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10 **Running head:** *Intraspecific variation in Grey-headed Albatrosses*

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

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37   The non-breeding period is critical for restoration of body condition and self-maintenance

38   in albatrosses, yet detailed information on diet and distribution during this stage of the annual

39   cycle is lacking for many species. Here, we use stable isotope values of body feathers (δ^{13}C, δ^{15}N)

40   to infer habitat use and trophic level of non-breeding adult Grey-headed Albatrosses *Thalassarche*

41   *chrysostoma* (n = 194) from South Georgia. Specifically, we: (i) investigate intrinsic drivers (sex,

42   age, previous breeding outcome) of variation in habitat use and trophic level; (ii) quantify

43   variation among feathers of the same birds; and (iii) examine potential carry-over effects of habitat

44   use and trophic level during the non-breeding period on subsequent breeding outcome. In

45   agreement with previous tracking studies, δ^{13}C values of individual feathers indicate that non-

46   breeding Grey-headed Albatrosses from South Georgia foraged across a range of oceanic habitats,

47   but mostly in subantarctic waters, between the Antarctic Polar Front and Subtropical Front. Sex

48   differences were subtle but statistically significant, and overlap in the core isotopic niche areas

49   was high (62%); however, males exhibited slightly lower δ^{13}C and higher δ^{15}N values than

50   females, indicating that males forage at higher latitudes and at a higher trophic level. Neither age

51   nor previous breeding outcome influenced stable isotope values, and we found no evidence of

52   carry-over effects of non-breeding habitat use or trophic level on subsequent breeding outcome.

53   Repeatability among feathers of the same individual was moderate in δ^{13}C and low in δ^{15}N. This

54   cross-sectional study demonstrates high variability in the foraging and migration strategies of this

55   albatross population.

56

57   **Key words:** seabirds; *Thalassarche chrysostoma*; Procellariiformes; intraspecific variation;

58   migration; Southern Ocean

59　　Individual seabirds within apparently generalist populations may differ in their resource use and

60　　foraging strategies (Phillips *et al.* 2017), with potential implications for community structure,

61　　evolutionary ecology and conservation management (Bolnick *et al.* 2003, Votier *et al.* 2010,

62　　Phillips *et al.* 2017). Variation among individuals is often attributed to the influence of intrinsic

63　　drivers, including sex (Bearhop *et al.* 2006, Phillips *et al.* 2011), age (Votier *et al.* 2017, Clay *et*

64　　*al.* 2018), and breeding status (Jaeger *et al.* 2014, Clay *et al.* 2016). However most studies of

65　　intraspecific variation in seabird foraging have focused on the breeding period, and less is known

66　　about the non-breeding period, when birds are free from reproductive constraints associated with

67　　incubation or provisioning, and can disperse widely.

68　　　　　There is increasing evidence for sex differences in seabird foraging strategies during the

69　　non-breeding period, including variation in diet, distribution and other aspects of behaviour

70　　(Bearhop *et al.* 2006, Phillips *et al.* 2009, De Felipe *et al.* 2019). These differences are thought to

71　　arise from size-related behavioural dominance and competitive exclusion (typically of the larger

72　　sex over the smaller), or habitat and dietary specialisation (Phillips *et al.* 2017). The degree of

73　　segregation in foraging ecology may be a function of sexual size dimorphism (SSD; Phillips *et al.*

74　　2011), though this appears to apply more to high-latitude than tropical species (Mancini *et al.*

75　　2013), and studies have also demonstrated sex-related foraging strategies in species with reduced

76　　SSD (e.g. Lamacchia *et al.* 2019). Less attention, however, has been paid to changes in foraging

77　　behaviour and distribution with age, despite some evidence that it may be an important driver

78　　(Phillips *et al.* 2017). Indeed, a recent study of non-breeding Wandering Albatrosses *Diomedea*

79　　*exulans* from South Georgia found evidence of age-related changes in activity patterns and stable

80　　isotope proxies for habitat use (Clay *et al.* 2018). There is also evidence that non-breeding

81　　Wandering Albatrosses in the Indian Ocean forage further south with age (Jaeger *et al.* 2014).

82　　　　　Stable isotope analyses have been validated as a powerful tool to study the foraging

83　　ecology of seabirds, including albatrosses (Cherel *et al.* 2000), and stable isotope values of adult

84　　feathers are routinely used to investigate diet and distribution during the non-breeding period

85　　(Cherel *et al.* 2013, Phillips *et al.* 2009). This is because moult rarely overlaps with breeding, and

86　　feathers are metabolically inert once grown and hence preserve an isotopic record of diet at time of

87　　formation (Hobson & Clark 1992, Bearhop *et al.* 2002, Catry *et al.* 2013). Stable isotope values of

88　　carbon (^{13}C/^{12}C, expressed as δ^{13}C) and nitrogen (^{15}N/^{14}N, δ^{15}N) in tissues reflect those of prey

89　　during the period of synthesis. δ^{15}N values increase in a stepwise manner by ~3 to 5 ‰ at each

90　　trophic level, whereas δ^{13}C values increase less with trophic level (~0.5 to 1 ‰), but can be used

91 to infer foraging habitat (DeNiro & Epstein 1981, Hobson & Clark 1992, Bearhop *et al*. 2002). In

92 the marine environment, this includes the relative reliance on an inshore versus offshore, benthic

93 versus pelagic diet, and latitude or water mass where a gradient exists, such as in the Southern

94 Ocean (Quillfeldt *et al*. 2005, 2010, Cherel & Hobson 2007, Jaeger *et al*. 2010).

95 The aim of this cross-sectional study is to provide detailed information on the foraging

96 ecology of Grey-headed Albatrosses *Thalassarche chrysostoma* from South Georgia during the

97 non-breeding period. The population at South Georgia constitutes the largest population at any

98 island group (50% globally; Poncet *et al*. 2017). This species exhibits male-biased SSD (Phillips *et*

99 *al*. 2004), is among the longest-lived birds (Catry *et al*. 2006) and is a population-level generalist

100 (Mills *et al*. 2020). Two studies analysing geolocator data from a small number of non-breeding

101 birds revealed that most target the Subantarctic Zone (SAZ: between the Antarctic Polar Front

102 [APF] and the Subtropical Front [STF]), with evidence for small-scale sexual segregation and

103 some consistency in habitat use within the same non-breeding period (Croxall *et al*. 2005, Clay *et*

104 *al*. 2016). Using the stable isotope method, we test the following *a priori* predictions: (i) most

105 feather δ^{13}C values should correspond to foraging in the SAZ; (ii) there will be sex differences in

106 stable isotope values, consistent with the degree of SSD; (iii) δ^{13}C values will decrease with age as

107 demonstrated in similar studies of Wandering Albatrosses (Jaeger *et al*. 2014, Clay *et al*. 2018);

108 (iv) stable isotope values of feathers sampled from the same individual should show high

109 variability given the protracted moult pattern in this species (see below); (v) there will be carry-

110 over effects of variation in diet and distribution. Previous breeding outcome may influence the

111 stable isotope values, or the latter may influence the subsequent breeding outcome; however,

112 without further information we make no *a priori* predictions about the directions of these

113 relationships.

114

115 **METHODS**

116 **Study site and colony**

117 Chicks have been ringed annually since the 1970s in the intensive study-colonies of Grey-headed

118 Albatrosses at Bird Island, South Georgia (54°00'S, 38°03'W) (Fig. 1). Daily to weekly visits

119 were made throughout the breeding season to record identities of breeders and non-breeders,

120 laying and fledging dates, and nest survival (Froy *et al*. 2017, Pardo *et al*. 2017), and the modal

121 age of first breeding at Bird Island is 12 years (Prince *et al*. 1994). All birds included in this study

122 were sexed from records of observed copulatory position, prey-laying attendance pattern, or using

123   DNA extracted from blood samples (Fridolfsson & Ellegren 1999); hence all birds were of known

124   age, sex and breeding history.

125

126   **Feather sampling and moult**

127   A random collection of relatively unworn body feathers were obtained from the breast region of

128   adults during the early chick-rearing period (December–January) in three separate breeding

129   seasons (2013/14–2015/16). Individuals ($n = 194$) were only sampled in a single season. Stable

130   isotope values of feathers can provide information on foraging ecology during the non-breeding

131   period with the underlying assumption that moult and breeding do not overlap. In a study of

132   albatross moulting patterns at South Georgia, no Grey-headed Albatrosses were in active body

133   feather moult at Bird Island between October and February (Prince *et al.* 1993). However,

134   albatrosses replace their body feathers gradually throughout the non-breeding period, indeed only

135   ~7% of body feathers may be moutled and regrown at any one time (Battam *et al.* 2010).

136   Therefore the exact timing of body feather synthesis during the non-breeding period (of ~16

137   months) is unknown. However, as our sampling was of relatively unworn feathers, most were

138   likely to have grown in the immediately preceding winter.

139

140   **Stable isotope analysis**

141   Three body feathers were selected per individual and analysed separately. Whole feathers were

142   analysed, excluding only the rachis. Feathers were cleaned of surface lipids and contaminants

143   using chloroform:methanol solution (2:1 v/v) followed by successive distilled water rinses.

144   Feathers were air-dried, cut into small fragments using stainless steel scissors and packed into tin

145   capsules (aliquots: 0.70 ± 0.01 mg [mean ± standard error]). Stable isotope analyses were

146   conducted at the Natural Environment Research Council (NERC) Life Sciences Mass

147   Spectrometry Facility in East Kilbride. Stable isotope ratios of carbon and nitrogen were

148   determined by a continuous-flow mass spectrometer (Thermo Scientific [Bremen, Germany] Delta

149   Plus XP) coupled to an elemental analyser (Elementar [Langenselbold, Germany] vario PYRO

150   cube). To correct for instrument drift, three internal laboratory standards were analysed for every

151   10 samples. Stable isotope ratios are reported as δ-values and expressed as ‰ according to the

152   equation: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 10^3$, where X is ^{13}C or ^{15}N, R is the corresponding ratio

153    $^{13}C/^{12}C$ or $^{15}N/^{14}N$, and $R_{standard}$ is the ratio of international references Vienna PeeDee Belemnite

154   for carbon and atmospheric N_2 (AIR) for nitrogen. Measurement precision (standard deviation

155   associated with replicate runs of USGS40) was ±0.1 ‰ for δ^{13}C and ±0.2 ‰ for δ^{15}N.

156

157   **Data analysis**

158   Stable isotope values were compared to δ^{13}C estimates associated with foraging at the APF (–21.2

159   ‰) and Subtropical Front (STF; –18.3 ‰), which are derived from tracked Wandering

160   Albatrosses (Jaeger *et al*. 2010). The SAZ was defined as the waters bound to the north by the STF

161   and to the south by the APF, and the Subtropical Zone (STZ) and Antarctic Zone (AZ) as the

162   waters to the north of the STF and to the south of the APF, respectively. Separate linear mixed-

163   effects models (LMMs) were constructed with feather δ^{13}C and δ^{15}N values as response variables

164   via the *lme4* package in R (Bates *et al*. 2015). Predictor variables were sampling year, sex, age

165   (12–37 years), previous breeding outcome and all two-way interactions. Grey-headed Albatrosses

166   are predominantly biennial breeders, however a minority attempts to breed annually (Ryan *et al*.

167   2007) and hence birds were grouped according to their breeding outcomes (successful, failed or

168   deferred) in the two years prior to sampling. Individual identity was included as a random effect.

169   All possible models were ranked using the Akaike Information Criteria adjusted for small sample

170   sizes (AIC_C) and models within 2 AIC_C units of the top model (≤ 2 AIC_C) were considered equally

171   plausible (Burnham & Anderson 2002). Repeatabilities (intraclass correlation coefficient) in δ^{13}C

172   and δ^{15}N values among different feathers of the same individual were calculated via the *rptR*

173   package in R (Stoffel *et al*. 2017). Repeatability (range: 0 to 1) is calculated as the between-

174   individual variance divided by the between- and within-individual variances (Carneiro *et al*.

175   2017), and our values are adjusted repeatabilities (R_{adj}) as we controlled for predictor variables

176   retained in the minimum adequate models (Nakagawa & Schielzeth 2010).

177   The isotopic niches of males and females were compared using the Stable Isotope

178   Bayesian Ellipses in R package (*SIBER*; Jackson *et al*. 2011). Standard Ellipse Areas corrected for

179   small sample sizes (SEA_C), which represent the core isotopic niche, and 95% ellipse areas were

180   calculated for each sex. Percentage overlaps in SEA_C and 95% ellipse areas were used to quantify

181   sex differences in the isotopic niche. Bayesian standard ellipse areas (SEA_B) are provided as

182   unbiased estimates of core isotopic niche areas (presented as modes and 95% credibility intervals).

183   Finally, ordinal logistic regression was used to assess carry-over effects of stable isotope

184   values on the subsequent breeding outcome using the *ordinal* package in R (Christensen 2019).

185   The breeding outcome response variable had a natural ordering (failed at incubation [*n* = 23];

186   chick hatched but failed to fledge [$n = 108$]; chick fledged [$n = 63$]); all birds bred in the year that

187   they were sampled. Two models were tested using the following predictors: (i) mean $\delta^{15}N$ and

188     $\delta^{13}C$ values of individual birds; and, (ii) variance of $\delta^{15}N$ and $\delta^{13}C$ values (normalised to range: 0

189   to 1) based on the three feathers analysed for each individual. These models allowed us to test

190   whether the absolute values or the variability is important. All intrinsic effects and sampling year

191   were included as covariates. Analyses were conducted using R version 3.4.4 (R Core Team 2019),

192   and significance was set at $\alpha = 0.05$.

193

194   **RESULTS**

195   **Intraspecific variation**

196   A total of 582 isotopic measurements were made on body feathers of 194 adults; mean (± SD)

197   stable isotope values ($\delta^{13}C$, $\delta^{15}N$) are presented in Table 1. Grey-headed Albatross feathers

198   exhibited high variability in $\delta^{13}C$ (range: –24.6 to –17.1 ‰) and $\delta^{15}N$ values (6.7 to 14.8 ‰) (Fig.

199   S1). According to the $\delta^{13}C$ values, individuals foraged across a range of oceanic habitats during

200   the non-breeding period, corresponding mostly to the SAZ and to a lesser extent the AZ and STZ

201   (Fig. 2; Table 2). The most parsimonious LMM ($\Delta AIC_C = 0.0$) explaining $\delta^{15}N$ values included sex

202   as a fixed effect ($F_{1, 191} = 7.2$, $P < 0.01$), reflecting higher $\delta^{15}N$ values in males compared to

203   females (Fig. 2; Table 1). Models including other predictor variables (sampling year, age, breeding

204   history) had less support (> 2 AIC_C) (Table S1). The most parsimonious LMM explaining $\delta^{13}C$

205   values also included sex as a fixed effect ($F_{1,191} = 3.2$, $P < 0.01$), reflecting lower $\delta^{13}C$ in males

206   compared to females (Fig. 2; Tables 1 and 2); however, the null model and a model containing

207   sampling year were equally competitive (Table S1). Models including other predictor variables

208   (age, breeding history) received less support (> 2 AIC_C), and young individuals had no different

209     $\delta^{13}C$ and $\delta^{15}N$ values than old individuals (Table 3). Repeatability among feathers of the same

210   individual was moderate in $\delta^{13}C$ values ($R_{adj} = 0.43 \pm 0.04$, 95% CIs = 0.37– 0.49, $P < 0.001$) and

211   low in $\delta^{15}N$ values ($R_{adj} = 0.15 \pm 0.05$, 95% CIs = 0.07–0.24, $P < 0.001$). Isotopic niches of males

212   and females were similar in size (Table 1), with a 62% overlap in SEA_C and 80% overlap for the

213   95% ellipse areas (Fig. 2).

214

215   **Potential carry-over effects**

216   Neither the mean (ordinal regression: $\chi^2 = 0.10$, $P = 0.75$) nor normalised variance in $\delta^{13}C$ values

217   ($\chi^2 = 1.3$, $P = 0.26$) had a significant effect on subsequent breeding outcome, and nor did the mean

218   ($\chi^2 = 0.53$, $P = 0.61$) or normalised variance in $\delta^{15}N$ values ($\chi^2 = 0.20$, $P = 0.53$). $\delta^{13}C$ values and

219      $\delta^{15}N$ (means and variances) among birds that failed at the incubation or chick stage were therefore

220   similar to those of individuals that successfully fledged their chick.

221

222   **DISCUSSION**

223   Stable isotope values of adult feathers are considered to be effective proxies of habitat use and

224   trophic level of albatrosses during the the comparatively understudied non-breeding season

225   (Cherel *et al*. 2000, 2013, Phillips *et al*. 2009). Albatrosses forage over marine isoscapes

226   (reflecting broad-scale isotopic variation), and spatial variation in $\delta^{13}C$ is reflected in their tissues

227   (Quillfeldt *et al*. 2005, Cherel & Hobson 2007). The specific threshold $\delta^{13}C$ values that we used to

228   assign moulting location to north or south of the APF and STF were derived from tracked

229   Wandering Albatrosses in the Indian Ocean (Jaeger *et al*. 2010). However, the paths of the main

230   oceanographic fronts in the Southern Ocean can be highly variable between years (Moore *et al*.

231   1997), and stable isotope values are therefore broadly indicative of water masses rather than

232   latitude *per se*. Allowing for some uncertainty, feather $\delta^{13}C$ values indicate that Grey-headed

233   Albatrosses sampled at the Bird Island colony in 2013/14–2015/16 foraged predominantly in the

234   SAZ, and to a lesser extent in the STZ and AZ, during the previous non-breeding period. This is

235   consistent with stable isotope data from other populations of this species (Cherel *et al*. 2013), and

236   with geolocator data from a much smaller sample of individuals tracked previously from South

237   Georgia (Croxall *et al*. 2005, Clay *et al*. 2016). Hence our first *a priori* hypothesis that most

238   individuals spent the non-breeding period in the SAZ is supported.

239

240   **Drivers of variation in habitat use and trophic level**

241   Our study highlights considerable intraspecific variation in the habitat use ($\delta^{13}C$) and trophic level

242   ($\delta^{15}N$) of Grey-headed Albatrosses during non-breeding period. Sexual segregation and other sex

243   differences in foraging ecology are well-documented among seabirds, including albatrosses

244   (Phillips *et al*. 2004, 2011, Weimerskirch *et al*. 2014, Froy *et al*. 2015). In our analyses, sex was

245   the best predictor of feather $\delta^{13}C$ and $\delta^{15}N$ values, though differences were small – mean feather

246      $\delta^{13}C$ values were slightly lower and $\delta^{15}N$ values slightly higher in males than females. Moreover,

247   our analyses of the isotopic niche show high, but not complete, overlap between sexes. These

248   differences indicate that males forage at higher latitudes and to a greater extent on higher trophic

249   level prey, and hence provide some support for our second *a priori* prediction. The

250   aforementioned geolocator data showed that males foraged at slightly higher latitudes (by c.1°),

251   and core areas but not overall distributions were segregated to some extent from females during

252   the non-breeding summer only (Clay *et al*. 2016). Moreover, a previous stable isotope study, albeit

253   with a much reduced sample size, also found that δ^{13}C values in body feathers of males were

254   lower than those of females (Phillips *et al*. 2009). Male Grey-headed Albatrosses are 15% heavier,

255   with overall wing area and wing loading greater by 5% and 10%, respectively, than females

256   (Phillips *et al*. 2004). This may confer a functional role in flight performance (Shaffer *et al*. 2001),

257   with males perhaps better able to take advantage of the stronger winds at higher latitudes with

258   associated flight cost reductions (Phillips *et al*. 2004, Jaeger *et al*. 2014). The slightly higher δ^{15}N

259   values could indicate that males consume a greater proportion of higher trophic level prey during

260   the non-breeding period, or larger individuals rather than different species as size-related increases

261   in δ^{15}N values in fish, squid and crustaceans are often apparent within taxa (Schmidt *et al*. 2003).

262   Male Grey-headed Albatrosses have a longer and deeper bill than females (Phillips *et al*. 2004),

263   which could conceivably enable them to manipulate larger prey. Given the difficulties in obtaining

264   samples, no complete conventional diet studies (i.e. for all prey taxa) exist outside the breeding

265   period. Despite differing foraging distributions in incubation (Phillips *et al*. 2004), there is no

266   evidence for consistent differences between sexes in activity patterns in Grey-headed Albatrosses

267   during the breeding season (Phalan *et al*. 2007). Nor do activity patterns differ between sexes in

268   the closely-related Black-browed Albatross *Thalassarche melanophris* or in Wandering

269   Albatrosses during the non-breeding season (Mackley *et al*. 2010). Spatial variation in δ^{15}N

270   baselines can confound interpretation; however, that is very unlikely to be problematic in our

271   comparison as δ^{15}N values actually decrease with latitude in the Southern Ocean (Jaeger *et al*.

272   2010), and males both had higher δ^{15}N values, and foraged at higher latitudes according to δ^{13}C.

273   Our analyses provided no support for our *a priori* prediction relating to age-related

274   variation in foraging (Table 3). This contrasts with previous studies of Wandering Albatrosses.

275   Tracking at the Crozet Islands showed that older males foraged further south with increasing age

276   during the breeding season (Lecomte *et al*. 2010), though this was not found at South Georgia

277   (Froy *et al*. 2015). An age-related decrease in δ^{13}C values in body feathers - representing the non-

278   breeding period - was observed in Wandering Albatrosses at South Georgia (Clay *et al*. 2018), and

279   at the Crozet Islands (Jaeger *et al*. 2014). Grey-headed Albatrosses show distinct age-specific

280   habitat preferences in terms of sea surface temperature during the breeding season (Frankish et al.

281   2020), and old birds ($\geq$ 35 years) took longer trips and had lower daily mass gains compared to

282 mid-aged ($\leq$ 28 years) birds (Catry *et al.* 2006). However, our results suggest that if there are age-
283 related changes in at-sea activity patterns, foraging habitat or trophic level in Grey-headed
284 Albatrosses at South Georgia during the non-breeding period, then they are at fine scales and not
285 evident from stable isotope values. Additionally, there is the caveat that most studies (including
286 the present study) are cross-sectional and hence the possibility of selective mortality of particular
287 phenotypes cannot be excluded except by carrying out longitudinal studies.

288

289 **Variation among feathers**
290 Jaeger *et al.* (2009) noted that measuring stable isotopes in multiple feathers from the same
291 individual could provide insights into within-individual variation, which contrasts with the
292 conventional procedure of pooling multiple feathers per individual. After accounting for sex
293 effects, repeatability among feathers was moderate in δ^{13}C and low in δ^{15}N, but significant in both
294 cases, for which there are two possible explanations. Firstly, repeatability may be a consequence
295 of sampling feathers that were regrown over broadly the same period. However, this is unlikely
296 given that body feathers are most likely replaced gradually over the non-breeding period (see
297 Methods). A second alternative explanation is that individuals showed some consistency in their
298 habitat use and, to a lesser extent, trophic level during the non-breeding period. Given that
299 seabirds are dependent on resources that are patchily distributed but predictable at large spatial
300 scales (Weimerskirch 2007), a degree of consistency in foraging areas would be unsurprising.
301 Moreover, from a limited number of tracked individuals, Croxall *et al.* (2005) found consistency
302 in the habitats used by Grey-headed Albatrosses in successive winters during the non-breeding
303 period. Finally, chick-rearing Grey-headed Albatrosses show individual foraging site fidelity and
304 specialisation in habitat use in terms of sea surface temperature, eddy kinetic energy and water
305 depth (Bonnet-Lebrun *et al.* 2018).

306

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

314 subsequent reproduction (Sorensen *et al.* 2009). Nonetheless, in our analyses, no significant

315 relationships were found between mean feather stable isotope values, or variance in such values,

316 and breeding outcome. Moreover, previous breeding outcome did not explain stable isotope

317 values. Any potential relationships between stable isotopes, reflecting distribution and diet, would

318 likely be mediated through variation in body condition on arrival at the colony. The decision to

319 breed in Grey-headed Albatrosses at South Georgia is influenced by body condition (Crossin *et al*.

320 2013). All birds in our study were sampled as breeders, from which we can infer that they returned

321 to the colony in relatively good condition..

322

323 **Conclusion**

324 Rather less is known about the foraging ecology of albatrosses during the non-breeding compared

325 with the breeding season. A novel insight from our study is the high level of variability in habitat

326 use and trophic levels of non-breeding Grey-headed Albatrosses from South Georgia. Grey-headed

327 Albatrosses are therefore population-level generalists during the non-breeding periods and utilise a

328 range of oceanic habitats, though they mainly target the SAZ according to feather $\delta^{13}C$ values and

329 this is confirmed by geolocator data from previous tracking studies of this population. Sex

330 differences were subtle, but signficant, and the overlap in the core isotopic niche was high but not

331 complete. Neither age or previous breeding outcome influenced stable isotope values. Future

332 research on albatross foraging ecology, particularly age-related changes, would benefit from

333 longitudinal studies and stable isotope studies would benefit from increased understanding of

334 moulting patterns.We also found no evidence of carry-over effects of non-breeding diet or

335 distribution on subsequent breeding outcome, and it would be useful to examine carry-over effects

336 on birds observed as non-breeders at the colony, which are likely to vary more in terms of

337 physiological condition.

338

345

346 **DATA AVAILABILITY**

347 *The data that support the findings of this study are available from the corresponding author upon*
348 *reasonable request.*
349

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Table 1. Mean (± standard deviation) stable isotope values (δ^{13}C, δ^{15}N) of three body feathers sampled from individual male and female Grey-headed Albatrosses *Thalassarche chrysostoma* at Bird Island, South Georgia (2013/14–2015/16). SEA$_C$ is standard ellipse area corrected for small sample size, and SEA$_B$ is the Bayesian esitimate of the standard ellipse (modes with 95% credibility intervals in parentheses).

Sex	n	δ^{13}C (‰)	δ^{15}N (‰)	SEA$_C$ (‰^{2})	SEA$_B$ (‰^{2})
Males	103	−20.1 ± 1.2	12.7 ± 1.5	5.32	5.32 (4.76, 5.94)
Females	91	−19.8 ± 1.2	12.3 ± 1.6	5.84	5.85 (5.19, 6.54)

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

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

Table 3. Mean (± standard deviation) stable isotope values (δ^{13}C, δ^{15}N) of three body feathers sampled from young, 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	δ^{13}C (‰)[a]	δ^{15}N (‰)[b]
Young (≤ 14 years)	13	−20.2 ± 0.7	12.6 ± 0.9
Mid-aged (15–27 years)	119	−20.0 ± 0.9	12.5 ± 1.0
Old (≥ 28 years)	62	−19.8 ± 1.0	12.7 ± 1.1

[a] No signficant differences among age classes (ANOVA, $F_{2,192} = 1.43$, $P = 0.24$).

[b] No signficant differences among age classes (ANOVA $F_{2,192} = 0.09$, $P = 0.92$).

Figure 1. Location of Bird Island, South Georgia (black cross), in relation to the Antarctic Polar Front (dashed line) and Subtropical Front (dot-dash line).
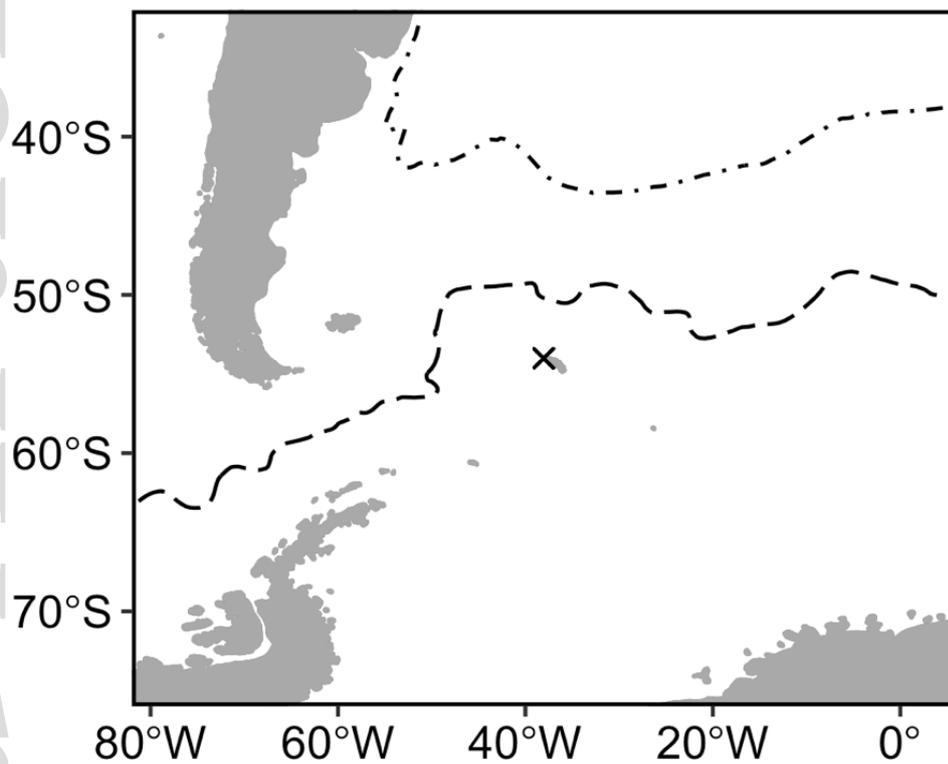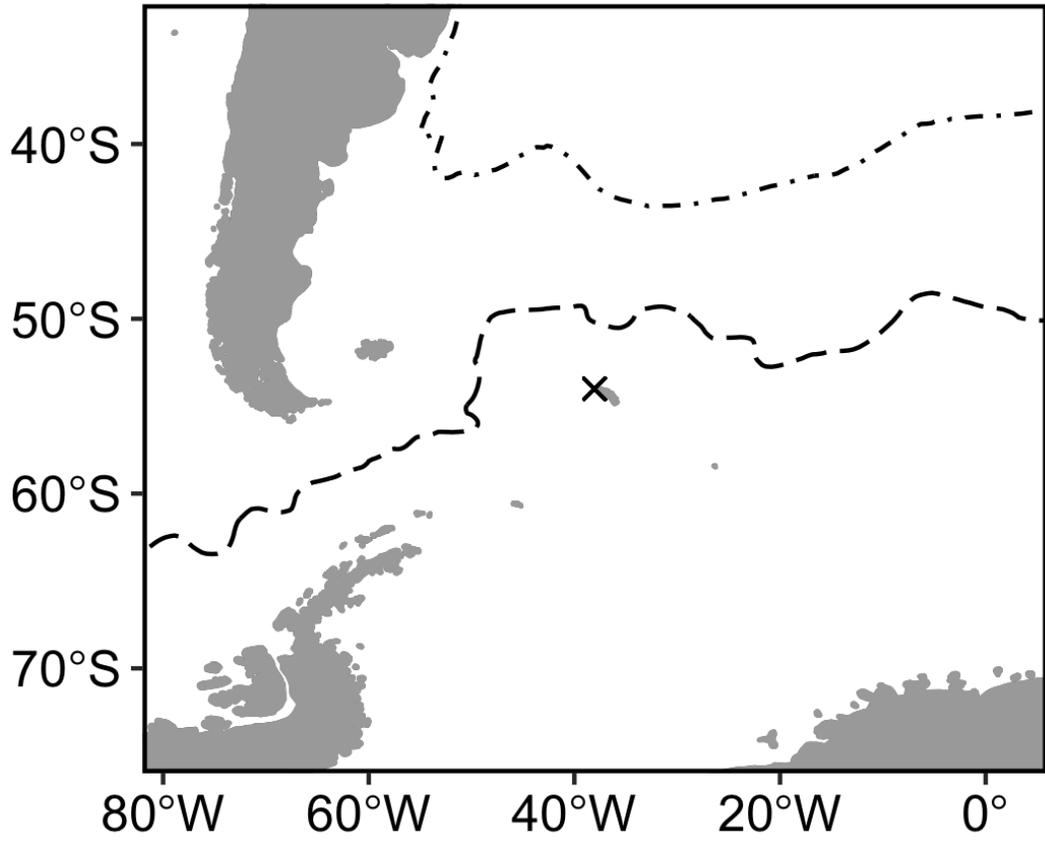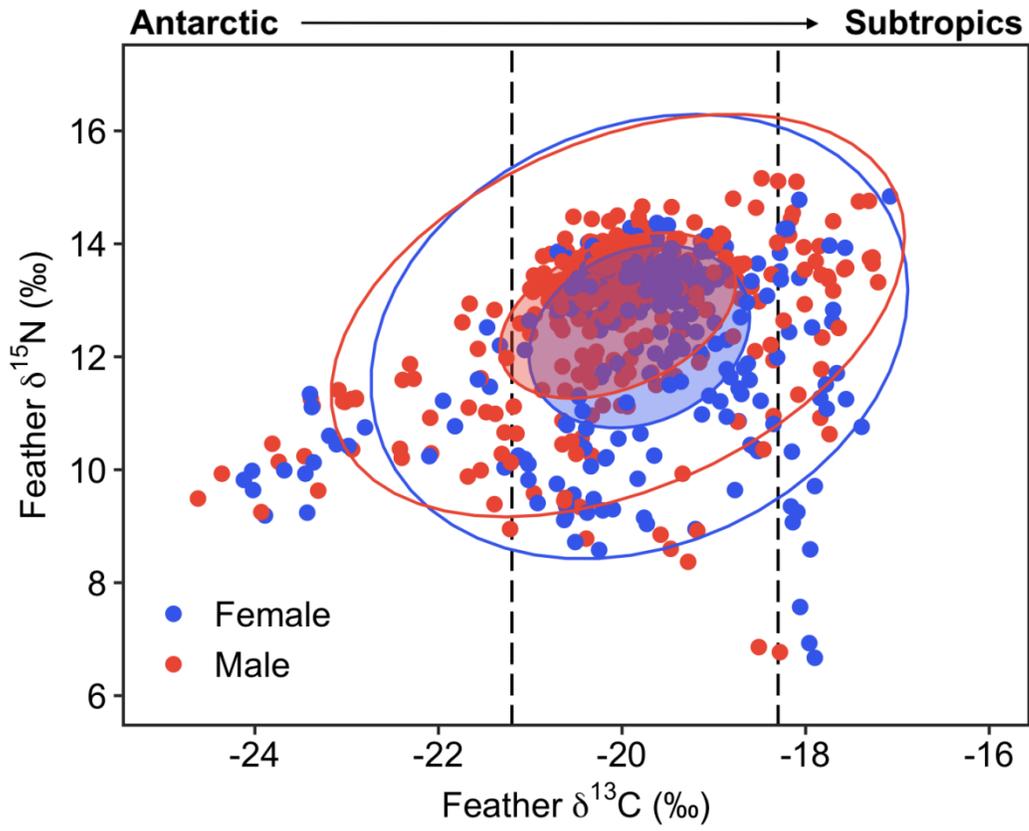
Figure 2. Stable isotope values (δ^{13}C, δ^{15}N) of individual body feathers from adult Grey-headed Albatrosses *Thalassarche chrysostoma* at Bird Island, South Georgia (2013/14–2015/16). Vertical lines are δ^{13}C estimates of the Antarctic Polar Front (–21.2 ‰) and Sub-Tropical Front (–18.3 ‰), separating the Antarctic Zone, Subantarctic Zone, and Subtropical Zone (Jaeger *et al.* 2010). Standard ellipse areas corrected for small sample sizes (SEA$_C$; shaded) and 95% ellipses areas are shown.

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