

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**

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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 (Zupping-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 al.*  
55 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 (Connors *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 al.*  
72 *et 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  $4.72 \pm 0.10$  kg and  $3.51 \pm 0.07$  kg, and of male and female Southern Giant Petrels was  
152  $4.35 \pm 0.10$  kg and  $3.64 \pm 0.09$  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 99<sup>th</sup>  
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



185 South Georgia, or as pelagic if outside this zone. On this basis, we calculated the proportion of each  
186 trip that was coastal, and if this exceeded 50% of fixes, the entire trip was classified as “coastal”; all  
187 other trips were classified as “pelagic”. Locations in each trip were interpolated at 30 min intervals  
188 using the *adehabitatLT* package (Calenge 2006). Each interpolated fix was classified as daylight or  
189 darkness (daylight includes civil twilight, i.e. sun higher than 6° below the horizon). Travel  
190 distance, trip duration and maximum distance from the colony (maximum range) were calculated  
191 for each trip from the interpolated data. In addition, each trip was binned into early, middle and late  
192 periods (hereafter “period”, a three-level factor) according to the calendar date at departure, with  
193 cut-off points defined by thirds of the distribution of all trips across both species.

194 Habitat use was analysed for pelagic trips by females only, as the few pelagic trips by males  
195 were unbalanced in terms of representing the different breeding stages. Using a 50 km grid across  
196 the entire study area, we calculated time spent per grid cell using the package *trip* (Sumner 2015).  
197 This was based only on fixes during daylight, as much of the night is spent resting in giant petrels  
198 and other large Procellariiformes (González-Solís *et al.* 2002; Phalan *et al.* 2007; but see Connors *et*  
199 *al.* 2015), and excluding cells that intersected with land at South Georgia. Habitat data were  
200 extracted as 8-day composites for each used grid cell in the relevant temporal period. These were  
201 remotely-sensed sea surface temperature (SST), chlorophyll a and non-directional wind speed  
202 obtained from the National Oceanic and Atmospheric Administration (BloomWatch 360;  
203 [http://coastwatch.pfel.noaa.gov/browsers/cwbrowser\\_global360.html](http://coastwatch.pfel.noaa.gov/browsers/cwbrowser_global360.html)) and bathymetry data  
204 (GEBCO) obtained from the British Oceanographic Data Centre. These rasterized data were  
205 projected and averaged from their original resolutions (0.05 degrees for SST, 0.05 degrees for  
206 chlorophyll a, 0.125 degrees for wind, and 0.5 degrees for bathymetry) onto the coarser 50 km grid  
207 used for the calculation of habitat usage.

208 Kernel density contours (utilisation distributions) were calculated from all interpolated  
209 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:  $1.54 \pm 0.15$ ,  $Z =$   
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 ( $\Delta AIC < 2$ ) 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  $\pm$  s.e. for Northern Giant Petrels,  $1775 \pm 426$   
311 km and for Southern Giant Petrels,  $3113 \pm 461$  km, Fig. 2; mean trip duration  $79.7 \pm 16.1$  h and  
312  $154.8 \pm 21.5$  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,  $399 \pm 43$  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,  $99.6 \pm 17.4$  h;  
318 for females  $160.6 \pm 25.6$  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,  $0.402 \pm 0.076$ , in brood-guarding,  
333  $0.473 \pm 0.048$ , and in post-brood,  $0.423 \pm 0.056$ ; 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  $71.3 \pm 11.2$  h; of pelagic trips,  $178.3 \pm 25.6$  h;  
336 in LMM accounting for species, sex and breeding stage, effect of trip type (pelagic vs. coastal)  $88.3$   
337  $\pm 22.8$  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  $1250 \pm 307$  km, middle period  $3827 \pm 1582$  km; for Southern Giant  
347 Petrels, early period  $5970 \pm 1134$  km, middle period  $1439 \pm 310$  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  $\Delta$ AIC of  $> -7$  compared to the best-fit period model ( $\Delta$ AIC 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  $\pm$   
366 s.e. used by Northern Giant Petrels in incubation, brood-guarding and post-brooding  $1.32 \pm 0.08$  °C,  
367  $1.82 \pm 0.07$  °C,  $4.05 \pm 0.12$  °C, respectively; and similarly by Southern Giant Petrels  $2.50 \pm 0.09$  °C,  
368  $2.76 \pm 0.06$  °C,  $2.07 \pm 0.06$  °C; 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  $\pm$  s.e. in cells used by Northern Giant  
371 Petrels  $0.86 \pm 0.05$  mg/m<sup>3</sup>, and by Southern Giant Petrels  $0.64 \pm 0.02$  mg/m<sup>3</sup>; 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  $\pm$  s.e. in used cells in early and middle  
377 periods,  $2.77 \pm 0.09$  °C and  $3.45 \pm 0.09$  °C respectively; mean wind speed  $\pm$  s.e.,  $8.76 \pm 0.04$  m/s  
378 and  $7.55 \pm 0.04$  m/s respectively; Supporting Information Table S2). In addition, birds foraged in  
379 deeper waters in the early than the middle period (mean depth  $\pm$  s.e. in used cells in early and  
380 middle periods,  $3062 \pm 48$  m and  $2476 \pm 54$  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).

384



385

386 **DISCUSSION**

387

388 The two closely-related species of sexually dimorphic giant petrels at South Georgia provide an  
389 opportunity to test the simultaneous roles of spatial and temporal segregation in enabling  
390 coexistence between and within species. By tracking both sexes over the entire breeding season, we  
391 have shown that foraging Northern and Southern Giant Petrels segregate in time, and that males and  
392 females within each species largely segregate in space. Both species employed similar strategies,  
393 showing broadly matching trip characteristics and habitat use under the same biological constraints  
394 (associated with breeding stage), but direct competition between the species is reduced by the  
395 considerably earlier breeding of Northern Giant Petrels (by six weeks; Brown *et al.* 2015). This is  
396 rare evidence supporting the importance of breeding allochrony in the coexistence of sister species.  
397 Tracked Northern Giant Petrels had a slightly smaller overall foraging range, and a much smaller  
398 range during incubation and brood-guarding than Southern Giant Petrels. The smaller range earlier  
399 in the season likely reflects their exploitation of carrion, associated with the recovery of the local  
400 Antarctic Fur Seal *Arctocephalus gazella* population, which may have contributed to the faster  
401 growth in numbers of breeding Northern than Southern Giant Petrels in recent decades (González-  
402 Solís *et al.* 2000a; Brown *et al.* 2015). Broadly, males of both species made shorter and more  
403 coastal trips (presumably scavenging) while females were more pelagic, yet both sexes were  
404 capable of long, pelagic trips. Thus the common perception that giant petrels, especially the males,  
405 are near-obligate scavengers through the breeding season needs to be reconsidered. Brood-guarding  
406 birds of both sexes tended to forage more coastally and to take shorter trips, as expected given that  
407 young chicks require frequent meals, and constant parental care to aid thermoregulation and reduce  
408 the risk of predation, as in other surface-breeding Procellariiformes (Catry *et al.* 2006). Overall, our  
409 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 Procellariiformes, 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.

523

524

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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.

541 **Tables**

542

Breeding stage	Sex	Northern Giant Petrels		Southern Giant Petrels	
		Trips	Individuals	Trips	Individuals
<b>For trip characteristics</b>					
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
<b>For habitat use</b>					
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

543

544 **Table 1.** Sample sizes by species, sex and breeding stage in analyses of trip characteristics for all  
545 deployments and habitat use for pelagic trips only of giant petrels tracked from Bird Island, South  
546 Georgia, in austral summer 2005/06. The number of deployments in which separate trips could not  
547 confidently be discriminated are indicated in parentheses. Note that very few males undertook  
548 pelagic trips and that these were unevenly distributed between breeding stages; analysis of habitat  
549 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	<i>0.167</i>	0.450	0.438	0.454	0.284	0.366	
		Males			<b>0.821</b>	<b>0.956</b>	0.360	<b>0.944</b>	<i>0.137</i>	<b>0.821</b>	0.359	<b>0.925</b>	0.219	0.432	
	Brood-guard	Females				<b>0.850</b>	0.510	<b>0.815</b>	<i>0.213</i>	<b>0.799</b>	0.496	<b>0.821</b>	0.336	0.457	
		Males					0.379	<b>0.939</b>	<i>0.142</i>	<b>0.839</b>	0.374	<b>0.931</b>	0.228	0.436	
	Post-brood	Females						0.353	0.326	0.379	0.602	0.368	0.462	0.470	
		Males							<i>0.134</i>	<b>0.852</b>	0.349	<b>0.974</b>	0.215	0.432	
Southern Giant Petrels	Incubation	Females								<i>0.203</i>	0.424	<i>0.139</i>	0.339	0.337	
		Males										0.432	<b>0.867</b>	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

551 **Table 2.** Overlap in utilisation distributions by species, sex and breeding stage of giant petrels  
552 tracked from Bird Island, South Georgia, in austral summer 2005/06. Values range from 0 (no  
553 overlap) to 1 (kernels completely intersect). For ease of interpretation, high overlaps (> 0.75) are  
554 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
<b>By breeding stage</b>					<b>By calendar date (period)</b>				
<i>Travel distance</i>					<i>Travel distance</i>				
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	
<i>Trip duration</i>					<i>Trip duration</i>				
<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	
<i>Max. range</i>					<i>Max. range</i>				
<u>Sex</u> + <u>Breeding stage</u>	6	0.00	0.425	*	<u>Sex</u> + <u>Species*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	
<i>Proportion of trip coastal</i>					<i>Proportion of trip coastal</i>				
<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	
<i>Trip start time</i>					<i>Trip start time</i>				
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
<b>By breeding stage</b>					<b>By calendar date (period)</b>				
<b><i>Temperature</i></b>					<b><i>Temperature</i></b>				
<u>Species * Breeding stage</u>	9	0.00	0.561	**	<u>Period</u>	5	0.00	0.318	*
Breeding stage	6	2.28	0.180		Species + <u>Period</u>	6	0.60	0.235	*
(intercept only)	4	2.80	0.138		Species * <u>Period</u>	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	
<b><i>Chlorophyll</i></b>					<b><i>Chlorophyll</i></b>				
<u>Species</u> + Breeding stage	7	0.00	0.466	*	<u>Species</u> + Period	6	0.00	0.375	*
<u>Species</u>	5	0.38	0.386	*	<u>Species</u>	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	
<b><i>Wind</i></b>					<b><i>Wind</i></b>				
(intercept only)	4	0.00	0.458	*	Species + <u>Period</u>	6	0.00	0.460	*
Species * Breeding stage	9	1.38	0.230	*	<u>Period</u>	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	
<b><i>Bathymetry</i></b>					<b><i>Bathymetry</i></b>				
(intercept only)	4	0.00	0.412	*	<u>Period</u>	5	0.00	0.479	*
Breeding stage	6	0.70	0.290	*	Species + <u>Period</u>	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

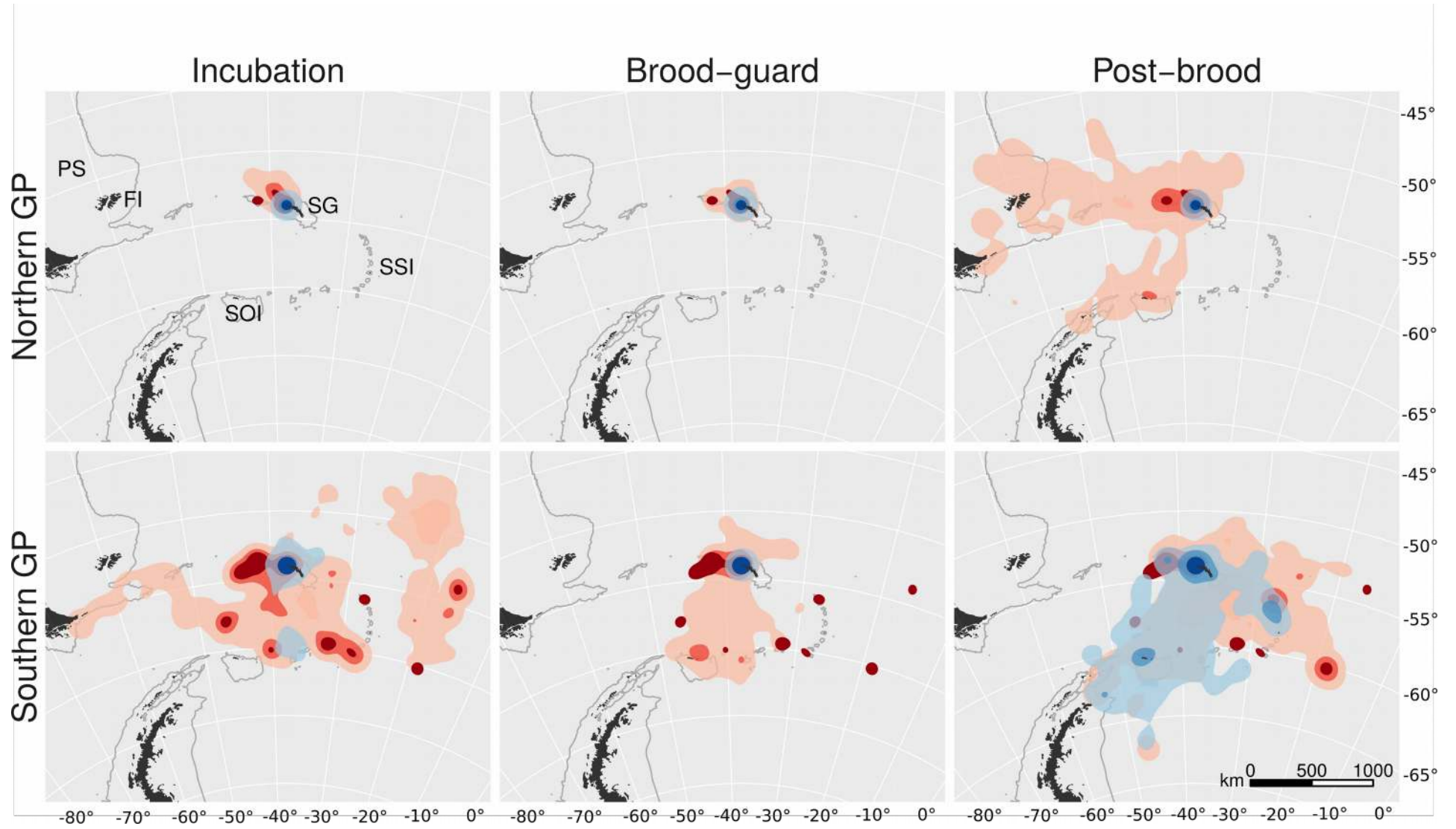
569 **Table 4.** The five best-fitting models describing habitat variables in cells used by female giant  
570 petrels on pelagic trips tracked from Bird Island, South Georgia, in austral summer 2005/06, in  
571 relation to either breeding stage (left model set) or period (reflecting calendar date; right model set).  
572 As sex was not investigated in this analysis, the candidate model set was: Species; Time (breeding  
573 stage or time slot); Species + Time; Species + Time+ Species:Time; null model (intercept only).  
574 Important variables (present in over half of models within 50% of the relative likelihood of the best-  
575 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).

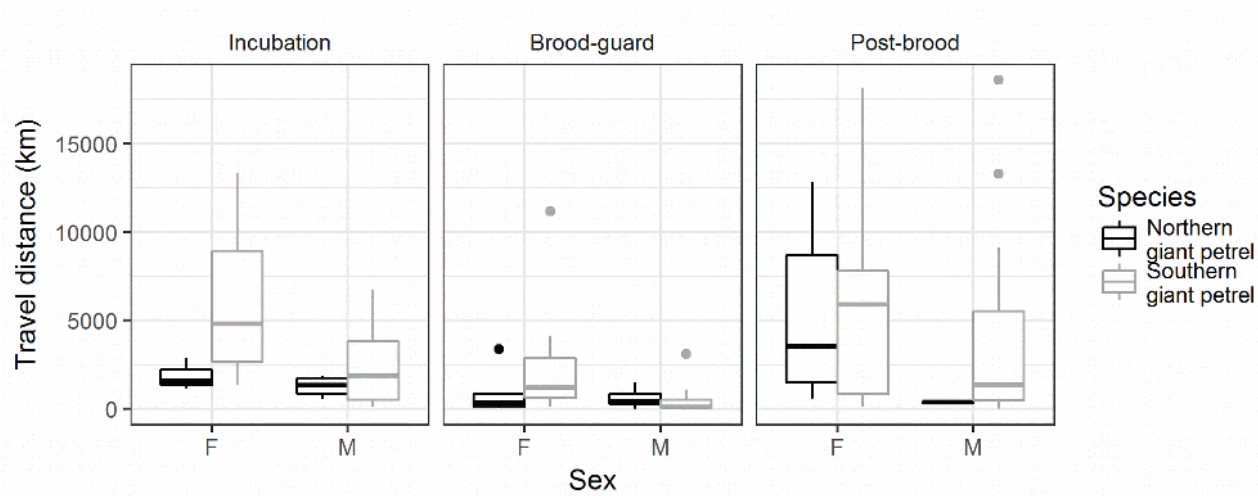
577 **Figures**

578

579



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.



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