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

HANNA M. V. GRANROTH-WILDING* & RICHARD A. PHILLIPS2

1Department of Biosciences, Division of Ecology and Evolution, University of Helsinki, Viikinkaari 1, 00014 Helsinki, Finland. ORCID iD: 0000-0002-4052-3821.

2British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge, CB3 0ET, United Kingdom.

* Corresponding author. Email: hanna@granroth-wilding.co.uk
Biological communities are shaped by competition between and within species. Competition is often reduced by inter- and intra-specific specialization on resources, such as differences in foraging areas or time, allowing similar species to coexist and potentially contributing to reproductive isolation. Here, we examine the simultaneous role of temporal and spatial foraging segregation within and between two sympatric sister species of seabirds, Northern *Macronectes halli* and Southern *M. giganteus* Giant Petrels. These species show marked sexual size dimorphism and allochrony (with earlier breeding by Northern Giant Petrels), but this is the first study to test for differences in foraging behaviours and areas across the entire breeding season both between the two species and between the sexes. We tracked males and females of both species in all breeding stages at Bird Island, South Georgia, to test how foraging distribution, behaviour and habitat use varies between and within species in biological time (incubation, brood-guard or post-brood stages) and in absolute time (calendar date). Within each breeding stage, both species took trips of comparable duration to similar areas, but due to breeding allochrony they segregated temporally. Northern Giant Petrels had a somewhat smaller foraging range than Southern Giant Petrels, reflecting their greater exploitation of local carrion and probably contributing to their recent higher population growth. Within species, segregation was spatial, with females generally taking longer, more pelagic trips than males. Both sexes of both species showed unexpectedly plastic foraging behaviour, and there was little evidence of inter-specific differences in habitat use. Thus, in giant petrels, temporal segregation reduces inter-specific competition and sexual segregation reduces intra-specific competition. These results demonstrate how both specialization and dynamic changes in foraging strategies at different scales underpin resource division within a community.

**Keywords:** Allochrony, inter-specific competition, intra-specific competition, niche differentiation, Procellariiformes, resource partitioning, sexual segregation, speciation, tracking
Competition in ecological communities, both between and within species, is a fundamental ecological process, with important evolutionary consequences. Coexistence between community members is promoted by a reduction in this competition, often because different members exploit different parts of the resource space, such as particular habitats or prey (Schoener 1974). This resource partitioning or niche differentiation can shape the structure of a community, driving evolutionary change in its constituent organisms (Zuppinger-Dingley et al. 2014) and promoting species coexistence in plants (Silvertown 2004), insects (Augustyn et al. 2016), fish (Bonin et al. 2015), mammals (Stewart et al. 2002; Nicholls & Racey 2006) and birds at local and regional scales (Gotelli et al. 2010; Young et al. 2010).

Among morphologically similar competitors, partitioning of habitat or prey resources can play an important role not only in maintaining coexistence but also in isolating diverging taxa during incipient speciation (Svanback & Bolnick 2007). In such contexts, resources are often partitioned through behavioural mechanisms (Nicholls & Racey 2006). Behaviour can change rapidly in response to increasing competitive pressure, often in ways consistent with existing morphological differences between sub-populations (Svanback & Bolnick 2007, Linnebjerg et al. 2013, Drago et al. 2015). Such behavioural divergence is frequently observed as segregation between species or sub-populations either in space or in time, for example with sympatric species reducing inter-specific competition by foraging in different areas during the breeding or nonbreeding seasons (Phillips et al. 2005, Rayner et al. 2016), at differing heights or depths (Nicholls & Racey 2006, Navarro et al. 2013), or at different times of day (Wilson 2010, Navarro et al. 2013). Particularly where it occurs on a variety of scales or in different foraging traits, segregation may nonetheless be difficult to resolve, even in systems where competitors differ morphologically (Conners et al. 2015).

Similar segregation patterns within species have also been well documented, with behavioural differences resulting in partitioning of food resources according to sex or age class...
(Lewis et al. 2001, Lecomte et al. 2010). The competition that drives such segregation is expected to be particularly intense when adults of both sexes congregate to breed (Phillips et al. 2011, Phillips et al. 2017, Drago et al. 2015), and sexual segregation in foraging, which can act to reduce intra-specific competition, is widespread among vertebrates (Lewis et al. 2001, Ruckstuhl & Neuhaus 2002, Catry et al. 2005, Breed et al. 2006). Males and females may forage in different areas, at different times, or take different prey, in sexually monomorphic as well as dimorphic species, although behavioural differentiation can be subtle even in species with extreme sexual dimorphism (Lewis et al. 2002, Ruckstuhl & Neuhaus 2002, Phillips et al. 2011, 2017, Harris et al. 2013, Griffiths et al. 2014, Baylis et al. 2016). Competition between the sexes has been implicated in the evolution of specialisation and segregation in many contexts, for example with males and females exploiting different habitat types or taking different roles when rearing offspring, even where segregation has proved difficult to resolve (Copello et al. 2011, Pinet et al. 2012, Ludynia et al. 2013, Cleasby et al. 2015, Baylis et al. 2016).

Both inter- and intra-specific differences in distribution and behaviour arise as dynamic responses to the biotic and abiotic environment and may therefore vary over time. Such flexibility in foraging strategy is particularly important when foraging is constrained, such as in central-place foragers when habitat use is spatially restricted, and energy and time budgets are limited by the changing demands of incubation and chick-rearing (Phillips et al. 2017). Breeding seabirds are typically subject to these foraging constraints, making them an informative model for investigating how the competition that such restrictions induce is resolved through variation in foraging behaviour on different scales. These constraints may differ between the sexes and occur on different schedules in otherwise similar species and habitats (Elliott et al. 2010, Beaulieu & Sockman 2012, Pinet et al. 2012). Inter-specific segregation in timing of breeding (allochrony) may therefore be a crucial mechanism enabling the coexistence of similar species, maintaining reproductive isolation in related taxa, or potentially driving sympatric speciation (Wilson 2010, Brown et al. 2015).
complete understanding of dynamic resource partitioning within a community requires consideration of both inter- and intra-specific segregation patterns not only in space but also in time. Moreover, while studies in a wide range of species have described certain components of the structure of inter- and intra-specific spatial and temporal segregation in foraging areas, only recently have such differences been linked explicitly to habitat variables (Pinet et al. 2012, Thiers et al. 2014, Cleasby et al. 2015). This is critical to understanding the mechanisms that give rise to observed patterns in foraging behaviour and hence allow predictive modelling of foraging distributions within a community.

The pattern of inter- and intra-specific (between-sex) segregation in foraging distributions has received much attention in Northern and Southern Giant Petrels, Macronectes halli and M. giganteus, two recently diverged (~500-200 kya, Techow et al. 2010) sister species of seabirds distributed from subtropical to Antarctic waters that breed sympatrically across most of their range. Both species are commonly thought of as scavengers, feeding predominantly on seal and penguin carrion, and in the males, scavenging is often considered to be near-obligate (Hunter 1983, González-Solís 2004, Forero et al. 2005). Indeed, several biologging, diet and isotope studies have shown that the sexes employ different foraging strategies: males tend to feed closer to the colony, presumed to be exploiting carrion on local beaches, while females undertake longer trips to capture more pelagic, live prey and are less frequently observed at carcasses on shore (Hunter 1983, González-Solís et al. 2000a, González-Solís et al. 2002, Forero et al. 2005, González-Solís et al. 2007, Copello et al. 2011, Thiers et al. 2014). This niche differentiation is considered to be linked with sexual size dimorphism: males of both species are ~20% larger than females and have more robust bills, which may equip them to more efficiently exploit carcasses on land (Hunter 1987, González-Solís 2004). However, tracking with sufficient accuracy to separate coastal (likely scavenging) trips from more pelagic trips has only been undertaken during a single breeding stage, or in multiple stages but from only one species at that site (González-Solís et al. 2000b, González-
Solís et al. 2002, Thiers et al. 2014), and the relative roles of sexual and inter-specific segregation across the entire breeding period therefore remain unclear. Crucially, the focus in previous work on breeding stages overlooks a marked difference between the species in timing of breeding. Northern Giant Petrels breed around 6 weeks earlier than Southern Giant Petrels (Hunter 1987, Brown et al. 2015), hence the breeding stages and associated constraints on foraging behaviour hardly overlap between the species. This allochrony (difference in timing of breeding) is assumed to have been a key factor in divergence of the two species (Hunter 1987 Friesen et al. 2007), but its importance in terms of inter- and intra-specific differences in foraging distribution and ecology is much less clear. Despite the similarity in their morphology, ecology and environment, Northern and Southern Giant Petrels breeding sympatrically at Bird Island in South Georgia have displayed different population trajectories over the last two decades, implying a role for behavioural differences in how resources are divided between and within the species. Here, we provide a full analysis of inter- and intra-specific segregation in foraging behaviour among giant petrels throughout breeding, investigating the simultaneous role of different axes of segregation – temporal and spatial – in supporting their coexistence. Previous work suggests that the two species segregate in both space and time and the sexes in space, but these predictions do not account for the temporal offset of breeding stages. We explicitly examine how segregation patterns vary both with competition in absolute time and with the biological constraints of breeding stage, and assess the importance of intra- and inter-specific differences in habitat use.

**METHODS**

**Study species and field data collection**

Tracking data were collected from male and female Northern and Southern Giant Petrels breeding
on Bird Island, South Georgia (54°00'S, 38°03'W) throughout the breeding season in the austral summer of 2005/06. Here, the two species breed sympatrically in the same areas and habitats, but in small groups that tend to consist of the same species. Two devices were deployed on each bird: a 3.6 g geolocator-immersion logger (Mk 4, Mk 5 or Mk 7; British Antarctic Survey, Cambridge, UK) attached with cable-ties to a plastic leg ring, and a 20 g or 30 g satellite tag (91 deployments: platform terminal transmitter, PTT-100; Microwave Telemetry) or a 68 g GPS logger (12 deployments: BGDL-II; Shizuoka University, Japan) to record locations, attached to mantle feathers using Tesa tape. The PTT transmitted at 90 s intervals, and an average of 25.0 locations were obtained per day (one location every 57 min) from each device using the ARGOS satellite system. The GPS devices were set to record a location every 60 min. The immersion loggers tested for saltwater immersion every 3 s, and then either recorded every change of state from wet-to-dry or vice versa that lasted ≥ 6 s (Mk 7) or binned these data into 10 min intervals, providing a value between 0 (completely dry) and 200 (completely wet) (Mk 4 and Mk 5). The combined mass of devices and attachments were always <1.5% of body mass, which is within the recommended 3% limit to avoid deleterious effects (Phillips et al. 2003) (heavier GPS devices deployed only on males; for 36 individuals with available data, mean mass ± s.e. of male and female Northern Giant Petrels was 4.72 ± 0.10 kg and 3.51 ± 0.07 kg, and of male and female Southern Giant Petrels was 4.35 ± 0.10 kg and 3.64 ± 0.09 kg, respectively). All birds were sexed from bill dimensions, and had been fitted previously with a standard British Trust for Ornithology ring and a plastic ring with a unique combination of colour and 3-character alphanumeric code as part of a long-term study programme (Brown et al. 2015). Nests were visited daily during incubation and brood-guarding, ringed adults were identified, and the dates when the chick hatched and was first left unattended (i.e. end of brood-guarding) were recorded; thereafter, nests were visited every few days.

Locations provided by PTTs are accurate to 1-10 km (median across all but the poorest-quality ARGOS Location Classes (LC) B and Z (Douglas et al. 2012)) which is not sufficiently high
resolution to distinguish between attendance at the nest and foraging on land nearby. Separate foraging trips to sea were therefore discriminated from the patterns of saltwater immersion. A trip was defined as any period of intermittent wet records that included no more than 12 hours of contiguous dry time, a conservative interval based on manual inspection of the immersion data in relation to daily observations of nest attendance. However, Mk 7 loggers (55 out of 103 deployments) frequently showed likely erroneous wet events, commonly occurring as a series of isolated, short (3-6 seconds) immersions, including from periods when visual records indicated that the bird was at the nest. In order to identify trip start and end times consistently across all logger types, we therefore disregarded all immersion events of ≤ 9 s if no immersion event of > 9 s occurred within the previous or following hour. Trip assignments were confirmed from attendance records for each individual (based on daily visits to nests during incubation and brood-guarding), with only one of the 139 trips identified to that point requiring further splitting. For 13 of the 103 deployments, the immersion data did not allow individual trips to be discriminated. The remaining deployments generated 127 trips from 71 individuals across all breeding stages (Table 1). Trips were assigned to incubation, brood-guarding or post-guard chick-rearing, according to nest status when the adult departed.

Tracking data analysis

All data preparation and analysis was done in R (R Core Team, 2015) using an azimuthal equal-area projection centred on Bird Island on a WGS 84 coordinate system. Low quality PTT fixes (LC Z) were removed and the retained fixes were iteratively speed-filtered to remove likely erroneous locations, using McConnell et al.’s (1992) algorithm implemented in the argosfilter package (Freitas 2012). A maximum speed of 30 m/s was allowed between two subsequent fixes, based on the 99th percentile of speeds between fixes (29.9 m/s, following González-Solís et al. (2000b)). Each filtered 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 6° 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
13 deployments in which individual trips could not be discriminated. We used a 10km grid with the
same smoothing parameter of 50 km for all species-sex-breeding stage combinations (the median
value of the least-squares cross-validated smoothing factors selected in each subgroup’s kernel
analysis) to avoid bias when comparing usage distributions. Pairwise overlaps were calculated
between the distributions of each species-sex-breeding stage combination as the volume of
intersection between the 100% kernels in the package adehabitatHR, providing a value ranging
from 0 (no overlap) to 1 (complete overlap).

**Analysis**

We investigated how species, sex and trip timing affected trip characteristics and habitat use. Trip
characteristics comprised: trip duration; travel distance; maximum range; the proportion of the trip
that was coastal, as an indication of scavenging; and trip start time (time of day of departure), which
in other dimorphic species varies with sex-specific breeding roles or constraints (Harris et al. 2013).
Habitat variables were compared across those grid cells in which either species was present. For all
these response variables, we first tested a set of models that included breeding stage as the temporal
predictor variable, examining how ecological constraints shape foraging behaviour across the
species and sexes. We then compared these results to an analysis including period (reflecting
calendar date; see above) rather than breeding stage as the temporal predictor, examining whether
real-time competition between the species and sexes alters behaviour and habitat use. Northern

Giant Petrels lay around 6 weeks earlier (Brown et al. 2015; mean first lay date across all monitored
nests in study year and area: Northern Giant Petrels \(n = 242\), 01 October 2005; Southern Giant
Petrels \(n = 126\), 10 November 2005); among tracked birds, all Southern Giant Petrel incubation
fell within Northern Giant Petrels’ brood-guarding, while later breeding stages overlapped by
around one week between the species. Due to this allochrony, only one individual Northern Giant
Petrel yielded discriminated trips in the late period. To prevent this restricted sample from skewing
model fits, all models examining period were fitted to tracks only from the early and middle periods, except those for maximum range and trip start time, for which non-discriminated trips were also used because locations at the nest would not affect these variables.

Activity patterns could not be reliably inferred from the immersion data due to the erroneous wet events recorded by the Mk 7 loggers (proportion of trip wet for Mk 7 compared to other Mk 4 and Mk 5 loggers, in a binomial generalized linear mixed model controlling for species, sex and breeding stage as fixed effects and individual as a random effect with a logit link: \(1.54 \pm 0.15, Z = 10.40, P < 0.001\)). Within any breeding stage, which is the main constraint on behaviour, there were insufficient numbers of individuals fitted with Mk 4 or Mk 5 loggers to allow robust comparison of species or sexes, and therefore we do not address activity patterns further. In the light of this malfunctioning of the saltwater sensing – likely oversensitivity, responding to wet nests, vegetation or salts washing off plumage in addition to full immersion – previous studies that have used BAS Mk 7 loggers may benefit from a reassessment of their conclusions.

We used the same model selection approach for all analyses: an information theoretic approach based on AIC to select the most informative variables from a set of 13 candidate models. This metric assesses the fit of the entire model and thus avoids type I errors associated with multiple testing in this extensive exploratory analysis, while penalizing over-fitting (Burnham & Anderson 2013). Our candidate models included 1, 2, or 3 main effects, and interactions between species and sex, and between species and the temporal variable (breeding stage or period), to test whether these variables influenced foraging behaviour differently in the two species. All models with an interaction also contained both component variables as main effects (full list in captions of Tables 3-4 and Supplementary tables 1-2) and all models were fitted using maximum likelihood. Models are generally considered to have an equivalent fit (i.e. similarly informative) if their AIC is within 2 units (\(\Delta \text{AIC} < 2\)) of the best-fitting model (Burnham & Anderson 2013). To assess the relative explanatory power of our two temporal variables, breeding stage or period, we compared the fits of
both model sets using a reduced dataset that allowed all models to be robustly fitted; removing the insufficient late period trips left the post-brooding stage insufficiently represented, so this comparison excludes both these temporal divisions. To help differentiate between models of similar fits, we also calculated the AIC weight (relative likelihood) of each model, normalized across the candidate model set to capture their relative fits. We considered a model to have “some” support if it was at least twice as likely relative to the next-best fit model, “good” support if its relative likelihood was over 0.5 (absolutely most likely), and “robust” support if both of these criteria applied. In model sets that did not yield a single, preferred model, we considered all models with likelihoods > 50% of that of the best-fit model, and considered those variables present in over half of these models to have “some” support. Models with a relative likelihood of < 50% of the best-fit model were not considered informative.

All models were linear or generalized linear mixed models ((G)LMMs) fitted using the *nlme* or *lme4* packages (Bates et al. 2015, Pinheiro et al. 2016). For trip characteristics, individual ID was fitted as a random intercept to account for multiple trips by the same individual. For habitat use, each response variable was modelled as its value in each grid square per trip with each value weighted by the time spent in that grid cell in that trip. As each trip covered many grid squares and each bird potentially undertook multiple trips, trip ID nested within individual ID was fitted as a random intercept. To ensure that all model assumptions were met, chlorophyll and wind were log-transformed to reduce skew in the raw data and normalize residuals.

**RESULTS**

**Foraging areas**

Northern and Southern Giant Petrels were both widely distributed in the south-west Atlantic in the
austral summer 2005/06, but with marked differences between sexes and breeding stages (Fig. 1).

Females tended to forage more widely in both species, and across both species, constraints on
distribution were strongest during brood-guarding (Fig. 1). Females of both species were recorded
from the Scotia Arc in the south and east, to the Patagonian Shelf and Antarctic Peninsula region in
the west. In contrast, male Northern Giant Petrels were always concentrated around the colony, and
male Southern Giant Petrels only exploited more distant areas south and south-west of the colony in
the post-brood chick-rearing period. Overall, Southern Giant Petrels travelled east and west of Bird
Island, whereas Northern Giant Petrels only travelled substantial distances to the west; neither
species made substantial use of pelagic waters to the north of the colony. The 50% kernels of
females of both species and male Southern Giant Petrels included the South Orkney Islands, and
these trips, though pelagic in range, may have included coastal scavenging. Southern Giant Petrels
of both sexes visited the South Sandwich Islands, and the females also consistently used a small
area to their west.

In pairwise comparisons, the mean overlap between the utilisation distributions of each
species-sex-breeding stage combination was 0.487 (Table 2). This reflected a mixture of generally
high overlaps between the distribution of certain groups – males of both species, male and female
Northern Giant Petrels in general, and between both species within the brood-guarding period – and
generally low overlaps between other groups – female Northern and Southern Giant Petrels during
incubation, and female Southern Giant Petrels in incubation or post-brood and males of both species
(Table 2).

Trip characteristics

In the model sets testing the effect of breeding stage on the characteristics of foraging trips, there
was weak support that trips of Southern Giant Petrels were longer in terms of both travel distance
and duration than those of Northern Giant Petrels, although the effect size of the species term in the
best-fit model overlapped zero (mean travel distance ± s.e. for Northern Giant Petrels, 1775 ± 426 km and for Southern Giant Petrels, 3113 ± 461 km, Fig. 2; mean trip duration 79.7 ± 16.1 h and 154.8 ± 21.5 h, respectively; Table 3, Supporting Information Table S1). In keeping with this, the maximum range of foraging trips – closely correlated with both travel distance and trip duration (Spearman's $r^2$ of 0.861 and 0.707, respectively, both $P < 0.001$), but tested with the larger sample that included non-discriminated trips it did not differ between the two species (overall mean maximum range, 399 ± 43 km). Regardless of species, the sex and breeding stage affected trip length: males travelled less far and for less time (Fig. 2; mean trip duration for males, 99.6 ± 17.4 h; for females 160.6 ± 25.6 h) and for both sexes, compared to incubation, trips during brood-guarding were somewhat shorter and trips in post-brood substantially longer (Fig. 2, Table 3, Supporting Information Table S1). These differences were reflected in the smaller maximum range of males than females, and the maximum range of both sexes during brood-guarding and post-brood were shorter and longer, respectively (Table 3, Supporting Information Table S1). There was some evidence that trips started progressively earlier in the day through the breeding stages, as breeding stage was included in all top-fitting models, but none had strong support, and mean trip start time did not vary between the species or sexes (Table 3, Supporting Information Table S1). There was no evidence that sex or breeding stage affected characteristics of foraging trips in different ways in the two species (i.e. no well-supported interactions with species, Table 3).

Clearer differences were seen in the proportion of the trip that birds spent within 10 km of South Georgia (coastal foraging). Males spent more time near the coast, but this effect was less pronounced in Northern than in Southern Giant Petrels (Table 3, Supporting Information Table S1, Fig. 3). In addition, birds spent more time near the coast during brood guarding than in incubation or post-brood (mean proportion of trip coastal in incubation, 0.402 ± 0.076, in brood-guarding, 0.473 ± 0.048, and in post-brood, 0.423 ± 0.056; Table 3, Supporting Information Table S1). Across both species and sexes and all breeding stages, coastal trips were shorter in duration than pelagic
trips (across all trips, mean duration of coastal trips 71.3 ± 11.2 h; of pelagic trips, 178.3 ± 25.6 h; in LMM accounting for species, sex and breeding stage, effect of trip type (pelagic vs. coastal) 88.3 ± 22.8 h, \( t = 3.87, P = 0.0003 \)). Among coastal trips, there was no strong evidence that species, sex, or breeding stage affected maximum range (null model best fit, AIC weight 0.407, next-best 0.182), suggesting that none of these factors influenced whether birds stayed close to the colony or foraged coastally elsewhere at South Georgia.

In model sets testing the effect of period instead of breeding stage, there were marked differences in the characteristics of foraging trips of Northern and Southern Giant Petrels, reflecting the interspecific difference in laying dates and therefore the relative (calendar) timing of breeding stages. Southern Giant Petrels made longer trips in the early period and shorter trips in the late period, whereas the reverse was true for Northern Giant Petrels (for Northern Giant Petrels, mean travel distance in early period 1250 ± 307 km, middle period 3827 ± 1582 km; for Southern Giant Petrels, early period 5970 ± 1134 km, middle period 1439 ± 310 km; Table 3, Supporting Information Table S1). Mirroring the patterns by breeding stage, Southern Giant Petrels had a greater maximum range overall, and across both species, later trips were to waters further from the colony, with weak support for an interaction between species and period. Also similar to the breeding stage models, the effect of period on the proportion of a trip that was coastal did not differ between the species, and the start time of trips was not explained by any of the factors examined alongside period (Table 3, Supporting Information Table S1). Overall, breeding stage explained more variation in all trip characteristics than period, with the best-fit breeding stage model having a \( \Delta \text{AIC} \) of > –7 compared to the best-fit period model (\( \Delta \text{AIC} \) between best-fit breeding stage and period models fitted to the same reduced dataset: for travel distance –7.8, for trip duration –9.9, for maximum range –10.8, for trip start time –7.1, for proportion of the trip that was coastal –28.3).

**Habitat use**
By comparison with the analyses of trip characteristics, there was limited evidence that females of
the two species differed in their habitat use on pelagic trips. In models examining the effect of
breeding stage, used grid cells did not differ notably in either wind or bathymetry between either
species or breeding stage (Table 4). Sea surface temperature of used grid cells was similar in both
species, although Northern Giant Petrels used areas of warmer SST across breeding stages whereas
SST used by Southern Giant Petrels was more consistent across the breeding season (mean SST ±
s.e. used by Northern Giant Petrels in incubation, brood-guarding and post-brooding 1.32 ± 0.08 °C,
1.82 ± 0.07 °C, 4.05 ± 0.12 °C, respectively; and similarly by Southern Giant Petrels 2.50 ± 0.09 °C,
2.76 ± 0.06 °C, 2.07 ± 0.06 °C; Table 4, Supporting Information Table S2). The species also differed
in chlorophylla concentrations in their foraging areas, which tended to be lower in grid cells used
by Southern than Northern Giant Petrels (mean chlorophyll a ± s.e. in cells used by Northern Giant
Petrels 0.86 ± 0.05 mg/m³, and by Southern Giant Petrels 0.64 ± 0.02 mg/m³; Table 4, Supporting
Information Table S2).

Models examining the effect of period provided little evidence for interspecific differences
in habitat use. Consistent with seasonal environmental changes, period affected both temperature
and winds experienced by tracked birds (Table 4), with all birds using areas of warmer water and
lower winds in the middle than early period (mean SST ± s.e. in used cells in early and middle
periods, 2.77 ± 0.09 °C and 3.45 ± 0.09 °C respectively; mean wind speed ± s.e., 8.76 ± 0.04 m/s
and 7.55 ± 0.04 m/s respectively; Supporting Information Table S2). In addition, birds foraged in
deeper waters in the early than the middle period (mean depth ± s.e. in used cells in early and
middle periods, 3062 ± 48 m and 2476 ± 54 m, respectively; Table 4, Supporting Information Table
S2). As in the analysis by breeding stage above, Southern Giant Petrels foraged in areas of
somewhat lower chlorophylla concentrations than Northern Giant Petrels (Table 4, Supporting
Information Table S2).
DISCUSSION

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

Although the tracked Northern and Southern Giant Petrels differed to some extent in
distribution and behaviour, sex and breeding stage had a stronger influence than species or period
(calendar date) on their foraging ecology, with little evidence that these effects differed between the
two species. The similarity in the foraging strategies of these sister taxa implies that intra-specific
segregation patterns have changed little in the 500-200ky since the species diverged (Techow et al.
2010) and hence suggests that they are ancestral to both species (Hunter 1987). Despite their similar
strategies in biological time (breeding stage), in absolute time (i.e. in terms of calendar date), many
aspects of foraging behaviour differed between the species. Thus, rather than partitioning
contemporaneous foraging resources through changes in a complex suite of behaviours, competition
between these ecologically and morphologically similar species appears instead to be resolved
through a shift in breeding phenology, a trait that in many species has the potential for rapid
evolution (Franks et al. 2007, Friesen et al. 2007, Tarka et al. 2015). In other systems, inter-specific
competition may be resolved through dynamic differentiation in other behavioural traits: Rock
Shags Phalacrocorax magellanicus undertake longer trips when breeding in sympatry with the Red-
legged Cormorant P. gaimardi than when breeding in single-species colonies (Frere et al. 2008).
Indeed, it has been suggested that behavioural modification is the most likely immediate response
of seabirds to environmental change (Lewis et al. 2006). In giant petrels, our results indicate that
several aspects of behaviour, most notably breeding phenology but also foraging strategies, appear
to be labile traits that may have allowed initial rapid responses to reduce competition through
resource partitioning. In addition to the temporal segregation, Southern Giant Petrels tended to
forage slightly further afield and exploit more westerly areas than Northern Giant Petrels. This
difference in foraging ranges is likely to reduce costs of reproduction to some extent in Northern
Giant Petrels, and hence may underlie the difference between the species in population growth rate.
The sexual segregation we observed in both species, with females typically foraging further afield than males, particularly in early breeding stages, is consistent with previous findings from a range of biologging, stable isotope and diet studies (Hunter 1983, González-Solís et al. 2000a, González-Solís et al. 2000b, González-Solís et al. 2002, Forero et al. 2005, Phillips et al. 2011, Raya Rey et al. 2012, Thiers et al. 2014). These behavioural differences are associated with pronounced sexual size dimorphism: size differences have been assumed to constrain the larger males, which presumably have higher costs of flying, to specialise on the exploitation of seal and penguin carrion on local beaches, excluding the slighter females from these resources and forcing them to forage further afield (Hunter 1983, González-Solís et al. 2000b). However, our finding that both sexes of both species undertook substantial (> 4 days and > 1800 km) pelagic trips as well as coastal trips shows that foraging distributions in the giant petrels are more plastic than commonly appreciated during the breeding season, and not tightly constrained by physiological limits such as wing loading or competitiveness. This supports previous findings from the non-breeding season and diet studies (Hunter 1983, González-Solís et al. 2007, but see Thiers et al. 2014). Although females in particular undertook long foraging trips that resembled other medium-to-large, wide-ranging Procellariformes, such as albatrosses and White-chinned Petrels Procellaria aequinoctialis (Phillips et al. 2004, Phillips et al. 2005, Phillips et al. 2006), males were far from exclusively coastal when not constrained by chick demands. Similarly, consistent with the morphological specializations of both sexes (but particularly males) for exploiting carrion (Hunter 1983, González-Solís 2004, Forero et al. 2005), coastal foraging by both males and females indicates that scavenging is less male-dominated than commonly assumed. Overall, this variability suggests that giant petrels, broadly considered to be specialist scavengers (Hunter 1983, González-Solís 2004, Forero et al. 2005), should more rightly be considered as generalists, with both sexes able to exploit both coastal and pelagic areas and hence consume both carrion and oceanic prey. Indeed, the high level of opportunism would explain why their population trends are not correlated with carrion availability.
The range of and plasticity in foraging strategies among giant petrels indicates that segregation patterns are less shaped by adult physiology, and more by the demands of reproduction (incubating the egg or feeding the growing chick). Indeed, breeding stage explained more variation in foraging behaviour than calendar date, and moreover the range of both species was most restricted around the colony during the brood-guard stage of chick-rearing, when the parents alternate at the nest to provide food, warmth and protection from predators, which may be facilitated by the shorter duration of the coastal trips favoured in this breeding stage. This change in behaviour in response to biotic conditions indicates that both male and female giant petrels make dynamic foraging decisions throughout the breeding season, and hence probably also throughout the rest of year, to meet changing demands. This behavioural diversity suggests that divergent selection on foraging strategies between males and females is not strong, and hence that morphological differences related to foraging are unlikely to completely explain intra-specific foraging segregation in this system. Indeed, rather than morphology driving segregation, as often assumed, it is not currently possible to rule out that intra-specific behavioural differences may have arisen first – as with the inter-specific differences above, a labile initial response to reduce competition – with the striking morphological differences emerging in consequence as further specialisation.

Although foraging behaviour displayed multi-faceted and dynamic variability, we found little evidence for consistent use of particular habitats among females on pelagic trips. Southern Giant Petrels appeared to forage in areas of lower chlorophyll (at the time of the trip) than Northern Giant Petrels, and males and females in later breeding stages, especially Northern Giant Petrels, used warmer waters than birds in earlier breeding stages. However, we cannot confidently discern whether these are active habitat choices to optimise nutrient intake or unavoidable consequences of the spatial and temporal segregation patterns. In particular, breeding allochrony in giant petrels is likely associated with variation in the habitats available to each species at each breeding stage; the
extent to which habitat use reflects real preferences for certain oceanographic features would require further investigation. Moreover, as the limited number of pelagic trips undertaken by males precluded a robust analysis of their habitat choices, we were not able to investigate the population-level importance of habitat preferences. Further, some trips that we classified as pelagic included time spent close or on land at the South Orkney and South Sandwich islands, and other parts of the Scotia Arc, where giant petrels may have been exploiting carrion on beaches rather than oceanic prey. Lastly, as with the trip characteristics discussed above, foraging habitat varied substantially across a relatively small number of trips (max. 22 trips per species/sex/temporal variable group); tracking more individuals may serve to reduce this variation and hence clarify real differences in foraging strategies between the groups. Due to these difficulties in interpreting the observed patterns in habitat use, the implications of interspecific differences in habitat preference for population trajectories remain unclear. Studies of habitat use at other colonies where the two species breed sympatrically but show different population growth rates (Delord et al. 2008; Ryan et al. 2009) would provide an informative natural experiment in which to fully assess the role of habitat availability in population trajectories. This would be of substantial value in moving from a descriptive to a predictive understanding of inter- and intra-specific resource partitioning in seabirds (Pinet et al. 2012, Thiers et al. 2014, Cleasby et al. 2015).

Our single-colony study has highlighted the importance of segregation along both spatial and temporal axes for the coexistence of two ecologically and morphologically similar seabird species. Sexual segregation was mainly spatial, constrained by breeding stage, whereas segregation between the species arose from breeding allochrony. Intra-specific competition had a stronger influence on distribution and behaviour than inter-specific competition, mirroring patterns in other sympatric vertebrates (seabirds: Weimerskirch et al. 2009, Young et al. 2010; reef fish: Forrester et al. 2006). These behavioural differences are not only of ecological and evolutionary importance but may also have conservation implications if they expose different parts of the population or
community to different threats (van Toor et al. 2011). However, while wider-ranging female giant petrels have historically been proposed to be more at risk of incidental mortality in longline fisheries than males (González-Solís et al. 2000a, Otley et al. 2006) and the same could apply to wider-ranging Southern compared to Northern Giant Petrels, current management of demersal fisheries at South Georgia and around the Falkland Islands includes strict bycatch mitigation methods and monitoring of compliance (Tancell et al. 2016), and so these range differences are unlikely to affect bycatch likelihood. Finally, while our investigation focussed on segregation of two species within the seabird community, foraging strategies within a multi-species assemblage also depend on those of other taxa, segregation at smaller scales (Navarro et al. 2013), and individual habitat preferences (Phillips et al. 2017). Given the structured segregation patterns of giant petrels at South Georgia that we have described, both within and between species, this species pair could be an informative model in which to extend our understanding of how simultaneous competition on many different scales shapes foraging strategies and habitat use.

We are grateful to Helen Taylor for assistance with retrieval of devices on Bird Island, to Andy Wood for collation of the tracking data, to Tommy Clay for informative discussions on the analysis and to Sue Lewis for helpful comments on a draft manuscript. Constructive comments from two anonymous reviewers substantially improved the paper. This study represents a contribution to the Ecosystems component of the British Antarctic Survey Polar Science for Planet Earth Programme, funded by NERC.

REFERENCES


Ryan PG, Jones MGW, Dyer BM, Upfold L, Crawford RJM. 2009. Recent population estimates and


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

**Table S1**: Full model outputs of the best-fit models describing trip characteristics of foraging Northern and Southern Giant Petrels tracked at Bird Island, South Georgia.

**Table S2**: Full model outputs of the best-fit models describing habitat use of foraging Northern and Southern Giant Petrels tracked at Bird Island, South Georgia.
### Tables

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**For trip characteristics**

| Incubation | Females | 3 | 3 | 10 | 10 |
| Brood-guarding | Females | 5 | 3 | 19 | 10 |
| Post-brood | Females | 8 | 6 | 7  | 6  |
| Males   | 0 | 0 | 7 | 6  |

**For habitat use**

| Incubation | Females | 0 | 0 | 1  | 1  |
| Brood-guarding | Females | 7 | 5 | 1  | 1  |
| Post-brood | Females | 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.
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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.
Table 3. The five best-fitting models describing trip characteristics of giant petrels 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). The full candidate model set for

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each response variable was: Species; Sex; Time (breeding stage or period); Species + Sex; Sex +
Time; Species + Time; Species + Sex + Species:Sex; Species + Time + Species:Time; Species + Sex
+ Time; Species + Sex + Time + Species:Sex; Species + Sex + 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 * indicates one of several models considered informative (full model selection criteria in main text).
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 *
indicates one of several models considered informative (full model selection criteria in main text).
Figure 1. Distributions of Northern and Southern Giant Petrels tracked from Bird Island, South Georgia, in 2005/06 by sex and breeding stage (calendar date differs between species), shown as 95%, 50% and 25% utilisation distributions. Females are shown in red and males in blue, with progressively higher-probability kernels in darker colours. Landmasses are shown in black, with the tip of South America on the left hand map edge and the Antarctic Peninsula on the bottom edge. Relevant island groups and features are marked on the first panel: the Patagonian Shelf (PS), Falkland Islands (FI), South Georgia (SG), South Sandwich Islands (SSI) and South Orkneys (SOI); the latter three island groups illustrate the line of the Scotia 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 the western tip of South Georgia.
Figure 2. Travel distance of Giant Petrels tracked from Bird Island, South Georgia, in austral summer 2005/06 for each species, sex and breeding 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 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 circles.
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, 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 quartiles. Whiskers show the data range 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 circles.