1   **Running head:** *Spatio-temporal segregation in giant petrels*

2

3   **Segregation in space and time explains the coexistence of two sympatric sub-Antarctic petrels**

4   HANNA M. V. GRANROTH-WILDING[1*] & RICHARD A. PHILLIPS[2]

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6   [1]*Department of Biosciences, Division of Ecology and Evolution, University of Helsinki, Viikinkaari*

7   *1, 00014 Helsinki, Finland. ORCID iD: 0000-0002-4052-3821.*

8   [2]*British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road,*

9   *Cambridge, CB3 0ET, United Kingdom.*

10

11   * Corresponding author. Email: hanna@granroth-wilding.co.uk

12 Biological communities are shaped by competition between and within species. Competition is

13 often reduced by inter- and intra-specific specialization on resources, such as differences in foraging

14 areas or time, allowing similar species to coexist and potentially contributing to reproductive

15 isolation. Here, we examine the simultaneous role of temporal and spatial foraging segregation

16 within and between two sympatric sister species of seabirds, Northern *Macronectes halli* and

17 Southern *M. giganteus* Giant Petrels. These species show marked sexual size dimorphism and

18 allochrony (with earlier breeding by Northern Giant Petrels), but this is the first study to test for

19 differences in foraging behaviours and areas across the entire breeding season both between the two

20 species and between the sexes. We tracked males and females of both species in all breeding stages

21 at Bird Island, South Georgia, to test how foraging distribution, behaviour and habitat use varies

22 between and within species in biological time (incubation, brood-guard or post-brood stages) and in

23 absolute time (calendar date). Within each breeding stage, both species took trips of comparable

24 duration to similar areas, but due to breeding allochrony they segregated temporally. Northern Giant

25 Petrels had a somewhat smaller foraging range than Southern Giant Petrels, reflecting their greater

26 exploitation of local carrion and probably contributing to their recent higher population growth.

27 Within species, segregation was spatial, with females generally taking longer, more pelagic trips

28 than males. Both sexes of both species showed unexpectedly plastic foraging behaviour, and there

29 was little evidence of inter-specific differences in habitat use. Thus, in giant petrels, temporal

30 segregation reduces inter-specific competition and sexual segregation reduces intra-specific

31 competition. These results demonstrate how both specialization and dynamic changes in foraging

32 strategies at different scales underpin resource division within a community.

33 **Keywords:** Allochrony, inter-specific competition, intra-specific competition, niche differentiation,

34 Procellariiformes, resource partitioning, sexual segregation, speciation, tracking

35 Competition in ecological communities, both between and within species, is a fundamental

36 ecological process, with important evolutionary consequences. Coexistence between community

37 members is promoted by a reduction in this competition, often because different members exploit

38 different parts of the resource space, such as particular habitats or prey (Schoener 1974). This

39 resource partitioning or niche differentiation can shape the structure of a community, driving

40 evolutionary change in its constituent organisms (Zuppinger-Dingley *et al.* 2014) and promoting

41 species coexistence in plants (Silvertown 2004), insects (Augustyn *et al.* 2016), fish (Bonin *et al.*

42 2015), mammals (Stewart *et al.* 2002; Nicholls & Racey 2006) and birds at local and regional scales

43 (Gotelli *et al.* 2010; Young *et al.* 2010).

44   Among morphologically similar competitors, partitioning of habitat or prey resources can

45 play an important role not only in maintaining coexistence but also in isolating diverging taxa

46 during incipient speciation (Svanback & Bolnick 2007). In such contexts, resources are often

47 partitioned through behavioural mechanisms (Nicholls & Racey 2006). Behaviour can change

48 rapidly in response to increasing competitive pressure, often in ways consistent with existing

49 morphological differences between sub-populations (Svanback & Bolnick 2007, Linnebjerg *et al.*

50 2013, Drago *et al.* 2015). Such behavioural divergence is frequently observed as segregation

51 between species or sub-populations either in space or in time, for example with sympatric species

52 reducing inter-specific competition by foraging in different areas during the breeding or

53 nonbreeding seasons (Phillips *et al.* 2005, Rayner *et al.* 2016), at differing heights or depths

54 (Nicholls & Racey 2006, Navarro *et al.* 2013), or at different times of day (Wilson 2010, Navarro *et*

55 *al.* 2013). Particularly where it occurs on a variety of scales or in different foraging traits,

56 segregation may nonetheless be difficult to resolve, even in systems where competitors differ

57 morphologically (Conners *et al.* 2015).

58   Similar segregation patterns within species have also been well documented, with

59 behavioural differences resulting in partitioning of food resources according to sex or age class

60 (Lewis *et al.* 2001, Lecomte *et al.* 2010). The competition that drives such segregation is expected

61 to be particularly intense when adults of both sexes congregate to breed (Phillips *et al.* 2011,

62 Phillips *et al.* 2017, Drago *et al.* 2015), and sexual segregation in foraging, which can act to reduce

63 intra-specific competition, is widespread among vertebrates (Lewis *et al.* 2001, Ruckstuhl &

64 Neuhaus 2002, Catry *et al.* 2005, Breed *et al.* 2006). Males and females may forage in different

65 areas, at different times, or take different prey, in sexually monomorphic as well as dimorphic

66 species, although behavioural differentiation can be subtle even in species with extreme sexual

67 dimorphism (Lewis *et al.* 2002, Ruckstuhl & Neuhaus 2002, Phillips *et al.* 2011, 2017, Harris *et al.*

68 2013, Griffiths *et al.* 2014, Baylis *et al.* 2016). Competition between the sexes has been implicated

69 in the evolution of specialisation and segregation in many contexts, for example with males and

70 females exploiting different habitat types or taking different roles when rearing offspring, even

71 where segregation has proved difficult to resolve (Copello *et al.* 2011, Pinet *et al.* 2012, Ludynia *et*

72 *al.* 2013, Cleasby *et al.* 2015, Baylis *et al.* 2016).

73   Both inter- and intra-specific differences in distribution and behaviour arise as dynamic

74 responses to the biotic and abiotic environment and may therefore vary over time. Such flexibility

75 in foraging strategy is particularly important when foraging is constrained, such as in central-place

76 foragers when habitat use is spatially restricted, and energy and time budgets are limited by the

77 changing demands of incubation and chick-rearing (Phillips *et al.* 2017). Breeding seabirds are

78 typically subject to these foraging constraints, making them an informative model for investigating

79 how the competition that such restrictions induce is resolved through variation in foraging

80 behaviour on different scales. These constraints may differ between the sexes and occur on different

81 schedules in otherwise similar species and habitats (Elliott *et al.* 2010, Beaulieu & Sockman 2012,

82 Pinet *et al.* 2012). Inter-specific segregation in timing of breeding (allochrony) may therefore be a

83 crucial mechanism enabling the coexistence of similar species, maintaining reproductive isolation in

84 related taxa, or potentially driving sympatric speciation (Wilson 2010, Brown *et al.* 2015). A

85   complete understanding of dynamic resource partitioning within a community requires

86   consideration of both inter- and intra-specific segregation patterns not only in space but also in time.

87   Moreover, while studies in a wide range of species have described certain components of the

88   structure of inter- and intra-specific spatial and temporal segregation in foraging areas, only recently

89   have such differences been linked explicitly to habitat variables (Pinet *et al.* 2012, Thiers *et al.*

90   2014, Cleasby *et al.* 2015). This is critical to understanding the mechanisms that give rise to

91   observed patterns in foraging behaviour and hence allow predictive modelling of foraging

92   distributions within a community.

93   The pattern of inter- and intra-specific (between-sex) segregation in foraging distributions

94   has received much attention in Northern and Southern Giant Petrels, *Macronectes halli* and *M.*

95   *giganteus*, two recently diverged (~500-200 kya, Techow *et al.* 2010) sister species of seabirds

96   distributed from subtropical to Antarctic waters that breed sympatrically across most of their range.

97   Both species are commonly thought of as scavengers, feeding predominantly on seal and penguin

98   carrion, and in the males, scavenging is often considered to be near-obligate (Hunter 1983,

99   González-Solís 2004, Forero *et al.* 2005). Indeed, several biologging, diet and isotope studies have

100   shown that the sexes employ different foraging strategies: males tend to feed closer to the colony,

101   presumed to be exploiting carrion on local beaches, while females undertake longer trips to capture

102   more pelagic, live prey and are less frequently observed at carcasses on shore (Hunter 1983,

103   González-Solís *et al.* 2000a, González-Solís *et al.* 2002, Forero *et al.* 2005, González-Solís *et al.*

104   2007, Copello *et al.* 2011, Thiers *et al.* 2014). This niche differentiation is considered to be linked

105   with sexual size dimorphism: males of both species are ~20% larger than females and have more

106   robust bills, which may equip them to more efficiently exploit carcasses on land (Hunter 1987,

107   González-Solís 2004). However, tracking with sufficient accuracy to separate coastal (likely

108   scavenging) trips from more pelagic trips has only been undertaken during a single breeding stage,

109   or in multiple stages but from only one species at that site (González-Solís *et al.* 2000b, González-

110 Solís *et al.* 2002, Thiers *et al.* 2014), and the relative roles of sexual and inter-specific segregation

111 across the entire breeding period therefore remain unclear. Crucially, the focus in previous work on

112 breeding stages overlooks a marked difference between the species in timing of breeding. Northern

113 Giant Petrels breed around 6 weeks earlier than Southern Giant Petrels (Hunter 1987, Brown *et al.*

114 2015), hence the breeding stages and associated constraints on foraging behaviour hardly overlap

115 between the species. This allochrony (difference in timing of breeding) is assumed to have been a

116 key factor in divergence of the two species (Hunter 1987 Friesen *et al.* 2007), but its importance in

117 terms of inter- and intra-specific differences in foraging distribution and ecology is much less clear.

118   Despite the similarity in their morphology, ecology and environment, Northern and Southern

119 Giant Petrels breeding sympatrically at Bird Island in South Georgia have displayed different

120 population trajectories over the last two decades, implying a role for behavioural differences in how

121 resources are divided between and within the species. Here, we provide a full analysis of inter- and

122 intra-specific segregation in foraging behaviour among giant petrels throughout breeding,

123 investigating the simultaneous role of different axes of segregation – temporal and spatial – in

124 supporting their coexistence. Previous work suggests that the two species segregate in both space

125 and time and the sexes in space, but these predictions do not account for the temporal offset of

126 breeding stages. We explicitly examine how segregation patterns vary both with competition in

127 absolute time and with the biological constraints of breeding stage, and assess the importance of

128 intra- and inter-specific differences in habitat use.

129

130

131 **METHODS**

132

133 **Study species and field data collection**

134 Tracking data were collected from male and female Northern and Southern Giant Petrels breeding

135 on Bird Island, South Georgia (54°00'S, 38°03'W) throughout the breeding season in the austral

136 summer of 2005/06. Here, the two species breed sympatrically in the same areas and habitats, but in

137 small groups that tend to consist of the same species. Two devices were deployed on each bird: a

138 3.6 g geolocator-immersion logger (Mk 4, Mk 5 or Mk 7; British Antarctic Survey, Cambridge, UK)

139 attached with cable-ties to a plastic leg ring, and a 20 g or 30 g satellite tag (91 deployments:

140 platform terminal transmitter, PTT-100; Microwave Telemetry) or a 68 g GPS logger (12

141 deployments: BGDL-II; Shizuoka University, Japan) to record locations, attached to mantle feathers

142 using Tesa tape. The PTT transmitted at 90 s intervals, and an average of 25.0 locations were

143 obtained per day (one location every 57 min) from each device using the ARGOS satellite system.

144 The GPS devices were set to record a location every 60 min. The immersion loggers tested for

145 saltwater immersion every 3 s, and then either recorded every change of state from wet-to-dry or

146 *vice versa* that lasted $\geq$ 6 s (Mk 7) or binned these data into 10 min intervals, providing a value

147 between 0 (completely dry) and 200 (completely wet) (Mk 4 and Mk 5). The combined mass of

148 devices and attachments were always <1.5% of body mass, which is within the recommended 3%

149 limit to avoid deleterious effects (Phillips *et al.* 2003) (heavier GPS devices deployed only on

150 males; for 36 individuals with available data, mean mass $\pm$ s.e. of male and female Northern Giant

151 Petrels was 4.72 ± 0.10 kg and 3.51 ± 0.07 kg, and of male and female Southern Giant Petrels was

152 4.35 ± 0.10 kg and 3.64 ± 0.09 kg, respectively). All birds were sexed from bill dimensions, and had

153 been fitted previously with a standard British Trust for Ornithology ring and a plastic ring with a

154 unique combination of colour and 3-character alphanumeric code as part of a long-term study

155 programme (Brown *et al.* 2015). Nests were visited daily during incubation and brood-guarding,

156 ringed adults were identified, and the dates when the chick hatched and was first left unattended

157 (i.e. end of brood-guarding) were recorded; thereafter, nests were visited every few days.

158   Locations provided by PTTs are accurate to 1-10 km (median across all but the poorest-

159 quality ARGOS Location Classes (LC) B and Z (Douglas *et al.* 2012)) which is not sufficiently high

160   resolution to distinguish between attendance at the nest and foraging on land nearby. Separate

161   foraging trips to sea were therefore discriminated from the patterns of saltwater immersion. A trip

162   was defined as any period of intermittent wet records that included no more than 12 hours of

163   contiguous dry time, a conservative interval based on manual inspection of the immersion data in

164   relation to daily observations of nest attendance. However, Mk 7 loggers (55 out of 103

165   deployments) frequently showed likely erroneous wet events, commonly occurring as a series of

166   isolated, short (3-6 seconds) immersions, including from periods when visual records indicated that

167   the bird was at the nest. In order to identify trip start and end times consistently across all logger

168   types, we therefore disregarded all immersion events of $\leq$ 9 s if no immersion event of > 9 s

169   occurred within the previous or following hour. Trip assignments were confirmed from attendance

170   records for each individual (based on daily visits to nests during incubation and brood-guarding),

171   with only one of the 139 trips identified to that point requiring further splitting. For 13 of the 103

172   deployments, the immersion data did not allow individual trips to be discriminated. The remaining

173   deployments generated 127 trips from 71 individuals across all breeding stages (Table 1). Trips

174   were assigned to incubation, brood-guarding or post-guard chick-rearing, according to nest status

175   when the adult departed.

176

177   **Tracking data analysis**

178   All data preparation and analysis was done in R (R Core Team, 2015) using an azimuthal equal-area

179   projection centred on Bird Island on a WGS 84 coordinate system. Low quality PTT fixes (LC Z)

180   were removed and the retained fixes were iteratively speed-filtered to remove likely erroneous

181   locations, using McConnell *et al.*'s (1992) algorithm implemented in the *argosfilter* package (Freitas

182   2012). A maximum speed of 30 m/s was allowed between two subsequent fixes, based on the 99th

183   percentile of speeds between fixes (29.9 m/s, following González-Solís *et al.* (2000b)). Each filtered

184   location was classified as coastal if it fell within 10 km (conservative ARGOS error) of land at

South Georgia, or as pelagic if outside this zone. On this basis, we calculated the proportion of each

trip that was coastal, and if this exceeded 50% of fixes, the entire trip was classified as "coastal"; all

other trips were classified as "pelagic". Locations in each trip were interpolated at 30 min intervals

using the *adehabitatLT* package (Calenge 2006). Each interpolated fix was classified as daylight or

darkness (daylight includes civil twilight, i.e. sun higher than 6º below the horizon). Travel

distance, trip duration and maximum distance from the colony (maximum range) were calculated

for each trip from the interpolated data. In addition, each trip was binned into early, middle and late

periods (hereafter "period", a three-level factor) according to the calendar date at departure, with

cut-off points defined by thirds of the distribution of all trips across both species.

Habitat use was analysed for pelagic trips by females only, as the few pelagic trips by males

were unbalanced in terms of representing the different breeding stages. Using a 50 km grid across

the entire study area, we calculated time spent per grid cell using the package *trip* (Sumner 2015).

This was based only on fixes during daylight, as much of the night is spent resting in giant petrels

and other large Procellariiformes (González-Solís *et al.* 2002; Phalan *et al.* 2007; but see Conners *et al.* 2015), and excluding cells that intersected with land at South Georgia. Habitat data were

extracted as 8-day composites for each used grid cell in the relevant temporal period. These were

remotely-sensed sea surface temperature (SST), chlorophyll a and non-directional wind speed

obtained from the National Oceanic and Atmospheric Administration (BloomWatch 360;

http://coastwatch.pfel.noaa.gov/browsers/cwbrowser_global360.html) and bathymetry data

(GEBCO) obtained from the British Oceanographic Data Centre. These rasterized data were

projected and averaged from their original resolutions (0.05 degrees for SST, 0.05 degrees for

chlorophyll a, 0.125 degrees for wind, and 0.5 degrees for bathymetry) onto the coarser 50 km grid

used for the calculation of habitat usage.

Kernel density contours (utilisation distributions) were calculated from all interpolated

locations (daylight and darkness) from both sexes, including pelagic and coastal trips, and also the

210 13 deployments in which individual trips could not be discriminated. We used a 10km grid with the

211 same smoothing parameter of 50 km for all species-sex-breeding stage combinations (the median

212 value of the least-squares cross-validated smoothing factors selected in each subgroup's kernel

213 analysis) to avoid bias when comparing usage distributions. Pairwise overlaps were calculated

214 between the distributions of each species-sex-breeding stage combination as the volume of

215 intersection between the 100% kernels in the package *adehabitatHR*, providing a value ranging

216 from 0 (no overlap) to 1 (complete overlap).

217

218 **Analysis**

219 We investigated how species, sex and trip timing affected trip characteristics and habitat use. Trip

220 characteristics comprised: trip duration; travel distance; maximum range; the proportion of the trip

221 that was coastal, as an indication of scavenging; and trip start time (time of day of departure), which

222 in other dimorphic species varies with sex-specific breeding roles or constraints (Harris *et al.* 2013).

223 Habitat variables were compared across those grid cells in which either species was present. For all

224 these response variables, we first tested a set of models that included breeding stage as the temporal

225 predictor variable, examining how ecological constraints shape foraging behaviour across the

226 species and sexes. We then compared these results to an analysis including period (reflecting

227 calendar date; see above) rather than breeding stage as the temporal predictor, examining whether

228 real-time competition between the species and sexes alters behaviour and habitat use. Northern

229 Giant Petrels lay around 6 weeks earlier (Brown *et al.* 2015; mean first lay date across all monitored

230 nests in study year and area: Northern Giant Petrels [$n = 242$], 01 October 2005; Southern Giant

231 Petrels [$n = 126$], 10 November 2005); among tracked birds, all Southern Giant Petrel incubation

232 fell within Northern Giant Petrels' brood-guarding, while later breeding stages overlapped by

233 around one week between the species. Due to this allochrony, only one individual Northern Giant

234 Petrel yielded discriminated trips in the late period. To prevent this restricted sample from skewing

235 model fits, all models examining period were fitted to tracks only from the early and middle

236 periods, except those for maximum range and trip start time, for which non-discriminated trips were

237 also used because locations at the nest would not affect these variables.

238   Activity patterns could not be reliably inferred from the immersion data due to the erroneous

239 wet events recorded by the Mk 7 loggers (proportion of trip wet for Mk 7 compared to other Mk 4

240 and Mk 5 loggers, in a binomial generalized linear mixed model controlling for species, sex and

241 breeding stage as fixed effects and individual as a random effect with a logit link: 1.54 ± 0.15, $Z =$

242 10.40, $P < 0.001$). Within any breeding stage, which is the main constraint on behaviour, there were

243 insufficient numbers of individuals fitted with Mk 4 or Mk 5 loggers to allow robust comparison of

244 species or sexes, and therefore we do not address activity patterns further. In the light of this

245 malfunctioning of the saltwater sensing – likely oversensitivity, responding to wet nests, vegetation

246 or salts washing off plumage in addition to full immersion – previous studies that have used BAS

247 Mk 7 loggers may benefit from a reassessment of their conclusions.

248   We used the same model selection approach for all analyses: an information theoretic

249 approach based on AIC to select the most informative variables from a set of 13 candidate models.

250 This metric assesses the fit of the entire model and thus avoids type I errors associated with multiple

251 testing in this extensive exploratory analysis, while penalizing over-fitting (Burnham & Anderson

252 2013). Our candidate models included 1, 2, or 3 main effects, and interactions between species and

253 sex, and between species and the temporal variable (breeding stage or period), to test whether these

254 variables influenced foraging behaviour differently in the two species. All models with an

255 interaction also contained both component variables as main effects (full list in captions of Tables 3-

256 4 and Supplementary tables 1-2) and all models were fitted using maximum likelihood. Models are

257 generally considered to have an equivalent fit (i.e. similarly informative) if their AIC is within 2

258 units (ΔAIC < 2) of the best-fitting model (Burnham & Anderson 2013). To assess the relative

259 explanatory power of our two temporal variables, breeding stage or period, we compared the fits of

260　both model sets using a reduced dataset that allowed all models to be robustly fitted; removing the

261　insufficient late period trips left the post-brooding stage insufficiently represented, so this

262　comparison excludes both these temporal divisions. To help differentiate between models of similar

263　fits, we also calculated the AIC weight (relative likelihood) of each model, normalized across the

264　candidate model set to capture their relative fits. We considered a model to have "some" support if

265　it was at least twice as likely relative to the next-best fit model, "good" support if its relative

266　likelihood was over 0.5 (absolutely most likely), and "robust" support if both of these criteria

267　applied. In model sets that did not yield a single, preferred model, we considered all models with

268　likelihoods > 50% of that of the best-fit model, and considered those variables present in over half

269　of these models to have "some" support. Models with a relative likelihood of < 50% of the best-fit

270　model were not considered informative.

271　　　　All models were linear or generalized linear mixed models ((G)LMMs) fitted using the *nlme*

272　or *lme4* packages (Bates *et al.* 2015, Pinheiro *et al.* 2016). For trip characteristics, individual ID was

273　fitted as a random intercept to account for multiple trips by the same individual. For habitat use,

274　each response variable was modelled as its value in each grid square per trip with each value

275　weighted by the time spent in that grid cell in that trip. As each trip covered many grid squares and

276　each bird potentially undertook multiple trips, trip ID nested within individual ID was fitted as a

277　random intercept. To ensure that all model assumptions were met, chlorophyll and wind were log-

278　transformed to reduce skew in the raw data and normalize residuals.

279

280

281　**RESULTS**

282

283　**Foraging areas**

284　Northern and Southern Giant Petrels were both widely distributed in the south-west Atlantic in the

285 austral summer 2005/06, but with marked differences between sexes and breeding stages (Fig. 1).

286 Females tended to forage more widely in both species, and across both species, constraints on

287 distribution were strongest during brood-guarding (Fig. 1). Females of both species were recorded

288 from the Scotia Arc in the south and east, to the Patagonian Shelf and Antarctic Peninsula region in

289 the west. In contrast, male Northern Giant Petrels were always concentrated around the colony, and

290 male Southern Giant Petrels only exploited more distant areas south and south-west of the colony in

291 the post-brood chick-rearing period. Overall, Southern Giant Petrels travelled east and west of Bird

292 Island, whereas Northern Giant Petrels only travelled substantial distances to the west; neither

293 species made substantial use of pelagic waters to the north of the colony. The 50% kernels of

294 females of both species and male Southern Giant Petrels included the South Orkney Islands, and

295 these trips, though pelagic in range, may have included coastal scavenging. Southern Giant Petrels

296 of both sexes visited the South Sandwich Islands, and the females also consistently used a small

297 area to their west.

298   In pairwise comparisons, the mean overlap between the utilisation distributions of each

299 species-sex-breeding stage combination was 0.487 (Table 2). This reflected a mixture of generally

300 high overlaps between the distribution of certain groups – males of both species, male and female

301 Northern Giant Petrels in general, and between both species within the brood-guarding period – and

302 generally low overlaps between other groups – female Northern and Southern Giant Petrels during

303 incubation, and female Southern Giant Petrels in incubation or post-brood and males of both species

304 (Table 2).

305

306 **Trip characteristics**

307 In the model sets testing the effect of breeding stage on the characteristics of foraging trips, there

308 was weak support that trips of Southern Giant Petrels were longer in terms of both travel distance

309 and duration than those of Northern Giant Petrels, although the effect size of the species term in the

310 best-fit model overlapped zero (mean travel distance ± s.e. for Northern Giant Petrels, 1775 ± 426

311 km and for Southern Giant Petrels, 3113 ± 461 km, Fig. 2; mean trip duration 79.7 ± 16.1 h and

312 154.8 ± 21.5 h, respectively; Table 3, Supporting Information Table S1). In keeping with this, the

313 maximum range of foraging trips – closely correlated with both travel distance and trip duration

314 (Spearman's r^2 of 0.861 and 0.707, respectively, both $P < 0.001$), but tested with the larger sample

315 that included non-discriminated trips it did not differ between the two species (overall mean

316 maximum range, 399 ± 43 km). Regardless of species, the sex and breeding stage affected trip

317 length: males travelled less far and for less time (Fig. 2; mean trip duration for males, 99.6 ± 17.4 h;

318 for females 160.6 ± 25.6 h) and for both sexes, compared to incubation, trips during brood-guarding

319 were somewhat shorter and trips in post-brood substantially longer (Fig. 2, Table 3, Supporting

320 Information Table S1). These differences were reflected in the smaller maximum range of males

321 than females, and the maximum range of both sexes during brood-guarding and post-brood were

322 shorter and longer, respectively (Table 3, Supporting Information Table S1). There was some

323 evidence that trips started progressively earlier in the day through the breeding stages, as breeding

324 stage was included in all top-fitting models, but none had strong support, and mean trip start time

325 did not vary between the species or sexes (Table 3, Supporting Information Table S1). There was no

326 evidence that sex or breeding stage affected characteristics of foraging trips in different ways in the

327 two species (i.e. no well-supported interactions with species, Table 3).

328   Clearer differences were seen in the proportion of the trip that birds spent within 10 km of

329 South Georgia (coastal foraging). Males spent more time near the coast, but this effect was less

330 pronounced in Northern than in Southern Giant Petrels (Table 3, Supporting Information Table S1,

331 Fig. 3). In addition, birds spent more time near the coast during brood guarding than in incubation

332 or post-brood (mean proportion of trip coastal in incubation, 0.402 ± 0.076, in brood-guarding,

333 0.473 ± 0.048, and in post-brood, 0.423 ± 0.056; Table 3, Supporting Information Table S1). Across

334 both species and sexes and all breeding stages, coastal trips were shorter in duration than pelagic

335 trips (across all trips, mean duration of coastal trips 71.3 ± 11.2 h; of pelagic trips, 178.3 ± 25.6 h;

336 in LMM accounting for species, sex and breeding stage, effect of trip type (pelagic vs. coastal) 88.3

337 ± 22.8 h, t = 3.87, P = 0.0003). Among coastal trips, there was no strong evidence that species, sex,

338 or breeding stage affected maximum range (null model best fit, AIC weight 0.407, next-best 0.182),

339 suggesting that none of these factors influenced whether birds stayed close to the colony or foraged

340 coastally elsewhere at South Georgia.

341　　　In model sets testing the effect of period instead of breeding stage, there were marked

342 differences in the characteristics of foraging trips of Northern and Southern Giant Petrels, reflecting

343 the interspecific difference in laying dates and therefore the relative (calendar) timing of breeding

344 stages. Southern Giant Petrels made longer trips in the early period and shorter trips in the late

345 period, whereas the reverse was true for Northern Giant Petrels (for Northern Giant Petrels, mean

346 travel distance in early period 1250 ± 307 km, middle period 3827 ± 1582 km; for Southern Giant

347 Petrels, early period 5970 ± 1134 km, middle period 1439 ± 310 km; Table 3, Supporting

348 Information Table S1). Mirroring the patterns by breeding stage, Southern Giant Petrels had a

349 greater maximum range overall, and across both species, later trips were to waters further from the

350 colony, with weak support for an interaction between species and period. Also similar to the

351 breeding stage models, the effect of period on the proportion of a trip that was coastal did not differ

352 between the species, and the start time of trips was not explained by any of the factors examined

353 alongside period (Table 3, Supporting Information Table S1). Overall, breeding stage explained

354 more variation in all trip characteristics than period, with the best-fit breeding stage model having a

355 ΔAIC of > −7 compared to the best-fit period model (ΔAIC between best-fit breeding stage and

356 period models fitted to the same reduced dataset: for travel distance −7.8, for trip duration −9.9, for

357 maximum range −10.8, for trip start time −7.1, for proportion of the trip that was coastal −28.3).

358

359 **Habitat use**

360   By comparison with the analyses of trip characteristics, there was limited evidence that females of

361   the two species differed in their habitat use on pelagic trips. In models examining the effect of

362   breeding stage, used grid cells did not differ notably in either wind or bathymetry between either

363   species or breeding stage (Table 4). Sea surface temperature of used grid cells was similar in both

364   species, although Northern Giant Petrels used areas of warmer SST across breeding stages whereas

365   SST used by Southern Giant Petrels was more consistent across the breeding season (mean SST ±

366   s.e. used by Northern Giant Petrels in incubation, brood-guarding and post-brooding 1.32 ± 0.08 ºC,

367   1.82 ± 0.07 ºC, 4.05 ± 0.12 ºC, respectively; and similarly by Southern Giant Petrels 2.50 ± 0.09 ºC,

368   2.76 ± 0.06 ºC, 2.07 ± 0.06 ºC; Table 4, Supporting Information Table S2). The species also differed

369   in chlorophyll a concentrations in their foraging areas, which tended to be lower in grid cells used

370   by Southern than Northern Giant Petrels (mean chlorophyll a ± s.e. in cells used by Northern Giant

371   Petrels 0.86 ± 0.05 mg/m^3, and by Southern Giant Petrels 0.64 ± 0.02 mg/m^3; Table 4, Supporting

372   Information Table S2).

373   Models examining the effect of period provided little evidence for interspecific differences

374   in habitat use. Consistent with seasonal environmental changes, period affected both temperature

375   and winds experienced by tracked birds (Table 4), with all birds using areas of warmer water and

376   lower winds in the middle than early period (mean SST ± s.e. in used cells in early and middle

377   periods, 2.77 ± 0.09 ºC and 3.45 ± 0.09 ºC respectively; mean wind speed ± s.e., 8.76 ± 0.04 m/s

378   and 7.55 ± 0.04 m/s respectively; Supporting Information Table S2). In addition, birds foraged in

379   deeper waters in the early than the middle period (mean depth ± s.e. in used cells in early and

380   middle periods, 3062 ± 48 m and 2476 ± 54 m, respectively; Table 4, Supporting Information Table

381   S2). As in the analysis by breeding stage above, Southern Giant Petrels foraged in areas of

382   somewhat lower chlorophyll a concentrations than Northern Giant Petrels (Table 4, Supporting

383   Information Table S2).

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DISCUSSION

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The two closely-related species of sexually dimorphic giant petrels at South Georgia provide an

opportunity to test the simultaneous roles of spatial and temporal segregation in enabling

coexistence between and within species. By tracking both sexes over the entire breeding season, we

have shown that foraging Northern and Southern Giant Petrels segregate in time, and that males and

females within each species largely segregate in space. Both species employed similar strategies,

showing broadly matching trip characteristics and habitat use under the same biological constraints

(associated with breeding stage), but direct competition between the species is reduced by the

considerably earlier breeding of Northern Giant Petrels (by six weeks; Brown *et al.* 2015). This is

rare evidence supporting the importance of breeding allochrony in the coexistence of sister species.

Tracked Northern Giant Petrels had a slightly smaller overall foraging range, and a much smaller

range during incubation and brood-guarding than Southern Giant Petrels. The smaller range earlier

in the season likely reflects their exploitation of carrion, associated with the recovery of the local

Antarctic Fur Seal *Arctocephalus gazella* population, which may have contributed to the faster

growth in numbers of breeding Northern than Southern Giant Petrels in recent decades (González-

Solís *et al.* 2000a; Brown *et al.* 2015). Broadly, males of both species made shorter and more

coastal trips (presumably scavenging) while females were more pelagic, yet both sexes were

capable of long, pelagic trips. Thus the common perception that giant petrels, especially the males,

are near-obligate scavengers through the breeding season needs to be reconsidered. Brood-guarding

birds of both sexes tended to forage more coastally and to take shorter trips, as expected given that

young chicks require frequent meals, and constant parental care to aid thermoregulation and reduce

the risk of predation, as in other surface-breeding Procellariiformes (Catry *et al.* 2006). Overall, our

results demonstrate the role of segregation along different axes of variation (temporal, in terms of

410 both breeding stage and absolute time, and spatial) in maintaining coexistence among similar

411 species.

412   Although the tracked Northern and Southern Giant Petrels differed to some extent in

413 distribution and behaviour, sex and breeding stage had a stronger influence than species or period

414 (calendar date) on their foraging ecology, with little evidence that these effects differed between the

415 two species. The similarity in the foraging strategies of these sister taxa implies that intra-specific

416 segregation patterns have changed little in the 500-200ky since the species diverged (Techow *et al*.

417 2010) and hence suggests that they are ancestral to both species (Hunter 1987). Despite their similar

418 strategies in biological time (breeding stage), in absolute time (i.e. in terms of calendar date), many

419 aspects of foraging behaviour differed between the species. Thus, rather than partitioning

420 contemporaneous foraging resources through changes in a complex suite of behaviours, competition

421 between these ecologically and morphologically similar species appears instead to be resolved

422 through a shift in breeding phenology, a trait that in many species has the potential for rapid

423 evolution (Franks *et al*. 2007, Friesen *et al*. 2007, Tarka *et al*. 2015). In other systems, inter-specific

424 competition may be resolved through dynamic differentiation in other behavioural traits: Rock

425 Shags *Phalacrocorax magellanicus* undertake longer trips when breeding in sympatry with the Red-

426 legged Cormorant *P. gaimardi* than when breeding in single-species colonies (Frere *et al*. 2008).

427 Indeed, it has been suggested that behavioural modification is the most likely immediate response

428 of seabirds to environmental change (Lewis et al. 2006). In giant petrels, our results indicate that

429 several aspects of behaviour, most notably breeding phenology but also foraging strategies, appear

430 to be labile traits that may have allowed initial rapid responses to reduce competition through

431 resource partitioning. In addition to the temporal segregation, Southern Giant Petrels tended to

432 forage slightly further afield and exploit more westerly areas than Northern Giant Petrels. This

433 difference in foraging ranges is likely to reduce costs of reproduction to some extent in Northern

434 Giant Petrels, and hence may underlie the difference between the species in population growth rate.

435   The sexual segregation we observed in both species, with females typically foraging further

436   afield than males, particularly in early breeding stages, is consistent with previous findings from a

437   range of biologging, stable isotope and diet studies (Hunter 1983, González-Solís *et al*. 2000a,

438   González-Solís *et al*. 2000b, González-Solís *et al*. 2002, Forero *et al*. 2005, Phillips *et al*. 2011,

439   Raya Rey *et al*. 2012, Thiers *et al*. 2014). These behavioural differences are associated with

440   pronounced sexual size dimorphism: size differences have been assumed to constrain the larger

441   males, which presumably have higher costs of flying, to specialise on the exploitation of seal and

442   penguin carrion on local beaches, excluding the slighter females from these resources and forcing

443   them to forage further afield (Hunter 1983, González-Solís *et al*. 2000b). However, our finding that

444   both sexes of both species undertook substantial (> 4 days and > 1800 km) pelagic trips as well as

445   coastal trips shows that foraging distributions in the giant petrels are more plastic than commonly

446   appreciated during the breeding season, and not tightly constrained by physiological limits such as

447   wing loading or competitiveness. This supports previous findings from the non-breeding season and

448   diet studies (Hunter 1983, González-Solís *et al*. 2007, but see Thiers *et al*. 2014). Although females

449   in particular undertook long foraging trips that resembled other medium-to-large, wide-ranging

450   Procellariformes, such as albatrosses and White-chinned Petrels *Procellaria aequinoctialis* (Phillips

451   *et al*. 2004, Phillips *et al*. 2005, Phillips *et al*. 2006), males were far from exclusively coastal when

452   not constrained by chick demands. Similarly, consistent with the morphological specializations of

453   both sexes (but particularly males) for exploiting carrion (Hunter 1983, González-Solís 2004,

454   Forero *et al*. 2005), coastal foraging by both males and females indicates that scavenging is less

455   male-dominated than commonly assumed. Overall, this variability suggests that giant petrels,

456   broadly considered to be specialist scavengers (Hunter 1983, González-Solís 2004, Forero *et al*.

457   2005), should more rightly be considered as generalists, with both sexes able to exploit both coastal

458   and pelagic areas and hence consume both carrion and oceanic prey. Indeed, the high level of

459   opportunism would explain why their population trends are not correlated with carrion availability

460   at another sub-Antarctic colony, Marion Island (De Bruyn *et al*. 2007).

461   The range of and plasticity in foraging strategies among giant petrels indicates that

462   segregation patterns are less shaped by adult physiology, and more by the demands of reproduction

463   (incubating the egg or feeding the growing chick). Indeed, breeding stage explained more variation

464   in foraging behaviour than calendar date, and moreover the range of both species was most

465   restricted around the colony during the brood-guard stage of chick-rearing, when the parents

466   alternate at the nest to provide food, warmth and protection from predators, which may be

467   facilitated by the shorter duration of the coastal trips favoured in this breeding stage. This change in

468   behaviour in response to biotic conditions indicates that both male and female giant petrels make

469   dynamic foraging decisions throughout the breeding season, and hence probably also throughout the

470   rest of year, to meet changing demands. This behavioural diversity suggests that divergent selection

471   on foraging strategies between males and females is not strong, and hence that morphological

472   differences related to foraging are unlikely to completely explain intra-specific foraging segregation

473   in this system. Indeed, rather than morphology driving segregation, as often assumed, it is not

474   currently possible to rule out that intra-specific behavioural differences may have arisen first – as

475   with the inter-specific differences above, a labile initial response to reduce competition – with the

476   striking morphological differences emerging in consequence as further specialisation.

477   Although foraging behaviour displayed multi-faceted and dynamic variability, we found

478   little evidence for consistent use of particular habitats among females on pelagic trips. Southern

479   Giant Petrels appeared to forage in areas of lower chlorophyll (at the time of the trip) than Northern

480   Giant Petrels, and males and females in later breeding stages, especially Northern Giant Petrels,

481   used warmer waters than birds in earlier breeding stages. However, we cannot confidently discern

482   whether these are active habitat choices to optimise nutrient intake or unavoidable consequences of

483   the spatial and temporal segregation patterns. In particular, breeding allochrony in giant petrels is

484   likely associated with variation in the habitats available to each species at each breeding stage; the

485 extent to which habitat use reflects real preferences for certain oceanographic features would

486 require further investigation. Moreover, as the limited number of pelagic trips undertaken by males

487 precluded a robust analysis of their habitat choices, we were not able to investigate the population-

488 level importance of habitat preferences. Further, some trips that we classified as pelagic included

489 time spent close or on land at the South Orkney and South Sandwich islands, and other parts of the

490 Scotia Arc, where giant petrels may have been exploiting carrion on beaches rather than oceanic

491 prey. Lastly, as with the trip characteristics discussed above, foraging habitat varied substantially

492 across a relatively small number of trips (max. 22 trips per species/sex/temporal variable group);

493 tracking more individuals may serve to reduce this variation and hence clarify real differences in

494 foraging strategies between the groups. Due to these difficulties in interpreting the observed

495 patterns in habitat use, the implications of interspecific differences in habitat preference for

496 population trajectories remain unclear. Studies of habitat use at other colonies where the two species

497 breed sympatrically but show different population growth rates (Delord et al. 2008; Ryan et al.

498 2009) would provide an informative natural experiment in which to fully assess the role of habitat

499 availability in population trajectories. This would be of substantial value in moving from a

500 descriptive to a predictive understanding of inter- and intra-specific resource partitioning in seabirds

501 (Pinet *et al*. 2012, Thiers *et al*. 2014, Cleasby *et al*. 2015).

502   Our single-colony study has highlighted the importance of segregation along both spatial

503 and temporal axes for the coexistence of two ecologically and morphologically similar seabird

504 species. Sexual segregation was mainly spatial, constrained by breeding stage, whereas segregation

505 between the species arose from breeding allochrony. Intra-specific competition had a stronger

506 influence on distribution and behaviour than inter-specific competition, mirroring patterns in other

507 sympatric vertebrates (seabirds: Weimerskirch *et al*. 2009, Young *et al*. 2010; reef fish: Forrester *et*

508 *al*. 2006). These behavioural differences are not only of ecological and evolutionary importance but

509 may also have conservation implications if they expose different parts of the population or

510 community to different threats (van Toor *et al*. 2011). However, while wider-ranging female giant

511 petrels have historically been proposed to be more at risk of incidental mortality in longline

512 fisheries than males (González-Solís *et al*. 2000a, Otley *et al*. 2006) and the same could apply to

513 wider-ranging Southern compared to Northern Giant Petrels, current management of demersal

514 fisheries at South Georgia and around the Falkland Islands includes strict bycatch mitigation

515 methods and monitoring of compliance (Tancell *et al*. 2016), and so these range differences are

516 unlikely to affect bycatch likelihood. Finally, while our investigation focussed on segregation of two

517 species within the seabird community, foraging strategies within a multi-species assemblage also

518 depend on those of other taxa, segregation at smaller scales (Navarro *et al*. 2013), and individual

519 habitat preferences (Phillips *et al*. 2017). Given the structured segregation patterns of giant petrels

520 at South Georgia that we have described, both within and between species, this species pair could

521 be an informative model in which to extend our understanding of how simultaneous competition on

522 many different scales shapes foraging strategies and habitat use.

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534 **SUPPORTING INFORMATION**

535

536 Additional Supporting Information can be found in the online version of this article:

537   **Table S1**: Full model outputs of the best-fit models describing trip characteristics of

538 foraging Northern and Southern Giant Petrels tracked at Bird Island, South Georgia.

539   **Table S2**: Full model outputs of the best-fit models describing habitat use of foraging

540 Northern and Southern Giant Petrels tracked at Bird Island, South Georgia.

Tables

Breeding stage	Sex	Northern Giant Petrels		Southern Giant Petrels	
		Trips	**Individuals**	**Trips**	**Individuals**
For trip characteristics					
Incubation	Females	3 (0)	3	10 (0)	10
	Males	4 (0)	4	9 (0)	9
Brood-guarding	Females	10 (2)	7	22 (0)	13
	Males	19 (3)	11	18 (1)	11
Post-brood	Females	11 (2)	9	10 (0)	8
	Males	8 (5)	6	16 (0)	12
For habitat use					
Incubation	Females	3	3	10	10
	Males	0	0	1	1
Brood-guarding	Females	5	3	19	10
	Males	7	5	1	1
Post-brood	Females	8	6	7	6
	Males	0	0	7	6

Table 1. Sample sizes by species, sex and breeding stage in analyses of trip characteristics for all deployments and habitat use for pelagic trips only of giant petrels tracked from Bird Island, South Georgia, in austral summer 2005/06. The number of deployments in which separate trips could not confidently be discriminated are indicated in parentheses. Note that very few males undertook pelagic trips and that these were unevenly distributed between breeding stages; analysis of habitat use were therefore carried out on females only.

| | | | Northern Giant Petrels | | | | | | Southern Giant Petrels | | | | | |
| | | | Incubation | | Brood-guard | | Post-brood | | Incubation | | Brood-guard | | Post-brood | |
			Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males
Northern Giant Petrels	Incubation	Females	■	0.459	0.569	0.488	0.463	0.448	*0.167*	0.450	0.438	0.454	0.284	0.366
		Males		■	**0.821**	**0.956**	0.360	**0.944**	*0.137*	**0.821**	0.359	**0.925**	*0.219*	0.432
	Brood-guard	Females			■	**0.850**	0.510	**0.815**	*0.213*	**0.799**	0.496	**0.821**	0.336	0.457
		Males				■	0.379	**0.939**	*0.142*	**0.839**	0.374	**0.931**	*0.228*	0.436
	Post-brood	Females					■	0.353	0.326	0.379	0.602	0.368	0.462	0.470
		Males						■	*0.134*	**0.852**	0.349	**0.974**	*0.215*	0.432
Southern Giant Petrels	Incubation	Females							■	*0.203*	0.424	*0.139*	0.339	0.337
		Males								■	0.432	**0.867**	0.261	0.498
	Brood-guard	Females									■	0.356	0.497	0.579
		Males										■	*0.221*	0.437
	Post-brood	Females											■	0.496
		Males												■

550

Table 2. Overlap in utilisation distributions by species, sex and breeding stage of giant petrels tracked from Bird Island, South Georgia, in austral summer 2005/06. Values range from 0 (no overlap) to 1 (kernels completely intersect). For ease of interpretation, high overlaps (> 0.75) are shown in bold and low overlaps (< 0.25) in italics.

Model terms	d.f.	ΔAIC	AIC weight	Support	Model terms	d.f.	ΔAIC	AIC weight	Support
By breeding stage					**By calendar date (period)**				
Travel distance					*Travel distance*				
Species + <u>Sex</u> + <u>Breeding stage</u>	7	0.00	0.402	*	<u>Sex</u> + <u>Species*Period</u>	7	0.00	0.985	**
<u>Sex</u> + <u>Breeding stage</u>	6	1.35	0.204	*	Species*Period	6	8.51	0.014	
Species*Sex + Breeding stage	8	1.68	0.173		Sex	4	16.62	0.000	
Sex + Species*Breeding stage	9	1.84	0.160		Sex + Period	5	18.15	0.000	
Species + Breeding stage	6	5.19	0.030		Species + Sex	5	18.15	0.000	
Trip duration					*Trip duration*				
<u>Sex</u> + <u>Species*Breeding stage</u>	9	0.00	0.397	*	<u>Sex</u> + <u>Species*Period</u>	7	0.00	0.896	**
<u>Species</u> + <u>Sex</u> + <u>Breeding stage</u>	7	1.19	0.219	*	Species*Period	6	4.33	0.103	
Species*Sex + Breeding stage	8	2.79	0.098		Sex	4	14.66	0.001	
Species*Breeding stage	8	2.85	0.095		Species + Sex	5	15.92	0.000	
Species + Breeding stage	6	2.91	0.092		Sex + Period	5	16.63	0.000	
Max. range					*Max. range*				
<u>Sex</u> + <u>Breeding stage</u>	6	0.00	0.425	*	<u>Sex</u> + <u>Species</u>*<u>Period</u>	9	0.00	0.427	*
Species + <u>Sex</u> + <u>Breeding stage</u>	7	0.49	0.332	*	<u>Sex</u> + <u>Period</u>	6	1.14	0.241	*
Species*Sex + Breeding stage	8	2.42	0.126		Species + Sex + Period	7	2.91	0.100	
Sex + Species*Breeding stage	9	2.61	0.115		Sex	4	3.00	0.095	
Breeding stage	5	13.68	0.000		Species + Sex	5	3.70	0.067	
Proportion of trip coastal					*Proportion of trip coastal*				
<u>Species*Sex</u> + <u>Breeding stage</u>	7	0.00	0.791	**	<u>Species*Sex</u> + <u>Period</u>	6	0.00	0.495	*
Species + Sex + Breeding stage	6	4.11	0.101		<u>Species</u> + <u>Sex</u> + <u>Period</u>	5	0.77	0.338	*
Sex + Breeding stage	5	4.52	0.083		Sex + Species*Period	6	2.49	0.143	
Sex + Species*Breeding stage	8	6.94	0.025		Sex + Period	4	6.00	0.025	
Species *Sex	5	52.57	0.000		Species *Sex	5	28.63	0.000	
Trip start time					*Trip start time*				
Species*<u>Breeding stage</u>	8	0.00	0.361	*	(intercept only)	3	0.00	0.370	**
<u>Breeding stage</u>	5	1.08	0.210	*	Species	4	1.68	0.160	
Sex + Species*Breeding stage	9	1.48	0.172		Sex	4	1.98	0.137	
Species + Breeding stage	6	2.92	0.084		Period	5	3.23	0.074	
Sex + Breeding stage	6	3.03	0.079		Species + Sex	5	3.66	0.059	

556

557 **Table 3.** The five best-fitting models describing trip characteristics of giant petrels tracked from

558 Bird Island, South Georgia, in austral summer 2005/06, in relation to either breeding stage (left

559 model set) or period (reflecting calendar date; right model set). The full candidate model set for

560 each response variable was: Species; Sex; Time (breeding stage or period); Species + Sex; Sex +

561 Time; Species + Time; Species + Sex+ Species:Sex; Species + Time + Species:Time; Species + Sex

562 + Time; Species + Sex+ Time + Species:Sex; Species + Sex + Time + Species:Time; null model

563 (intercept only). Important variables (present in over half of models within 50% of the relative

564 likelihood of the best-fit model) are underlined. In the "Support" column, ** indicates a single best-

565 fit model and * indicates one of several models considered informative (full model selection criteria

566 in main text).

Model terms	d.f.	ΔAIC	AIC weight	Support	Model terms	d.f.	ΔAIC	AIC weight	Support
By breeding stage					**By calendar date (period)**				
Temperature					*Temperature*				
Species * Breeding stage	9	0.00	0.561	**	Period	5	0.00	0.318	*
Breeding stage	6	2.28	0.180		Species + Period	6	0.60	0.235	*
(intercept only)	4	2.80	0.138		Species * Period	7	0.82	0.211	*
Species + Breeding stage	7	4.25	0.067		(intercept only)	5	3.03	0.167	*
Species	5	4.66	0.055		Species	5	3.03	0.070	
Chlorophyll					*Chlorophyll*				
Species + Breeding stage	7	0.00	0.466	*	Species + Period	6	0.00	0.375	*
Species	5	0.38	0.386	*	Species	5	0.20	0.339	*
Species * Breeding stage	9	3.21	0.094		Species * Period	7	1.99	0.139	
(intercept only)	4	4.65	0.045		(intercept only)	4	2.52	0.106	
Breeding stage	6	7.97	0.009		Period	5	4.39	0.042	
Wind					*Wind*				
(intercept only)	4	0.00	0.458	*	Species + Period	6	0.00	0.460	*
Species * Breeding stage	9	1.38	0.230	*	Period	5	0.52	0.355	*
Species	5	1.91	0.177		Species * Period	7	2.00	0.169	
Breeding stage	6	3.08	0.098		(intercept only)	4	7.52	0.011	
Species + Breeding stage	7	4.99	0.038		Species	5	9.23	0.005	
Bathymetry					*Bathymetry*				
(intercept only)	4	0.00	0.412	*	Period	5	0.00	0.479	*
Breeding stage	6	0.70	0.290	*	Species + Period	6	0.50	0.373	*
Species	5	2.00	0.152		Species * Period	7	2.41	0.144	
Species + Breeding stage	7	2.70	0.107		(intercept only)	4	9.79	0.004	
Species * Breeding stage	9	4.67	0.040		Species	5	11.78	0.001	

568

Table 4. The five best-fitting models describing habitat variables in cells used by female giant petrels on pelagic trips tracked from Bird Island, South Georgia, in austral summer 2005/06, in relation to either breeding stage (left model set) or period (reflecting calendar date; right model set). As sex was not investigated in this analysis, the candidate model set was: Species; Time (breeding stage or time slot); Species + Time; Species + Time+ Species:Time; null model (intercept only). Important variables (present in over half of models within 50% of the relative likelihood of the best-fit model) are underlined. In the "Support" column, ** indicates a single best-fit model and *

576   indicates one of several models considered informative (full model selection criteria in main text).
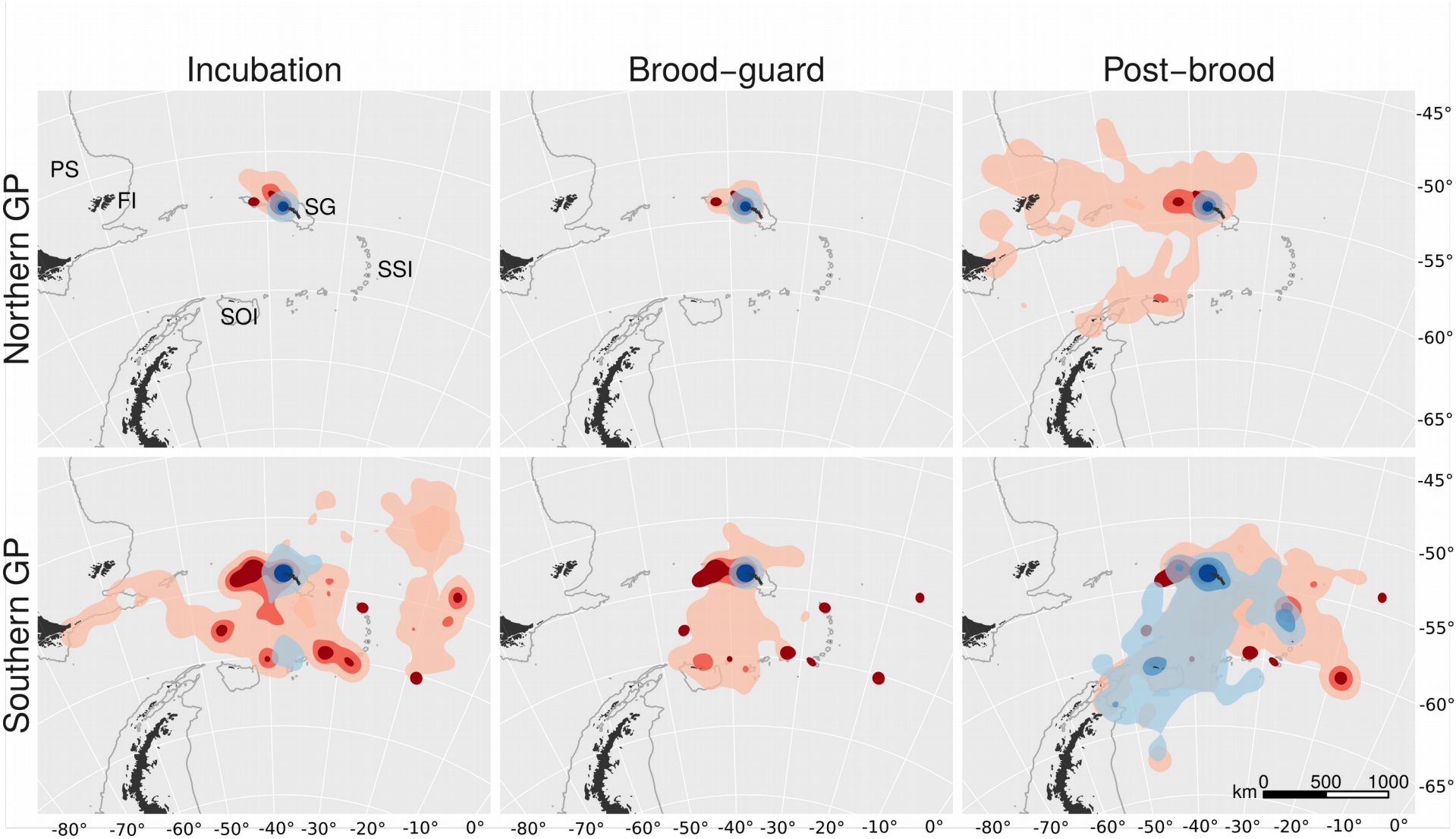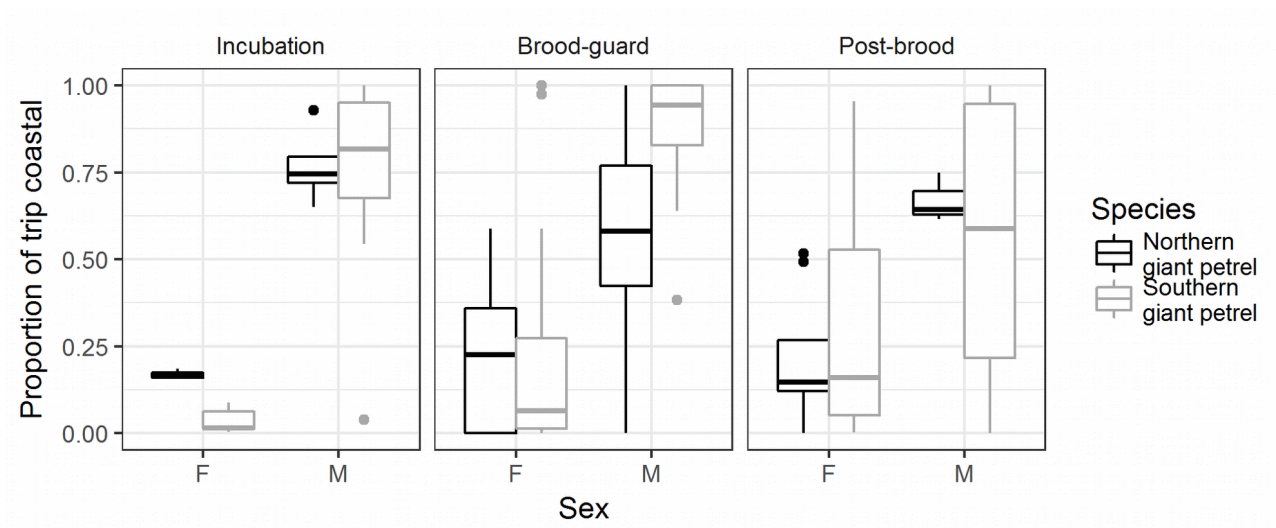
Figures

580   **Figure 1.** Distributions of Northern and Southern Giant Petrels tracked from Bird Island, South Georgia, in 2005/06 by sex and breeding stage

581   (calendar date differs between species), shown as 95%, 50% and 25% utilisation distributions. Females are shown in red and males in blue, with

582   progressively higher-probability kernels in darker colours. Landmasses are shown in black, with the tip of South America on the left hand map edge

583   and the Antarctic Peninsula on the bottom edge. Relevant island groups and features are marked on the first panel: the Patagonian Shelf (PS), Falkland

584   Islands (FI), South Georgia (SG), South Sandwich Islands (SSI) and South Orkneys (SOI); the latter three island groups illustrate the line of the Scotia

585   Arc. Pale grey lines show bathymetric contours at 1000 m. The map is in an azimuthal equal area projection centred on the colony at Bird Island, on

586   the western tip of South Georgia.

587
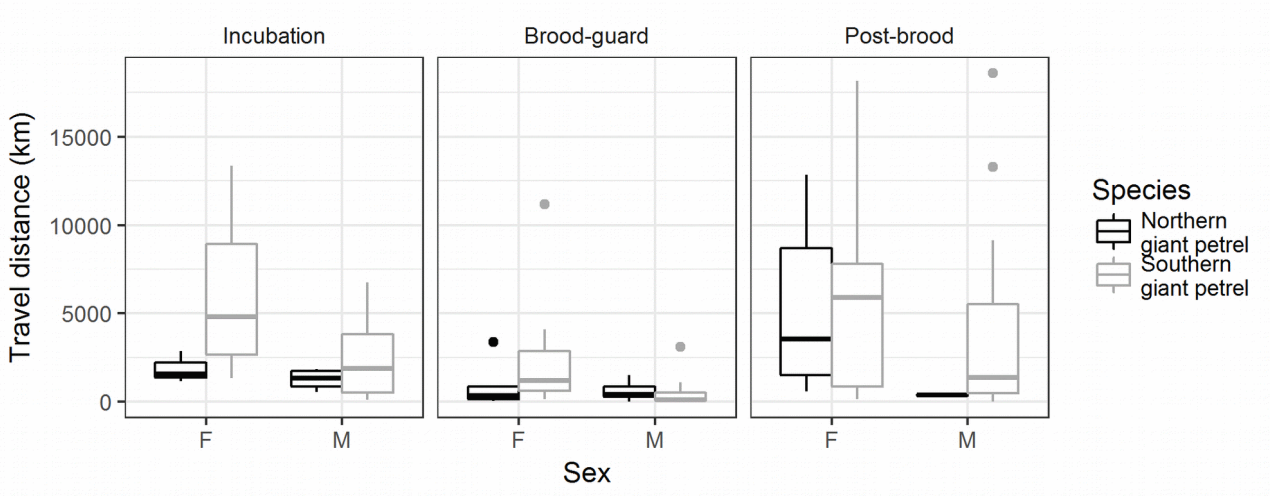
588 **Figure 2.** Travel distance of Giant Petrels tracked from Bird Island, South Georgia, in austral summer 2005/06 for each species, sex and breeding

589 stage, shown as box plots of the raw data for each subgroup. Boxes show the median with upper and lower quartiles. Whiskers show the data range

590 excluding observations more than 1.5 times the inter-quartile range from the median; if any subgroup contains such outliers, they are shown as filled

591 circles.

592   **Figure 3.** The proportion of each trip spent within 10 km of South Georgia (coastal foraging) by Giant Petrels tracked from Bird Island, South Georgia,

593   in austral summer 2005/06, shown for each species, sex and breeding stage as boxplots of the raw data. Boxes show the median with upper and lower

594   quartiles. Whiskers show the data range excluding observations more than 1.5 times the inter-quartile range from the median; if any subgroup contains

595   such outliers, they are shown as filled circles.

596