Stable isotopes demonstrate intraspecific variation in habitat use and trophic level of non-breeding albatrosses

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The non-breeding period is critical for restoration of body condition and self-maintenance in albatrosses, yet detailed information on diet and distribution during this stage of the annual cycle is lacking for many species. Here, we use stable isotope values of body feathers ($\delta^{13}C$, $\delta^{15}N$) to infer habitat use and trophic level of non-breeding adult Grey-headed Albatrosses Thalassarche chrysostoma ($n = 194$) from South Georgia. Specifically, we: (1) investigate intrinsic drivers (sex, age, previous breeding outcome) of variation in habitat use and trophic level; (2) quantify variation among feathers of the same birds; and (3) examine potential carry-over effects of habitat use and trophic level during the non-breeding period on subsequent breeding outcome. In agreement with previous tracking studies, $\delta^{13}C$ values of individual feathers indicate that non-breeding Grey-headed Albatrosses from South Georgia foraged across a range of oceanic habitats, but mostly in subantarctic waters, between the Antarctic Polar Front and Subtropical Front. Sex differences were subtle but statistically significant, and overlap in the core isotopic niche areas was high (62%); however, males exhibited slightly lower $\delta^{13}C$ and higher $\delta^{15}N$ values than females, indicating that males forage at higher latitudes and at a higher trophic level. Neither age nor previous breeding outcome influenced stable isotope values, and we found no evidence of carry-over effects of non-breeding habitat use or trophic level on subsequent breeding outcome. Repeatability among feathers of the same individual was moderate in $\delta^{13}C$ and low in $\delta^{15}N$. This cross-sectional study demonstrates high variability in the foraging and migration strategies of this albatross population.

Keywords: intraspecific variation, migration, Procellariiformes, seabirds, Southern Ocean, Thalassarche chrysostoma.

Individual seabirds within apparently generalist populations may differ in their resource use and foraging strategies (Phillips et al. 2017), with potential implications for community structure, evolutionary ecology and conservation management (Bolnick et al. 2003, Votier et al. 2010, Phillips et al. 2017). Variation among individuals is often attributed to the influence of intrinsic drivers, including sex (Bearhop et al. 2006, Phillips et al. 2011), age (Votier et al. 2017, Clay et al. 2018) and breeding status (Jaeger et al. 2014, Clay et al. 2016). However, most studies of intraspecific variation in seabird foraging have focused on the breeding period and less is known
about the non-breeding period, when birds are free from reproductive constraints associated with incubation or provisioning, and can disperse widely.

There is increasing evidence for sex differences in seabird foraging strategies during the non-breeding period, including variation in diet, distribution and other aspects of behaviour (Bearhop et al. 2006, Phillips et al. 2009, De Felipe et al. 2019). These differences are thought to arise from size-related behavioural dominance and competitive exclusion (typically of the larger sex over the smaller) or habitat and dietary specialization (Phillips et al. 2017). The degree of segregation in foraging ecology may be a function of sexual size dimorphism (SSD; Phillips et al. 2011), although this appears to apply more to high-latitude than to tropical species (Mancini et al. 2013), and studies have also demonstrated sex-related foraging strategies in species with reduced SSD (e.g. Lamacchia et al. 2019). Less attention, however, has been paid to changes in foraging behaviour and distribution with age, despite some evidence that it may be an important driver (Phillips et al. 2017). Indeed, a recent study of non-breeding Wandering Albatrosses Diomedea exulans from South Georgia found evidence of age-related changes in activity patterns and stable isotope proxies for habitat use (Clay et al. 2018). There is also evidence that non-breeding Wandering Albatrosses in the Indian Ocean forage further south with age (Jaeger et al. 2014).

Stable isotope analyses have been validated as a powerful tool to study the foraging ecology of seabirds, including albatrosses (Cherel et al. 2000), and stable isotope values of adult feathers are routinely used to investigate diet and distribution during the non-breeding period (Phillips et al. 2009, Cherel et al. 2013). This is because moult rarely overlaps with breeding, and feathers are metabolically inert once grown and hence preserve an isotopic record of diet at the time of formation (Hobson & Clark 1992, Bearhop et al. 2002, Catry et al. 2013). Stable isotope values of carbon ($^{13}$C/$^{12}$C, expressed as $\delta^{13}$C) and nitrogen ($^{15}$N/$^{14}$N, expressed as $\delta^{15}$N) in tissues reflect those of prey during the period of synthesis. $\delta^{15}$N values increase in a stepwise manner by $\sim 3$–5‰ at each trophic level, whereas $\delta^{13}$C values increase less with trophic level ($\sim 0.5$–1‰) but can be used to infer foraging habitat (DeNiro & Epstein 1981, Hobson & Clark 1992, Bearhop et al. 2002). In the marine environment, this includes the relative reliance on an inshore vs. offshore, benthic vs. pelagic diet, and latitude or water mass where a gradient exists, such as in the Southern Ocean (Quillfeldt et al. 2005, 2010, Cherel & Hobson 2007, Jaeger et al. 2010).

The aim of this cross-sectional study is to provide detailed information on the foraging ecology of Grey-headed Albatrosses Thalassarche chrysotoma from South Georgia during the non-breeding period. The population at South Georgia constitutes the largest population at any island group (50% globally; Poncet et al. 2017). This species exhibits male-biased SSD (Phillips et al. 2004), is among the longest-lived birds (Catry et al. 2006) and is a population-level generalist (Mills et al. 2020). Two studies analysing geolocator data from a small number of non-breeding birds revealed that most target the Sub-Antarctic Zone (SAZ: between the Antarctic Polar Front (APF) and the Subtropical Front (STF)), with evidence for small-scale sexual segregation and some consistency in habitat use within the same non-breeding period (Croxall et al. 2005, Clay et al. 2016). Using the stable isotope method, we test the following a priori predictions: (1) most feather $\delta^{13}$C values should correspond to foraging in the SAZ; (2) there will be sex differences in stable isotope values, consistent with the degree of SSD; (3) $\delta^{13}$C values will decrease with age, as demonstrated in similar studies of Wandering Albatrosses (Jaeger et al. 2014, Clay et al. 2018); (4) stable isotope values of feathers sampled from the same individual should show high variability given the protracted moult pattern in this species (see below); and (5) there will be carry-over effects of variation in diet and distribution. Previous breeding outcome may influence the stable isotope values, or the latter may influence the subsequent breeding outcome; however, without further information we make no a priori predictions about the directions of these relationships.

**METHODS**

**Study site and colony**

Chicks have been ringed annually since the 1970s in the intensive study-colonies of Grey-headed Albatrosses at Bird Island, South Georgia (54°00’S, 38°03’W) (Fig. 1). Daily to weekly visits were made throughout the breeding season to record identities of breeders and non-breeders, laying and
fledging dates, and nest survival (Froy et al. 2017, Pardo et al. 2017), and the modal age of first breeding at Bird Island is 12 years (Prince et al. 1994). All birds included in this study were sexed from records of observed copulatory position, from pre-laying attendance pattern or using DNA extracted from blood samples (Fridolfsson & Ellegren 1999); hence all birds were of known age, sex and breeding history.

**Feather sampling and moult**

A random collection of relatively unworn body feathers were obtained from the breast region of adults during the early chick-rearing period (December–January) in three separate breeding seasons (2013/14–2015/16). Individuals (n = 194) were only sampled in a single season. Stable isotope values of feathers can provide information on foraging ecology during the non-breeding period with the underlying assumption that moult and breeding do not overlap. In a study of albatross moult patterns at South Georgia, no Grey-headed Albatrosses were in active body feather moult at Bird Island between October and February (Prince et al. 1993). However, albatrosses replace their body feathers gradually throughout the non-breeding period; indeed, only ~7% of body feathers may be moulted and regrown at any one time (Battam et al. 2010). Therefore, the exact timing of body feather synthesis during the non-breeding period (of ~16 months) is unknown.

However, as our sampling was of relatively unworn feathers, most were likely to have grown in the immediately preceding winter.

**Stable isotope analysis**

Three body feathers were selected per individual and analysed separately. Whole feathers were analysed, excluding only the rachis. Feathers were cleaned of surface lipids and contaminants using a chloroform/methanol solution (2 : 1 v/v) followed by successive distilled water rinses. Feathers were air-dried, cut into small fragments using stainless steel scissors and packed into tin capsules (aliquots: 0.70 ± 0.01 mg (mean ± standard error)). Stable isotope analyses were conducted at the Natural Environment Research Council (NERC) Life Sciences Mass Spectrometry Facility in East Kilbride. Stable isotope ratios of carbon and nitrogen were determined by a continuous-flow mass spectrometer (Delta Plus XP; Thermo Scientific, Bremen, Germany) coupled to an elemental analyser (vario PYRO cube; Elementar, Langenselbold, Germany). To correct for instrument drift, three internal laboratory standards were analysed for every 10 samples. Stable isotope ratios are reported as δ-values and expressed as %oo according to the equation:

\[ \delta X = \left[ \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 10^3 \]

where \( X \) is \( ^{13}\text{C} \) or \( ^{15}\text{N} \), \( R \) is the corresponding ratio \( ^{13}\text{C}/^{12}\text{C} \) or \( ^{15}\text{N}/^{14}\text{N} \), and \( R_{\text{standard}} \) is the ratio of international references Vienna PeeDee Belemnite for carbon and atmospheric N\(_2\) (AIR) for nitrogen. Measurement precision (standard deviation associated with replicate runs of USGS40) was ± 0.1‰ for \( \delta^{13}\text{C} \) and ± 0.2‰ for \( \delta^{15}\text{N} \).

**Data analysis**

Stable isotope values were compared with \( \delta^{13}\text{C} \) estimates associated with foraging at the APF (−21.2‰) and STF (−18.3‰), which are derived from tracked Wandering Albatrosses (Jaeger et al. 2010). The SAZ was defined as the waters bound to the north by the STF and to the south by the APF, and the Subtropical Zone (STZ) and Antarctic Zone (AZ) as the waters to the north of the STF and to the south of the APF, respectively. Separate linear mixed-effects models (LMMs) were constructed with feather \( \delta^{13}\text{C} \) and \( \delta^{15}\text{N} \) values as response variables via the lme4 package in R (Bates et al. 2015). Predictor variables were...
sampling year, sex, age (12–37 years), previous breeding outcome and all two-way interactions. Grey-headed Albatrosses are predominantly biennial breeders; however, a minority attempt to breed annually (Ryan et al. 2007) and hence birds were grouped according to their breeding outcomes (successful, failed or deferred) in the 2 years prior to sampling. Individual identity was included as a random effect. All possible models were ranked using the Akaike information criterion adjusted for small sample sizes (AICc) and models within 2 AICc units of the top model (≤ 2 AICc) were considered equally plausible (Burnham & Anderson 2002). Repeatabilities (intraclass correlation coefficient) in δ13C and δ15N values among different feathers of the same individual were calculated via the rptR package in R (Stoffel et al. 2017). Repeatability (range: 0–1) is calculated as the between-individual variance divided by the between- and within-individual variances (Cavero et al. 2017) and our values are adjusted repeatabilities (Radj), as we controlled for predictor variables retained in the minimum adequate models (Nakagawa & Schielzeth 2010).

The isotopic niches of males and females were compared using the Stable Isotope Bayesian Ellipses in R package (SIBER; Jackson et al. 2011). Standard Ellipse Areas corrected for small sample sizes (SEAC), which represent the core isotopic niche, and 95% ellipse areas were calculated for each sex. Percentage overlaps in SEAC and 95% ellipse areas were used to quantify sex differences in the isotopic niche. Bayesian standard ellipse areas (SEAS) are provided as unbiased estimates of core isotopic niche areas (presented as modes and 95% credibility intervals).

Finally, ordinal logistic regression was used to assess carry-over effects of stable isotope values on the subsequent breeding outcome using the ordinal package in R (Christensen 2019). The breeding outcome response variable had a natural ordering (failed at incubation (n = 23); chick hatched but failed to fledge (n = 108); chick fledged (n = 63)); all birds bred in the year that they were sampled. Two models were tested using the following predictors: (1) mean δ15N and δ13C values of individual birds and (2) variance of δ15N and δ13C values (normalized to the range: 0–1) based on the three feathers analysed for each individual. These models allowed us to test whether the absolute values or the variability is important. All intrinsic effects and sampling year were included as covariates. Analyses were conducted using R version 3.4.4 (R Core Team 2019) and significance was set at α = 0.05.

RESULTS

Intraspecific variation

A total of 582 isotopic measurements were made on body feathers of 194 adults; mean (±sd) stable isotope values (δ13C, δ15N) are presented in Table 1. Grey-headed Albatross feathers exhibited high variability in δ13C (range: −24.6 to −17.1‰) and δ15N values (6.7–14.8‰) (Fig. S1). According to the δ13C values, individuals foraged across a range of oceanic habitats during the non-breeding period, corresponding mostly to the SAZ and to a lesser extent to the AZ and STZ (Fig. 2; Table 2). The most parsimonious LMM (ΔAICc = 0.0) explaining δ15N values included sex as a fixed effect (F1,191 = 7.2, P < 0.01), reflecting higher δ15N values in males than in females (Fig. 2; Table 1). Models including other predictor variables (sampling year, age, breeding history) had less support (> 2 AICc) (Table S1). The most parsimonious LMM explaining δ13C values also included sex as a fixed effect (F1,191 = 3.2, P < 0.01), reflecting lower δ13C in males than in females (Fig. 2; Tables 1 and 2); however, the null model and a model containing sampling year were equally competitive (Table S1). Models including other predictor variables (age, breeding history) received less support (> 2 AICc) and the δ13C and δ15N values of younger individuals did not differ from those of older individuals (Table 3). Repeatability among feathers of the same individual was moderate in δ13C values (Radj = 0.43 ± 0.04, 95% CI 0.37–0.49, P < 0.001) and low in δ15N values (Radj = 0.15 ± 0.05, 95% CI 0.07–0.24, P < 0.001). Isotopic niches of males and females were similar in size (Table 1), with a 62% overlap in SEAC and 80% overlap for the 95% ellipse areas (Fig. 2).

Potential carry-over effects

Neither the mean (ordinal regression: χ2 = 0.10, P = 0.75) nor normalized variance in δ13C values (χ2 = 1.3, P = 0.26) had a significant effect on subsequent breeding outcome, and neither did the mean (χ2 = 0.53, P = 0.61) nor normalized variance in δ15N values (χ2 = 0.20, P = 0.53). δ13C

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values and $\delta^{15}N$ (means and variances) among birds that failed at the incubation or chick stage were therefore similar to those of individuals that successfully fledged their chick.

**DISCUSSION**

Stable isotope values of adult feathers are considered to be effective proxies of habitat use and trophic level of albatrosses during the comparatively understudied non-breeding season (Cherel *et al.* 2000, 2013, Phillips *et al.* 2009). Albatrosses forage over marine isoscapes (reflecting broad-scale isotopic variation), and spatial variation in $\delta^{13}C$ is reflected in their tissues (Quillfeldt *et al.* 2005, Cherel & Hobson 2007). The specific threshold $\delta^{13}C$ values that we used to assign moulting location to north or south of the APF and STF were derived from tracked Wandering Albatrosses in the Indian Ocean (Jaeger *et al.* 2010). However, the paths of the main oceanographic fronts in the Southern Ocean can be highly variable between years (Moore *et al.* 1997) and stable isotope values are therefore broadly indicative of water masses rather than latitude per se. Allowing for some uncertainty, feather $\delta^{13}C$ values indicate that Grey-headed Albatrosses sampled at the Bird Island colony in 2013/14–2015/16 foraged

| Sex      | $n$ | $\delta^{13}C$ ($\%$) | $\delta^{15}N$ ($\%$) | SEA$_C$ ($\%$) | SEA$_B$ ($\%$) |
|----------|----|------------------------|-----------------------|----------------|----------------|
| Males    | 103| $-20.1 \pm 1.2$        | $12.7 \pm 1.5$        | 5.32           | 5.32 (4.76, 5.94) |
| Females  | 91 | $-19.8 \pm 1.2$        | $12.3 \pm 1.6$        | 5.84           | 5.85 (5.19, 6.54) |

SEA$_C$ is the standard ellipse area corrected for small sample size, and SEA$_B$ is the Bayesian estimate of the standard ellipse (modes with 95% credibility intervals in parentheses).

**Table 2.** Numbers of Grey-headed Albatross *Thalassarche chrysostoma* body feathers with $\delta^{13}C$ values corresponding to $\delta^{13}C$ estimates of foraging in the Antarctic Zone, Subantarctic Zone and Subtropical Zone (Jaeger *et al.* 2010).

| Age class | Females | Males | Total |
|-----------|---------|-------|-------|
| Antarctic Zone | 22 (8.0) | 38 (12.4) | 60 (10.3) |
| Subantarctic Zone | 228 (82.6) | 238 (77.8) | 466 (80.1) |
| Subtropical Zone | 26 (9.4) | 30 (9.8) | 56 (9.6) |

Percentages are in parentheses. All sampled birds were from Bird Island, South Georgia (2013/14–2015/16).

**Table 3.** Mean ($\pm$ sd) stable isotope values ($\delta^{13}C$, $\delta^{15}N$) of three body feathers sampled from younger, mid-aged and older Grey-headed Albatrosses *Thalassarche chrysostoma* at Bird Island, South Georgia (2013/14–2015/16). Age classes are delineated following Catry *et al.* (2006).

| Age class | $n$ | $\delta^{13}C$ ($\%$)* | $\delta^{15}N$ ($\%$)* |
|-----------|----|------------------------|------------------------|
| Younger ($\leq$ 14 years) | 13 | $-20.2 \pm 0.7$ | $12.6 \pm 0.9$ |
| Mid-aged (15–27 years) | 119 | $-20.0 \pm 0.9$ | $12.5 \pm 1.0$ |
| Older ($\geq$ 28 years) | 62 | $-19.8 \pm 1.0$ | $12.7 \pm 1.1$ |

*No significant differences among age classes (ANOVA, $F_{2,192} = 1.43$, $P = 0.24$). *No significant differences among age classes (ANOVA, $F_{2,192} = 0.09$, $P = 0.92$).
predominantly in the SAZ, and to a lesser extent in the STZ and AZ, during the previous non-breeding period. This is consistent with stable isotope data from other populations of this species (Cherel et al. 2013) and with geolocator data from a much smaller sample of individuals tracked previously from South Georgia (Croxall et al. 2005, Clay et al. 2016). Hence, our first a priori hypothesis that most individuals spent the non-breeding period in the SAZ is supported.

Drivers of variation in habitat use and trophic level

Our study highlights considerable intraspecific variation in the habitat use (δ¹³C) and trophic level (δ¹⁵N) of Grey-headed Albatrosses during the non-breeding period. Sexual segregation and other sex differences in foraging ecology are well-documented among seabirds, including albatrosses (Phillips et al. 2004, 2011, Weimerskirch et al. 2014, Froy et al. 2015). In our analyses, sex was the best predictor of feather δ¹³C and δ¹⁵N values, although differences were small – mean feather δ¹³C values were slightly lower and δ¹⁵N values slightly higher in males than in females. Moreover, our analyses of the isotopic niche show high, but not complete, overlap between sexes. These differences indicate that males forage at higher latitudes and to a greater extent on higher trophic level prey, hence providing some support for our second a priori prediction. The aforementioned geolocator data showed that males foraged at slightly higher latitudes (by c. 1°), and core areas but not overall distributions were segregated to some extent from females during the non-breeding summer only (Clay et al. 2016). Moreover, a previous stable isotope study, albeit with a much reduced sample size, also found that δ¹³C values in body feathers of males were lower than those of females (Phillips et al. 2009). Male Grey-headed Albatrosses are 15% heavier, with overall wing area and wing loading greater by 5 and 10%, respectively, than females (Phillips et al. 2004). This may confer a functional role in flight performance (Shaffer et al. 2001), with males perhaps better able to take advantage of the stronger winds at higher latitudes with associated flight cost reductions (Phillips et al. 2004, Jaeger et al. 2014). The slightly higher δ¹⁵N values could indicate that males consume a greater proportion of higher trophic level prey during the non-breeding period, or larger individuals rather than different species, as size-related increases in δ¹⁵N values in fish, squid and crustaceans are often apparent within taxa (Schmidt et al. 2003). Male Grey-headed Albatrosses have a longer and deeper bill than females (Phillips et al. 2004), which could conceivably enable them to manipulate larger prey. Given the difficulties in obtaining samples, no complete conventional diet studies (i.e. for all prey taxa) exist outside the breeding period. Despite differing foraging distributions in incubation (Phillips et al. 2004), there is no evidence for consistent differences between sexes in activity patterns in Grey-headed Albatrosses during the breeding season (Phalan et al. 2007). Nor do activity patterns differ between sexes in the closely related Black-browed Albatross Thalassarche melanophris or in Wandering Albatrosses during the non-breeding season (Mackley et al. 2010). Spatial variation in δ¹⁵N baselines can confound interpretation; however, that is very unlikely to be problematic in our comparison, as δ¹⁵N values actually decrease with latitude in the Southern Ocean (Jaeger et al. 2010) and males both had higher δ¹⁵N values and foraged at higher latitudes according to δ¹³C.

Our analyses provided no support for our a priori prediction relating to age-related variation in foraging (Table 3). This contrasts with previous studies of Wandering Albatrosses. Tracking at the Crozet Islands showed that older males foraged further south with increasing age during the breeding season (Lecomte et al. 2010), although this was not found at South Georgia (Froy et al. 2015). An age-related decrease in δ¹³C values in body feathers—representing the non-breeding period—was observed in Wandering Albatrosses at South Georgia (Clay et al. 2018) and at the Crozet Islands (Jaeger et al. 2014). Grey-headed Albatrosses show distinct age-specific habitat preferences in terms of sea surface temperature during the breeding season (Frankish et al. 2020) and older birds (≥ 35 years) took longer trips and had lower daily mass gains compared with mid-aged birds (≤ 28 years) (Catry et al. 2006). However, our results suggest that if there are age-related changes in at-sea activity patterns, foraging habitat or trophic level in Grey-headed Albatrosses at South Georgia during the non-breeding period, then they are at fine scales and not evident from stable isotope values. Additionally, there is the caveat that most studies (including the present study) are cross-sectional and hence the possibility
of selective mortality of particular phenotypes cannot be excluded except by carrying out longitudinal studies.

Variation among feathers

Jaeger et al. (2009) noted that measuring stable isotopes in multiple feathers from the same individual could provide insights into within-individual variation, which contrasts with the conventional procedure of pooling multiple feathers per individual. After accounting for sex effects, repeatability among feathers was moderate in $\delta^{13}$C and low in $\delta^{15}$N, but significant in both cases, for which there are two possible explanations. First, repeatability may be a consequence of sampling feathers that were regrown over broadly the same period. However, this is unlikely given that body feathers are most likely replaced gradually over the non-breeding period. Given that seabirds are dependent on resources that are patchily distributed but predictable at large spatial scales (Weimerskirch 2007), a degree of consistency in foraging areas would be unsurprising. Moreover, from a limited number of tracked individuals, Croxall et al. (2005) found consistency in the habitats used by Grey-headed Albatrosses in successive winters during the non-breeding period. Finally, chick-rearing Grey-headed Albatrosses show individual foraging site fidelity and specialization in habitat use in terms of sea surface temperature, eddy kinetic energy and water depth (Bonnet-Lebrun et al. 2018).

Carry-over effects

Behaviour or conditions experienced during the non-breeding period have an influence on subsequent breeding outcome in some albatrosses (Crossin et al. 2013, Clay et al. 2018). Grey-headed Albatrosses lay a single egg clutch with no replacement, and consistently successful birds at South Georgia arrive earlier at the colony, have shorter incubation shifts, and hatch larger chicks with higher growth rates compared with less successful birds (Cobley et al. 1998). Diet in the preceding non-breeding period may influence body condition, which can have consequences for subsequent reproduction (Sorensen et al. 2009).

Nonetheless, in our analyses, no significant relationships were found between mean feather stable isotope values, or variance in such values, and breeding outcome. Moreover, previous breeding outcome did not explain stable isotope values. Any potential relationships between stable isotopes, reflecting distribution and diet, would probably be mediated through variation in body condition on arrival at the colony. The decision to breed in Grey-headed Albatrosses at South Georgia is influenced by body condition (Crossin et al. 2013). All birds in our study were sampled as breeders, from which we can infer that they returned to the colony in relatively good condition.

CONCLUSION

Rather less is known about the foraging ecology of albatrosses during the non-breeding compared with the breeding season. A novel insight from our study is the high level of variability in habitat use and trophic levels of non-breeding Grey-headed Albatrosses from South Georgia. Grey-headed Albatrosses are therefore population-level generalists during the non-breeding periods and utilize a range of oceanic habitats, although they mainly target the SAZ according to feather $\delta^{13}$C values; this is confirmed by geolocator data from previous tracking studies of this population. Sex differences were subtle, but significant, and the overlap in the core isotopic niche was high but not complete. Neither age nor previous breeding outcome influenced stable isotope values. Future research on albatross foraging ecology, particularly age-related changes, would benefit from longitudinal studies, and stable isotope studies would benefit from increased understanding of moultting patterns. We also found no evidence of carry-over effects of non-breeding diet or distribution on subsequent breeding outcome and it would be useful to examine carry-over effects on birds observed as non-breeders at the colony, which are likely to vary more in terms of physiological condition.

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**AUTHOR CONTRIBUTION**

William F. Mills: Conceptualization (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Visualization (lead); Writing—original draft (lead). Rona A. R. McGill: Investigation (equal); Methodology (equal); Writing—review & editing (equal). Yves Cherel: Supervision (equal); Writing—review & editing (equal). Stephen C. Votier: Supervision (equal); Writing—review & editing (equal). Richard A. Phillips: Conceptualization (equal); Resources (lead); Supervision (equal); Methodology (equal); Visualization (lead); Writing—original draft (lead).

**Data Availability Statement**

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** Model selection for factors explaining variation in stable isotope values (δ¹³C, δ¹⁵N) of Grey-headed Albatross *Thalassarche chrysostoma* body feathers at Bird Island, South Georgia (2013/14–2015/16).

**Figure S1.** Mean (± standard deviation) stable isotope values (δ¹³C, δ¹⁵N) of body feathers from adult Grey-headed Albatrosses *Thalassarche chrysostoma* at Bird Island, South Georgia (2013/14–2015/16).