Since $\delta^{13}\text{C}$ has a trophic component, we used the residuals of the relationship with $\delta^{15}\text{N}$ in the same tissue (plasma: $F_{1,33} = 15.2$, $P < 0.001$, $r = 0.562$; RBC: $F_{1,33} = 14.8$, $P < 0.001$, $r = 0.556$) to determine the degree of short-term repeatability in $\delta^{13}\text{C}$ (between RBC and plasma), independently of trophic effects (Bearhop et al. 2006; Votier et al. 2010). Each tissue has a different turnover rate and therefore represents different timescales. However, integration of prey isotopes into body tissues is a continuous, dynamic process, and the analyses of short-term consistency were performed using the same blood sample, separated into plasma and RBC, which could lead to a temporal overlap in the synthesis of these tissues. Longer-term foraging consistency was estimated by regressing stable isotope values in RBC with those in feathers. We used again the residuals to correct the

trophic component associated with $\delta^{13}\text{C}$ by regressing these values upon $\delta^{15}\text{N}$ signatures in feathers ($F_{1,33} = 27.2$, $P \ll 0.001$, $r = 0.672$). Overlap between samples in this comparison will be negligible as wandering albatrosses do not replace breast feathers during breeding. Residuals from the significant relationships were used as a measure of consistency of each individual. We used the absolute value of the residuals for statistical analyses and assumed that values greater or less than the median represented, respectively, more or less consistent individuals. However, to establish the degree of foraging consistency within the population, we cautiously assumed residual values below 0.2 as consistent individuals. This is a conservative estimation, as 0.2 was always lower than the median of the residuals for all individuals. One outlier that had a significant influence on the results for $\delta^{13}\text{C}$ (1.0 in Fig. 2b) even after data transformation was excluded from further analyses. Although birds were sampled from May to October, month had no influence in the stable isotope and consistency values. This was expected because this study was carried out only during the chick-rearing period. Therefore, data for the 6-month period were pooled to analyse foraging consistency patterns.

Mixing models can be used to estimate the relative proportion of different dietary sources. We adopted a Bayesian multisource stable isotope mixing model (SIAR: Stable Isotope Analyses in R; Parnell et al. 2010) to estimate ranges of probable contributions of each prey to the diet of each individual and hence its specialization on particular prey items. All possible combinations of each source contribution were examined using the isotope values from plasma and RBC for each bird, and the mean and standard deviation of each of the four main prey sources. There are no diet–blood fractionation factors available for wandering albatrosses; hence, we used the average values generally accepted for birds: 1 and 3 ‰ enrichment for carbon and nitrogen, respectively (Kelly 2000; Caut et al. 2009), as adopted in studies of other seabirds (Hobson and Clark 1992; Bearhop et al. 2002; Cherel et al. 2005a). A standard deviation of ± 0.5 ‰ was taken into account, considering potential differences in fractionation factors among species.

Table 1 Comparison of stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in plasma, red blood cells (RBC) and feathers of male and female wandering albatrosses

Tissue type	All birds ($n = 35$)	Males ($n = 18$)	Females ($n = 17$)	T value	P
$\delta^{13}\text{C}$ (‰)					
Plasma	-20.0 ± 0.6	-20.2 ± 0.5	-19.9 ± 0.5	1.9	0.070
RBC	-20.1 ± 0.5	-20.3 ± 0.3	-19.9 ± 0.6	2.1	0.042
Feathers	-17.5 ± 0.8	-17.8 ± 0.8	-17.1 ± 0.6	3.3	0.002
$\delta^{15}\text{N}$ (‰)					
Plasma	14.3 ± 0.4	14.3 ± 0.5	14.4 ± 0.4	0.4	0.673
RBC	14.1 ± 0.3	14.1 ± 0.2	14.2 ± 0.4	0.9	0.385
Feathers	16.0 ± 0.3	16.0 ± 0.7	16.0 ± 0.6	0.3	0.774

Values are mean \pm SD.
Significant results in bold

We used the standard residuals of the relationship between body mass (at initial capture) and bill length ($F_{1,33} = 42.3$, $P \ll 0.001$, $r = 0.749$) to estimate the body mass index (BMI) of all sampled birds, an index primarily reflecting body lipid reserves (Zwarts et al. 1996).

All data were tested for departures from a normal distribution; trip duration was \log_{10} -transformed, maximum distance to colony and number of prey ingestions overall were square-root-transformed, and all proportions were arcsine-transformed. If no transformation normalized the data, non-parametric tests were used. The proportion of consumed prey types were compared between males and females and between the more and the less consistent individuals, using ANOVA (for data obtained with the SIAR mixing model) and Mann–Whitney U test (for data from the stomach contents). All statistical tests were performed with Statistica 7.0.

Results

General diet and stable isotope analysis

The diet of the 35 wandering albatrosses sampled was composed mainly of fish (59.4 % by mass) and cephalopods (38.4 %), a small amount of carrion (2.2 %) and trace crustaceans (0.02 %). No significant differences were found between sexes in the proportion of each of these components. Similarly, mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of plasma, which provides an indication of recent meals, did not differ significantly between sexes (Table 1). However, there were significant differences between sexes in $\delta^{13}\text{C}$, but not in $\delta^{15}\text{N}$, in RBC and feathers; females showed enrichment in ^{13}C , suggesting some sexual segregation of foraging habitat.

The most frequent fresh prey found in stomach samples from wandering albatrosses were Patagonian toothfish *Dissostichus eleginoides* (Smitt, 1898), blue antimora *Antimora rostrata* (Günther, 1878), giant warty squid *Kondakovia longimana* (Filippova, 1972) and glass squid *Taonius* sp. B (Voss) (Steenstrup, 1861). Mean $\delta^{15}\text{N}$ was much higher in the two fish species, *D. eleginoides* and

A. rostrata, than in the squid, reflecting their higher trophic position (Table 2). As expected, $\delta^{15}\text{N}$ in the blood of wandering albatrosses was higher than in their prey.

SIAR mixing model indicated that based on blood and prey isotope values, fish was the largest component (56.4 %) in the diet of the sampled birds, followed by cephalopods (43.6 %), proportions that were similar to those from analysis of regurgitates. According to the

model, some individuals obtained a much greater proportion of their diet from cephalopods than others (Fig. 1). Although the credibility intervals overlapped, the model revealed a high degree of heterogeneity in the proportion of the four main prey types in the diet of different individuals, with the exception of *A. rostrata* that was relatively constant for all individuals. Several individuals (e.g., 2, 12, 28, 31 and 34 in Fig. 1) appeared to have specialized on particular types of prey. This was unrelated to sex, as there were no significant differences in the proportions of the four prey items in the diet estimated by the model between males and females.

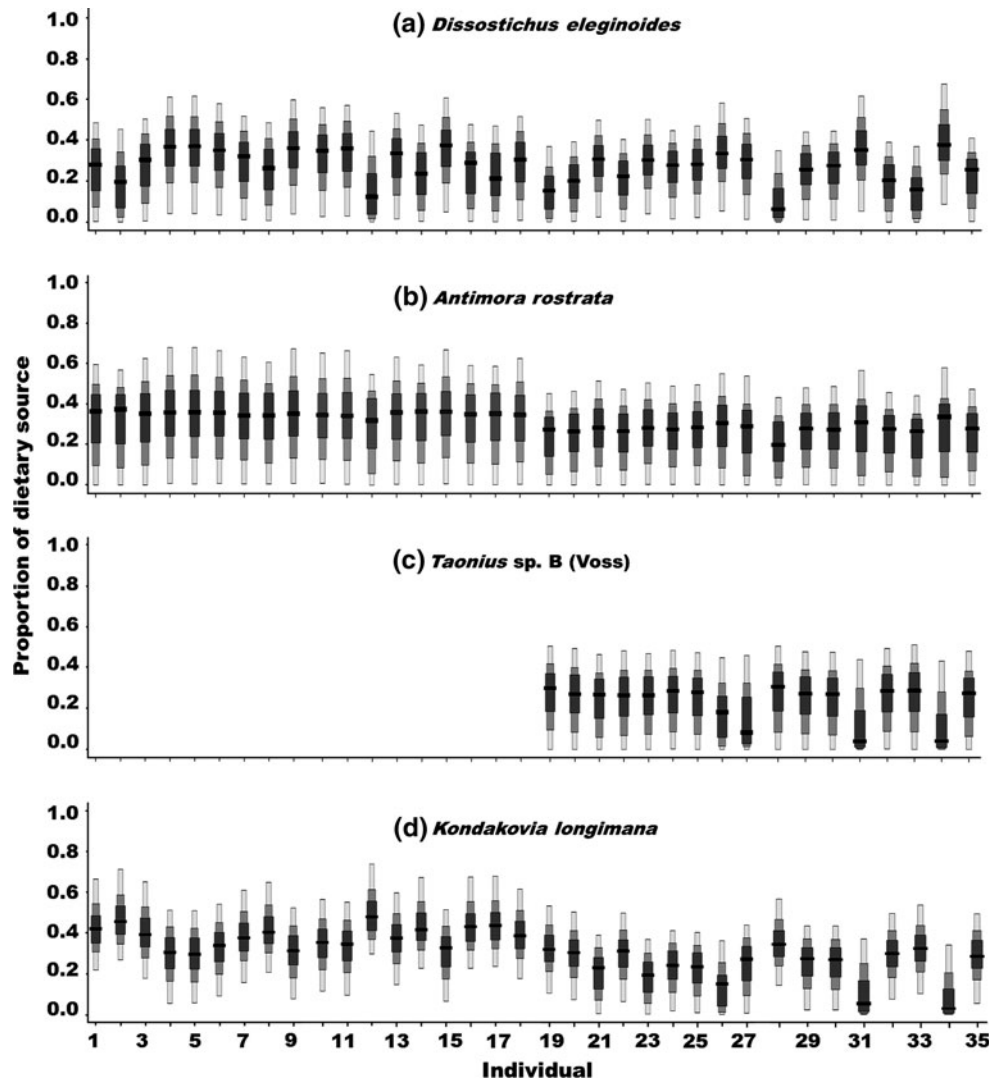
Table 2 Stable isotopic signature of carbon and nitrogen and C/N mass ratio (means \pm SD) of the four main prey species recorded in regurgitates collected from wandering albatrosses breeding in Bird Island

Prey species	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C/N
<i>D. eleginoides</i>	5	-19.9 ± 0.4	13.8 ± 0.9	3.17 ± 0.06
<i>A. rostrata</i>	4	-20.7 ± 0.3	12.2 ± 0.8	3.13 ± 0.02
<i>Taonius</i> sp. B (Voss)	2	-21.4 ± 0.3	11.3 ± 0.8	3.14 ± 0.02
<i>K. longimana</i>	4	-22.5 ± 0.8	8.7 ± 1.2	3.12 ± 0.07

Short- and long-term consistency in foraging niche

Strong significant positive relationships were found in residual $\delta^{13}\text{C}$ (hereafter $\delta^{13}\text{C}$) and in $\delta^{15}\text{N}$ between RBC and plasma of individual adults ($F_{1,33} = 35.0$, $P \ll 0.001$, $r = 0.718$, and $F_{1,33} = 18.7$, $P < 0.001$,

Fig. 1 Range of possible proportions of **a** *D. eleginoides*, **b** *A. rostrata*, **c** *Taonius* sp. B (Voss) and **d** *K. longimana* in the diet of individual wandering albatrosses during chick-rearing. Decreasing bar widths represent 5, 50, 75 and 95 % Bayesian credibility intervals computed by Stable Isotope Analysis in R (SIAR; Parnell et al. 2010)



$r = 0.601$, respectively; Fig. 2). These results suggest short-term foraging consistency within individuals in relation to both the use of particular water masses and trophic level (\approx relative proportion of fish and squid). Males and females showed similarly significant correlations between RBC and plasma in $\delta^{13}\text{C}$ (males: $n = 18$, $P = 0.001$, $r = 0.710$; females: $n = 17$, $P = 0.003$, $r = 0.674$) and in $\delta^{15}\text{N}$ (males: $n = 18$, $P = 0.007$, $r = 0.614$; females: $n = 17$, $P = 0.006$, $r = 0.641$).

A significant positive relationship was found between feathers and RBC in $\delta^{13}\text{C}$ ($F_{1,33} = 8.6$, $P = 0.006$, $r = 0.454$), which suggests consistent longer-term use of specific water masses (Fig. 2e). However, when split by sex, this relationship was not significant, although stronger in males (males: $n = 18$, $P = 0.089$, $r = 0.413$; females: $n = 17$, $P = 0.223$, $r = 0.312$). No relationship was found between $\delta^{15}\text{N}$ in feathers and RBC in the pooled sample ($F_{1,33} = 0.7$, $P = 0.405$, $r = 0.145$) or in separate analyses for each sex (males: $n = 18$, $P = 0.940$, $r = 0.019$; females: $n = 17$, $P = 0.274$, $r = 0.281$). Hence, birds apparently did not show long-term consistency in trophic level.

Individual foraging consistency

Absolute value of residuals for the level of consistency in tissue isotope values within individuals ranged from 0 to 1 for short and long terms (Fig. 2b, d, f). The median values were 0.22 for short term (plasma vs. RBC) in $\delta^{13}\text{C}$, 0.31 for short term (plasma vs. RBC) in $\delta^{15}\text{N}$ and 0.31 for long term (RBC vs. feathers) in $\delta^{13}\text{C}$, and the percentage of individuals that were consistent (based on the absolute value of residual of <0.2 ; see “Methods”) was 42.9, 37.1 and 28.6 %, respectively. These results suggest that around 40 % of the individuals in this population show short-term consistency in both prey carbon source (foraging habitat) and trophic level, and 29 % of individuals showed long-term consistency in foraging habitat. Despite a slight tendency for greater short-term consistency in foraging habitat use of males ($\delta^{13}\text{C}$) and in trophic level of females ($\delta^{15}\text{N}$), no differences were found between sexes for the absolute values of residuals for short term (plasma vs. RBC; Fig. 2b, d). However, significant differences were found between sexes for the absolute values of residuals for long term in $\delta^{13}\text{C}$ (RBC vs. feathers; T test: $df = 33$, T value = 2.6, $P = 0.014$), with males showing higher consistency in the longer term than females (Fig. 2f).

Linking foraging niche consistency with diet, foraging behaviour, age and body mass index

The proportion of fish and cephalopods found in the diet of wandering albatrosses collected using conventional

sampling and the proportion of the four main prey items estimated by the SIAR mixing model applied to prey and blood values did not differ significantly between the more and the less consistent individuals in $\delta^{15}\text{N}$ (Table 3). From the 35 individuals, 14 consumed more than 80 % fish (fish specialists), 13 consumed more than 80 % cephalopods (squid specialists) and eight combined the consumption of both these prey groups (generalists) during their last trip, which suggests that individuals specialized in specific prey items during trips. However, results from SIA of plasma and RBC suggest that the less consistent individuals changed the proportion of prey items consumed during preceding weeks.

Trip duration in the last foraging trip was significantly greater in individuals that showed greater consistency in $\delta^{13}\text{C}$ in RBC and plasma (Table 4). No differences in trip characteristics were found between sexes. Absolute value of residuals for short term in $\delta^{13}\text{C}$ was negatively correlated with trip duration ($F_{1,32} = 5.0$, $P = 0.032$, $r = -0.368$; Fig. 3). However, when split by sex, this relationship was significant only in males (males: $n = 18$, $P < 0.001$, $r = -0.592$; females: $n = 16$, $P = 0.525$, $r = -0.172$). No relationships were found between foraging consistency in trophic level and any foraging behaviour parameters recorded during the previous trip.

No relationships were found between the age or body mass index (BMI) and their level of short- and long-term consistency in $\delta^{13}\text{C}$ (age: $F_{1,25} = 0.0$, $P = 0.835$, $r = 0.042$ and $F_{1,26} = 2.7$, $P = 0.115$, $r = 0.305$, respectively; BMI: $F_{1,32} = 0.8$, $P = 0.382$, $r = 0.158$ and $F_{1,33} = 0.0$, $P = 0.946$, $r = 0.012$, respectively) or short-term consistency in $\delta^{15}\text{N}$ (age: $F_{1,26} = 0.6$, $P = 0.436$, $r = 0.153$; BMI: $F_{1,33} = 0.1$, $P = 0.817$, $r = 0.041$).

Discussion

Our results suggest that there is a high level of short-term consistency within individuals in the use of particular water masses and in trophic level (proportion of fish vs. cephalopods) in wandering albatrosses during chick-rearing at South Georgia. Correlations in stable isotope ratios between different tissues (RBC and plasma for short term, and feathers and RBC for long term) can highlight particular details of seabird ecology, such as the degree of foraging specialization. Previous work has shown foraging specialization in a large range of species, mainly reflecting high site fidelity or a consistent pattern in foraging behaviour (data loggers: Weimerskirch et al. 2005; Cook et al. 2006; Elliott et al. 2009; stable isotopes: Cherel et al. 2007; Anderson et al. 2009; Jaeger et al. 2010a; or in combination: Phillips et al. 2009; Weimerskirch et al.

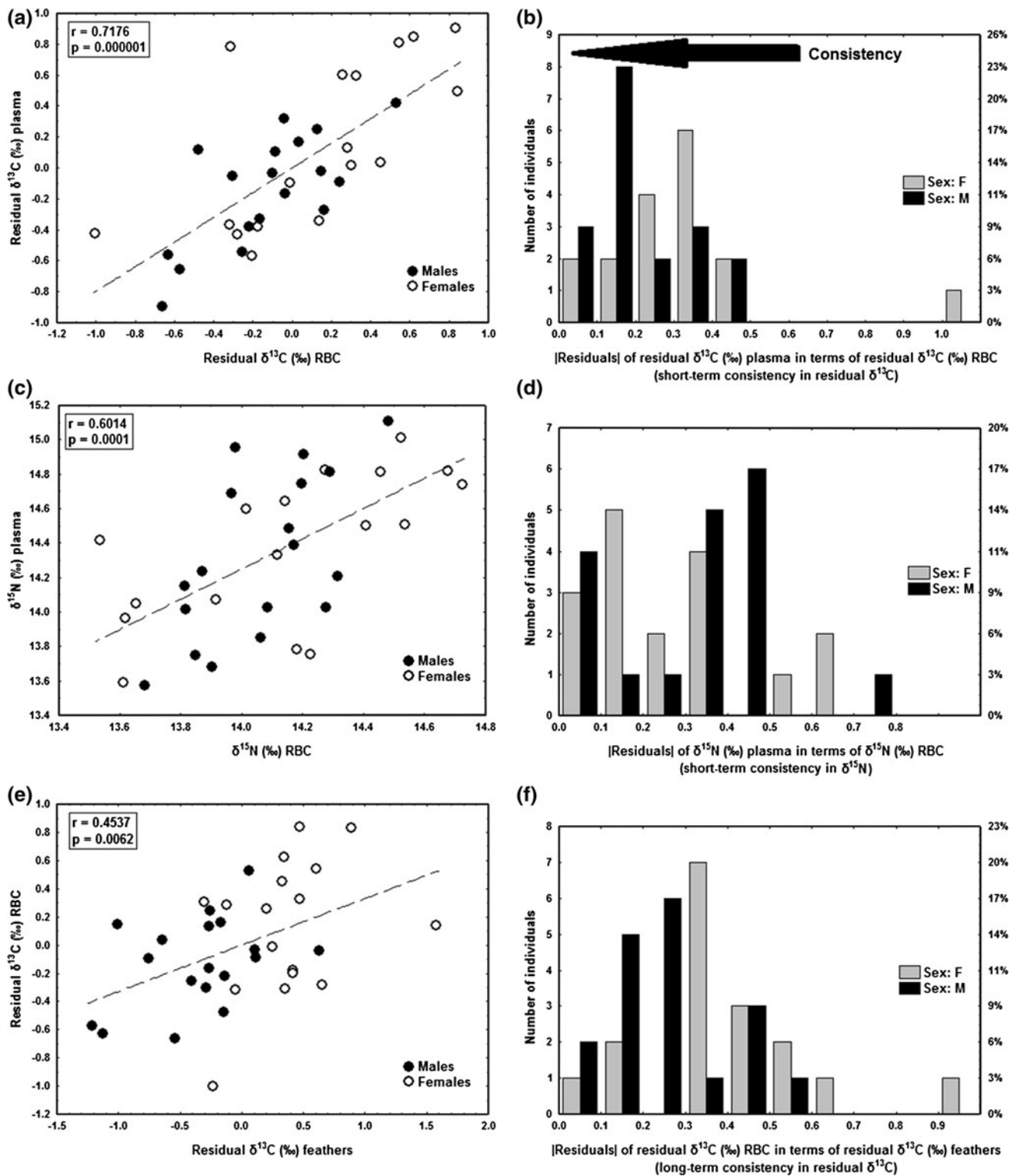


Fig. 2 Relationships between **a** residual $\delta^{13}\text{C}$ values in red blood cells (RBC) and plasma, **c** $\delta^{15}\text{N}$ values in RBC and plasma and **e** residual $\delta^{13}\text{C}$ values in feathers and RBC of wandering albatrosses. Histograms indicate the number of males and females showing varying degrees of consistency in residual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values

b short-term consistency in residual $\delta^{13}\text{C}$, **d** short-term consistency in $\delta^{15}\text{N}$ and **f** long-term consistency in residual $\delta^{13}\text{C}$ ($n = 35$). Individual wandering albatrosses with consistency values below 0.2 were considered as consistent

Table 3 Proportion of fish and cephalopods (based on the stomach contents) and the four main prey species (based on the SIAR mixing model) recorded in regurgitates collected from wandering albatrosses

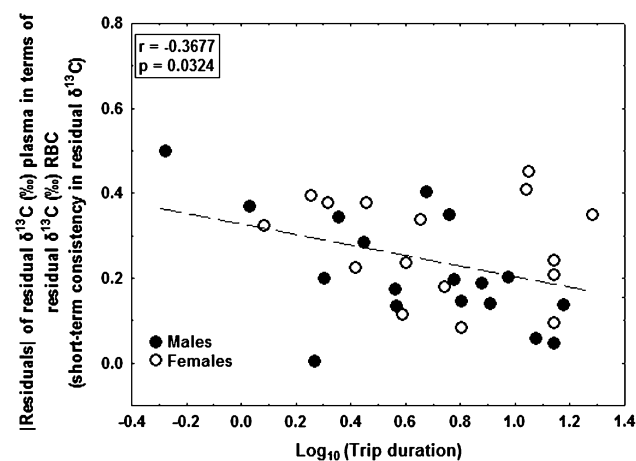
	All birds ($n = 35$)	More consistent (short term in $\delta^{15}\text{N}$; $n = 17$)	Less consistent (short term in $\delta^{15}\text{N}$; $n = 18$)
Fish (%)	50.9 \pm 43.2 (0–100)	55.5 \pm 40.2 (0–100)	46.6 \pm 46.6 (0–100)
Cephalopods (%)	44.9 \pm 43.2 (0–100)	43.2 \pm 41.3 (0–100)	46.5 \pm 46.1 (0–100)
<i>D. eleginoides</i> (%)	26.8 \pm 5.8 (16–39)	27.7 \pm 6.4 (18–39)	26.0 \pm 5.2 (16–35)
<i>A. rostrata</i> (%)	29.5 \pm 4.3 (22–36)	29.6 \pm 4.3 (23–36)	29.5 \pm 4.5 (22–36)
<i>Taonius</i> sp. B (Voss) (%)	11.9 \pm 12.5 (0–27)	12.6 \pm 12.4 (0–27)	11.2 \pm 13.0 (0–27)
<i>K. longimana</i> (%)	31.7 \pm 9.3 (14–50)	30.1 \pm 9.6 (14–48)	33.3 \pm 9.0 (19–50)

Values are mean \pm SD (minimum–maximum)

Table 4 Comparison of foraging parameters of wandering albatrosses showing high or low levels of short-term consistency in residual $\delta^{13}\text{C}$ (foraging habitat) and for all birds

	All birds	More consistent (short term in residual $\delta^{13}\text{C}$)	Less consistent (short term in residual $\delta^{13}\text{C}$)	<i>T</i> value	<i>P</i>
Trip duration (days)	6.4 \pm 5.0 (35)	7.6 \pm 4.4 (17)	5.1 \pm 5.3 (18)	−2.4	0.020
Latitude (point of inflection)	−47.3 \pm 7.2 (30)	−46.2 \pm 7.2 (13)	−48.1 \pm 7.3 (17)		
Longitude (point of inflection)	−44.0 \pm 8.1 (30)	−48.1 \pm 9.6 (13)	−42.6 \pm 6.1 (17)		
Maximum distance from colony (km)	1,071 \pm 793 (30)	1,338 \pm 738 (13)	867 \pm 794 (17)	−1.8	0.087
Percentage of time spent flying overall	62.4 \pm 14.1 (35)	58.3 \pm 12.1 (17)	66.3 \pm 15.2 (18)	1.8	0.080
Percentage of time spent flying during daylight	69.3 \pm 14.6 (35)	64.6 \pm 15.3 (17)	73.7 \pm 12.9 (18)	2.0	0.059
Percentage of time spent flying during darkness	57.6 \pm 17.4 (35)	53.5 \pm 14.2 (17)	61.4 \pm 19.7 (18)	1.5	0.142
Number of prey ingestions overall	16.3 \pm 14.1 (22)	25.9 \pm 14.6 (10)	8.3 \pm 7.0 (12)	−3.5	0.003
Number of prey ingestions per day	3.3 \pm 1.6 (22)	3.2 \pm 1.4 (10)	3.3 \pm 1.8 (12)	0.2	0.856

Some data transformed before analysis. Civil twilight (cut-off between daylight and darkness). Values are mean \pm SD (sample size). Significant results in bold

**Fig. 3** Relationship between \log_{10} (trip duration) and short-term consistency in residual $\delta^{13}\text{C}$ of wandering albatrosses [estimated from the absolute value of the residuals between red blood cells (RBC) and plasma in residual $\delta^{13}\text{C}$ values; $n = 34$]

2009; Votier et al. 2010). However, as far as we are aware, ours is the first study to estimate the proportion of consistent individuals within a population.

showing high or low levels of consistency in $\delta^{15}\text{N}$ (diet and distribution) and for all birds

Wandering albatrosses are top predator species consuming varying proportions of prey according to local or regional resource availability (review in Cherel and Klages 1998; Xavier et al. 2004; Weimerskirch et al. 2005). However, focusing at an individual level, perceptible preferences in diet were found within the study population at South Georgia. Analyses of regurgitates showed that several birds fed mainly (>80 % of prey items by mass) on fish or on cephalopods in their last trip (42.9 and 34.3 %, respectively), whereas others (22.8 %) consumed both prey in different proportions. SIAR mixing model estimated that fish were the most consumed resource in the short term based on analysis of stable isotope ratios in blood (Fig. 1). However, the relative contribution to the diet from different prey species varied considerably among individuals. For some individuals, the proportion of cephalopods was higher. According to Bolnick et al. (2007), the use of a narrow range of resources by each individual (specialization) might minimize intraspecific competition. Specialization in particular prey items does not seem to be related to sex in wandering albatrosses from South Georgia,

because no differences were found between males and females in ratio of the components found in regurgitates or in the diet predicted by the SIAR mixing model, although Weimerskirch et al. (1997) showed that males deliver fish more often than females at Crozet Islands.

A high, positive correlation in $\delta^{13}\text{C}$ (corrected for trophic fractionation) between RBC and plasma (Fig. 2a) indicates that individual wandering albatrosses foraged in isotopically similar areas in the short term. However, it does not mean necessarily that individuals show fine-scale site fidelity, but that they consistently use the same water mass. $\delta^{15}\text{N}$ values were also strongly correlated in RBC and plasma (Fig. 2c), suggesting short-term consistency in trophic level. Such relationships, however, are partly attributable to temporal overlap in the synthesis of plasma and RBC (Votier et al. 2010). Nevertheless, the correlation in $\delta^{13}\text{C}$ between feathers and RBC indicates that individuals exhibit longer-term consistency in habitat use that persists over many months, since $\delta^{13}\text{C}$ in RBC represents the breeding period (at least a few weeks before sampling) and that in body feathers represents the previous non-breeding season. This relationship was stronger in males than in females (corroborated by the relative proportion of consistent individuals; Fig. 2f). These results are in accordance with differences in $\delta^{13}\text{C}$ values in feathers, which suggest sexual segregation in habitat during the non-breeding season (Weimerskirch and Wilson 2000; Jaeger et al. 2009; Phillips et al. 2009). Presumably, males are more likely to forage consistently in isotopically similar water masses throughout the year, whereas females may shift their distribution further to the north, to exploit warmer waters during the non-breeding season, which may reduce competition for resources (Weimerskirch and Wilson 2000; Phillips et al. 2011).

A significant degree of foraging consistency within a population does not necessarily mean that all individuals are consistent. Our estimation of the proportion of individuals that were consistent was conservative, by selecting only those with very small residuals (absolute value <0.2) from the fitted regression line. Still, there were high proportions of individuals that showed short-term consistency in habitat use (43 %) and trophic level (37 %) and longer-term consistency in habitat use (29 %). Therefore, this characteristic may be widespread in this population and related species. In this context, we explored relationships between short-term foraging consistency and several other characteristics, including diet and foraging behaviour recorded using data loggers in order to clarify this phenomenon. In terms of diet, our results shows that of the more consistent individuals, around 42 % were specialists on fish and 29 % on cephalopods, and 29 % were generalists. Consistent generalists must consume similar proportions of all prey items over time in order to show similar

isotope values. On the other hand, the great majority (78 %) of individuals classified as generalists nevertheless seemed to have specialized on a particular prey category during the last trip, based on the single conventional diet sample collected on their return. However, these individuals must, in fact, be generalists that fed on different prey during previous weeks. This underlines the problem in determining the ratio of specialists to generalists from a “snapshot” diet analysis, particularly as a generalist predator might have ingested one prey species immediately prior to capture and collection of stomach contents (Warburton et al. 1998). In contrast, stable isotopes are much more suitable for analysing temporal diet consistency from days to weeks or months, depending on the tissue sampled (Araújo et al. 2007).

Similar to other studies of marine predators, we found differences in foraging behaviour at an individual level (see Weimerskirch 2007 for review), in this case, linked to foraging consistency. Presumably, the significant correlation of trip duration with short-term consistency in $\delta^{13}\text{C}$ (plasma vs. RBC; Fig. 3) simply reflects a greater proportion of RBC that was synthesized during the trip in birds that have been at sea (feeding on the same carbon source/in the same water mass) for longer. On the other hand, birds that made short trips would have produced more of their RBC during previous trips where they could have been feeding somewhere different. Nevertheless, it is equally possible that differences in trip duration could indicate foraging behaviour segregation between the more and the less consistent individuals in foraging habitat (mainly males), corroborated by the significant correlation of trip duration with short-term consistency in $\delta^{13}\text{C}$, as a result of more targeted specialization. At least around 43 % of birds were consistent and selective in foraging habitat during longer trips. Performing shorter trips at smaller spatial scales, the immediate prey encounter rate is expected to play a major role and prey predictability is assumed to be smaller in contrast with longer trips (Weimerskirch 2007), as birds travelling longer distances to find food may consistently seek specific water masses, in order to refill their condition and compensate for travelling longer distances. Consistency in foraging behaviour during the chick-rearing period has rarely been investigated in the past, but previously reported for other species (Quillfeldt et al. 2008; Woo et al. 2008; Jaeger et al. 2010a). Thus, short-term consistency in foraging habitat of wandering albatrosses, particularly males, during the chick-rearing period could be related to the regularity that many birds perform longer trips to specific water masses. This suggestion is in accordance with the fact that many seabird species concentrate their efforts on persistent and predictable food sources (Weimerskirch et al. 2005; Woo et al. 2008; Votier et al. 2010).

The adaptive significance of the foraging specializations observed in wandering albatrosses remains unclear. Some studies clearly demonstrate that intrapopulation variation is due to age or sex, while others attribute it to individual preference (Bolnick et al. 2003). Despite no significant differences in absolute value of residuals in the short term between sexes, the slight tendency of higher short-term consistency in habitat use by males, as well as significant differences in $\delta^{13}\text{C}$ values in RBC, could reflect sexual segregation in habitat use during chick-rearing (Weimerskirch et al. 1997; this study). This has also been inferred for the non-breeding season from differences in stable isotope ratios in feathers (Jaeger et al. 2009; this study) and considered to reflect habitat specialization, possibly driven by competitive exclusion of females by males (Phillips et al. 2011). However, the variation in short-term consistency in the foraging niche was unrelated to sex, indicating that other factors were responsible. We found no evidence that foraging niche consistency was related with age and hence probably not with experience. However, we sampled only breeding adults (11–33 years) and not immature birds. Weimerskirch et al. (2005, 2007) and Lecomte et al. (2010) found differences in behaviour between age classes and suggested that younger birds may have different foraging strategies, perhaps resulting from a poorer knowledge of the foraging habitat. However, there was apparently no difference in foraging success of young compared with older birds. Moreover, in the present work, there was no relationship between foraging consistency and body mass index, suggesting that the specialists and generalists have similar levels of body condition.

Foraging consistency in wandering albatrosses is not a consequence of experience in adult breeders and does not appear to confer an advantage in terms of body condition, so it remains unclear why there are such a high number of consistent individuals within the population. The advantages may relate to improvements in several traits such as reproductive success, chick food delivery rates, or chick condition, which requires further investigation. It may also contribute to reduce intraspecific competition among individuals.

In summary, we observed that (1) wandering albatrosses from South Georgia showed high short-term consistency at both habitat use and trophic level and long-term consistency in habitat use; (2) the degree of individual consistency within the population was around 40 % in the short-term habitat use and trophic level and 29 % in the long-term habitat use; (3) foraging consistency was not related to age or body mass index and so is not a consequence of experience nor does it affect body condition; and (4) consistency in habitat use tended to be greater over long time periods in males than in females. As well as documenting the existence of individual specialization, further studies

should explore the relative incidence in different populations, species and communities, and the implications for fecundity and survival.

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