Offshore spatial segregation in giant petrels Macronectes spp.: *differences between species, sexes and seasons*

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ABSTRACT

1. Investigations were made to determine whether the two giant petrel species segregate by gender and species in relation to the stage of the annual cycle. The individual foraging behaviour of 14 male and 11 female northern giant petrels (*Macronectes halli*) and 13 male and 15 female southern giant petrels (*M. giganteus*) breeding at South Georgia were tracked over 1 year using geolocators (global location sensing loggers).

2. Males of both species showed a flexible foraging strategy, switching from coastal to pelagic habits, probably governed by spatio-temporal changes in carrion availability. In contrast, marine areas exploited by females were more consistent over the year and similar for the two species, with most foraging locations concentrated over the same pelagic waters.

3. This study provides support for the differences in foraging between sexes as the main mechanism reducing intraspecific competition. Although the two species are morphologically similar and can easily access each other's foraging habitat, they differ in the foraging areas exploited. Thus, interspecific competition seems mainly relaxed by spatial segregation, particularly between males in winter, probably mediated by different competitive abilities and physical tolerances to temperature and winds. Foraging southern giant petrels from South Georgia were not restricted to the areas within the line of equidistance to other colonies, but their foraging range overlapped with feeding grounds of conspecifics breeding in the Falkland Islands and the Antarctic Continent.

4. Taken together, these findings suggest that foraging selection on marine habitat heterogeneity reduces interspecific competition, whereas carrion availability reduces intersexual competition, in giant petrels. Copyright © 2008 John Wiley & Sons, Ltd.

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INTRODUCTION

Intensive competition is expected between similar species occupying similar niches, usually leading to competitive exclusion of one of the two species. As a consequence, closely related species generally do not occur sympatrically but replace each other geographically (Odum, 1971; Arthur, 1987; Pianka, 2000). In some cases, however, some species of almost identical appearance coexist in the same area (Grant, 1975; Arlettaz et al., 1997). The way sympatric and closely related species partition resources has always been a prime issue in ecology (Lack, 1947; Connell, 1980; Schluter, 2000). In addition to interspecific competition, intersexual competition is also of considerable ecological interest, and has been extensively debated in the last decade, especially that among various vertebrate groups (Ruckstuhl and Neuhaus, 2005). Nevertheless, processes governing the coexistence of competitors are still poorly understood. Two main types of competition can occur: (1) exploitation competition when individuals compete indirectly for the same limiting resource depleting the amount available to others; and (2) interference competition, when individuals directly interfere with the foraging, survival, or reproduction of others (Birch, 1957). Detailed studies on foraging behaviour and habitat heterogeneity open up new avenues to approach the nature of competition between closely related species and the mechanisms for coexistence (Brown, 2000). An evolutionary response to competition is resource partitioning by displacing the niche at various spatio-temporal scales (Williams, 1972; Connell, 1980; Diamond, 1986; Brown, 2000). Spatial segregation can be defined as a non-random distribution of individuals in space use, and is usually intimately related to habitat segregation. Very recently, some radio and satellite tracking studies have addressed the foraging overlap between sexes and species (González-Solís et al., 2000a; Lewis et al., 2002; Phillips et al., 2004b). In addition, a few studies have related spatial segregation while foraging to differences in marine habitat exploitation (Hyrenbach et al., 2002; Waugh and Weimerskirch, 2003). However, owing to the costs and the limitations in the attachment methods of satellite tracking, most studies are restricted to the breeding period and have been conducted over short periods and for a few trips. This usually precludes the simultaneous comparison of foraging ranges of both sexes of more than one species at different breeding stages, but particularly over the wintering period. A significant technical advance in the study of foraging behaviour in the pelagic environment has been the development of lightweight geolocators; global location sensing (GLS) devices that can be deployed on seabirds all year round attached to a leg ring (Wilson et al., 1992; Afanasyev, 2004; Phillips et al., 2004a; Croxall et al., 2005). Because their cost is modest, many devices can be deployed, allowing for broader temporal overviews of foraging behaviour and habitat use.

Among seabirds, several pairs of sibling petrel species nest on the same islands. One of the most striking examples of coexistence is the sympatric distribution of the two sibling species of giant petrels at several subAntarctic archipelagos (Hunter, 1987). Results from satellite tracking indicate that during incubation and chick-rearing periods there is a remarkable sexual segregation between the species in foraging strategies and areas (González-Solís et al., 2000a, b). Both species showed a much larger foraging range than previously thought, travelling up to 2000 km from the breeding colony. However, this information is based on a small number of trips during the incubation period. As in most pelagic species, information on their foraging grounds and sexual segregation during the non-breeding period is very scarce. Giant petrels are particularly appropriate for studies of intersexual and interspecific resource competition. First, although the northern species, *Macronectes halli*, is 5–8% lighter than the southern species, *M. giganteus*, they have such a similar morphology and phylogenetic relationship that hybridization sometimes occurs and a few decades ago they were considered conspecific (Hunter, 1987). Second, both species have a marked sexual size dimorphism, with males being on average 25% heavier than females, giving opportunities for sexual segregation (Phillips et al., 2004b; González-Solís and Croxall, 2005). Third, although some sexual and interspecific differences have been noted, there is substantial diet overlap. Both species and sexes feed mainly on penguin and seal carrion (at several localities, including South Georgia), although males are known to feed more extensively on such prey than females, which feed the chicks with a greater proportion

of krill, squid and fish collected at sea (Hunter, 1983). Fourth, these species are known to compete intensively at penguin and seal carcasses (Johnstone, 1979; Bruyn and Cooper, 2005). In contrast with many seabirds, which compete only indirectly through the exploitation and depletion of resources, the regular intra- and interspecific aggressions among giant petrels at penguin and seal carcasses indicate that interference competition also occurs, imposing access restrictions on subordinate individuals (pers. obs.). Fifth, although a 6 week difference in the timing of breeding between the two species exists at the four subAntarctic localities where both species breed sympatrically; there is overall a substantial overlap in the 6 month breeding period (Hunter, 1987). Moreover, both species show similar requirements for nesting, often breeding close together and sometimes intermingled. In this study geolocators were used to study the spatial and temporal distribution over 1 year of the males and females of northern and southern giant petrels breeding at Bird Island, South Georgia. The study examines whether the two giant petrel species segregate offshore by gender and species in relation to the stage of the annual cycle.

MATERIAL AND METHODS

Fieldwork

Fieldwork was carried out on Bird Island, South Georgia (54° 03′S, 38° 36′W) in the period October to March 1999 to 2001 (Figure 1). On this island, the estimated number of breeding pairs of northern and southern giant petrels in 1996 was 2062 and 521, respectively (D R Briggs and R Humpidge *in litt.* to González-Solís *et al.*, 2000a). The study colony comprised a few breeding aggregations of giant petrels from both species, sometimes breeding intermingled, totalling more than 150 nests for each species. In November 1999, 100 geolocators mounted on a Darvic ring were deployed in equal proportions on male and female northern and southern giant petrels during the incubation period. Geolocators were deployed on a single member of each pair to minimize any potential impact of the geolocator on the breeding performance. Sixty-three, seven and one geolocators were recovered after 1, 2 and 3 years, respectively, and complete data was downloaded from 14 male and 11 female northern giant petrels and 13 male and 15 female southern
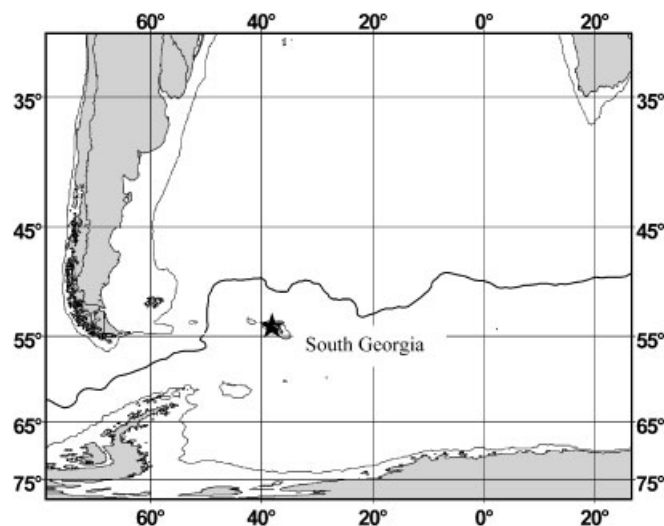

Figure 1. Colony site at South Georgia (indicated with a star) and study area in the Southern Ocean. Grey lines show the 100 m isobath and bold line shows the position of the Antarctic Polar Front (according to Orsi *et al.*, 1995).

giant petrels. Eleven geolocators could not be recovered because they had fallen off the Darvic ring; the remaining 18 instrumented birds were not seen in the area over the following two years. The geolocators used in this study were developed by the British Antarctic Survey and weighed 16 g. The geolocator was equipped with an internal clock and measured the light levels every 60 s, recording the maximum reading within each 10 min interval (full details in Afanasyev, 2004). From this information two positions per day (one corresponding to midday and the other to midnight) can be inferred with an average accuracy of 186 km ± 114 km (Phillips *et al.*, 2004a).

Geographical procedures

All data were converted to a cylindrical equal-area projection centred at the breeding colony to minimize the projection deformation and to ensure area conservation. To study the seasonal distribution of the positions kernel density distribution maps were derived using the kernel function implemented in the Animal Movement extension (Hooge *et al.*, 1999) of ArcView GIS 3.2 (ESRI). The smoothing parameter was set to 200 000 m and grid size to 10 000 m. Positions obtained from the same animal are not truly independent, but it has been shown that assessing ranges using kernel density procedures does not require serial independence of data (De Solla *et al.*, 1999).

For the instrumented birds the timing of the main events of the breeding season (laying, hatching and fledging) were monitored over the whole breeding period. Since foraging strategies were expected to change according to the stage of the breeding cycle and breeding status, kernel analyses were performed accordingly. That is, kernel maps were produced for groups of birds comprising individuals at a similar breeding stage (incubation, guarding, post-guarding), breeding status (breeding or failed birds (from failure date until the mean population fledging date)) and season (breeding season or wintering period (from fledging to mid August)). Note that each of these periods varied among birds, depending on the species, the laying and hatching date and the failure date/fledging date. The guarding period was assumed to last for 32 days (northern) and 21 days (southern) after the hatching date (Hunter, 1984).

Spatial segregation

To study the monthly spatial segregation, the frequency of positions per cell was calculated for each sex and species separately for each month. Habitat selection and segregation is dependent on the spatio-temporal scales of observation (Conradt *et al.*, 1999; Brown, 2000). Since the movements of giant petrels were tracked using geolocators with a nominal accuracy of 186 km (Phillips *et al.*, 2004a), large-scale segregation was analysed, setting cell size to 200×200 km. MiraMon (Pons, 2000) and ArcView GIS 3.2 (ESRI) were used for work on spatial data.

To estimate the degree of sex and species differences in spatial use between male and female northern and southern giant petrels, the segregation coefficient (Conradt *et al.*, 1999) was used, based on the monthly frequency of positions in 200×200 km spatial quadrats, for those quadrats within 2000 km radius of the breeding colony. The spatial segregation coefficient can be calculated as follows (Conradt *et al.*, 1999):

$$SC = \sqrt{1 - \frac{N-1}{XY} \sum\nolimits_{i=0}^{k} \frac{x_i y_i}{n_i - 1}}$$

where X is the total number of observed positions of the group 1 (males, females or species); Y the total number of observed positions of the group 2 (males, females or species); N the total number of observed positions $(X + Y)$; x_i the number of group 1 positions in ith spatial quadrat; y_i the number of group 2 positions in ith spatial quadrat; n_i the number of positions in ith spatial quadrat $(x_i + y_i)$; k the number of spatial quadrats.

Quadrats without positions or with a single position are excluded, since solitary positions separate from other positions of their own group (sex or species) as much as from positions of the opposite group. This

measure is equivalent to the geometric mean proportion of segregated positions and can range from '0' (no segregation) to '1' (complete segregation). It is suitable for quantitative studies of segregation because it is stochastically independent of the group ratio of positions and the number of positions within each square. Because the segregation coefficient is calculated on multiple positions from a few animals rather than numerous independent animals, a spurious segregation could emerge if many positions of the same animal are recorded before the animal moves to another quadrat. However, although positions from the same bird are not truly independent, each position is at least 12 h apart from the previous position, which ensures that the bird can readily move from quadrat to quadrat between two consecutive positions. Moreover, because positions of all birds were recorded at the same time interval, relative comparisons among groups and seasons are consistent.

Positioning and filtering procedures

Positions were calculated using Multitrace-3/16 light (Jensen Software Systems, 1997) by inspecting the integrity of the light curve day by day and fitting dawn and dusk times. The elevation angle of the sun was set at -5.5. To filter unrealistic positions, the following were removed: (a) those obtained from light curves showing interferences at dawn or dusk (mainly due to the bird sitting on the ground or to the proximity of artificial light); (b) those inferred from days or nights longer than 23 h; (c) those with a speed index (V_i) above 60 km h^{-1}, as calculated by the root of the square speed average of the segments formed with the two preceding and the two following positions (McConnell *et al.*, 1992):

$$V_i = \sqrt{\frac{1}{4} \sum\nolimits_{j=-2, j\neq 0}^{j=2} (v_{i,j+i})^2}$$

where $V_{i,j+i}$ is the velocity between successive positions i and $j+i$; (d) those within the equinox periods ranging from 19 March to 9 April and from 3 to 29 September (the equinox periods were set after a graphical inspection of the behaviour of the speed index over the year). Using this procedure, 24.9% of 44 349 positions were discarded.

RESULTS

Interspecific and sexual segregation in space use over the year

Activity ranges derived from kernel analyses in relation to gender and species are shown in Figure 2 organized according to the annual cycle of the animals (Figure 3). During the incubation period females showed a larger and more pelagic activity range compared to males of their own species (Figure 2(a)). Northern males and females showed a smaller activity range than southern giant petrel males and females, respectively. The interspecific difference may reflect the late deployment of the geolocators, at a time when most northern giant petrels were at the end of the incubation period, resulting in relatively few incubation locations for the northern giant petrels, mostly concentrated close to the time when birds start reducing the duration of the foraging trips (González-Solís, 2004b). During the guarding period there was an obvious contraction of the foraging range for all four groups compared to the preceding and following stages (Figure 2(b)). During the post-guarding stage the activity range expanded for all four groups, but northern giant petrels foraged mainly north, and southern giant petrels mainly south of the breeding colony (Figure 2(c)). In winter, northern giant petrels, particularly males, moved their main foraging areas to the Patagonian shelf break. In contrast, southern giant petrel males were nearly restricted to South Georgia and adjacent areas to the south, although some females also foraged on the Patagonian Shelf (Figure 2(d)). Failed birds during the incubation or chick rearing stages at any time from November to May showed some differences compared to breeding birds. Whereas northern giant petrel females only slightly expanded their
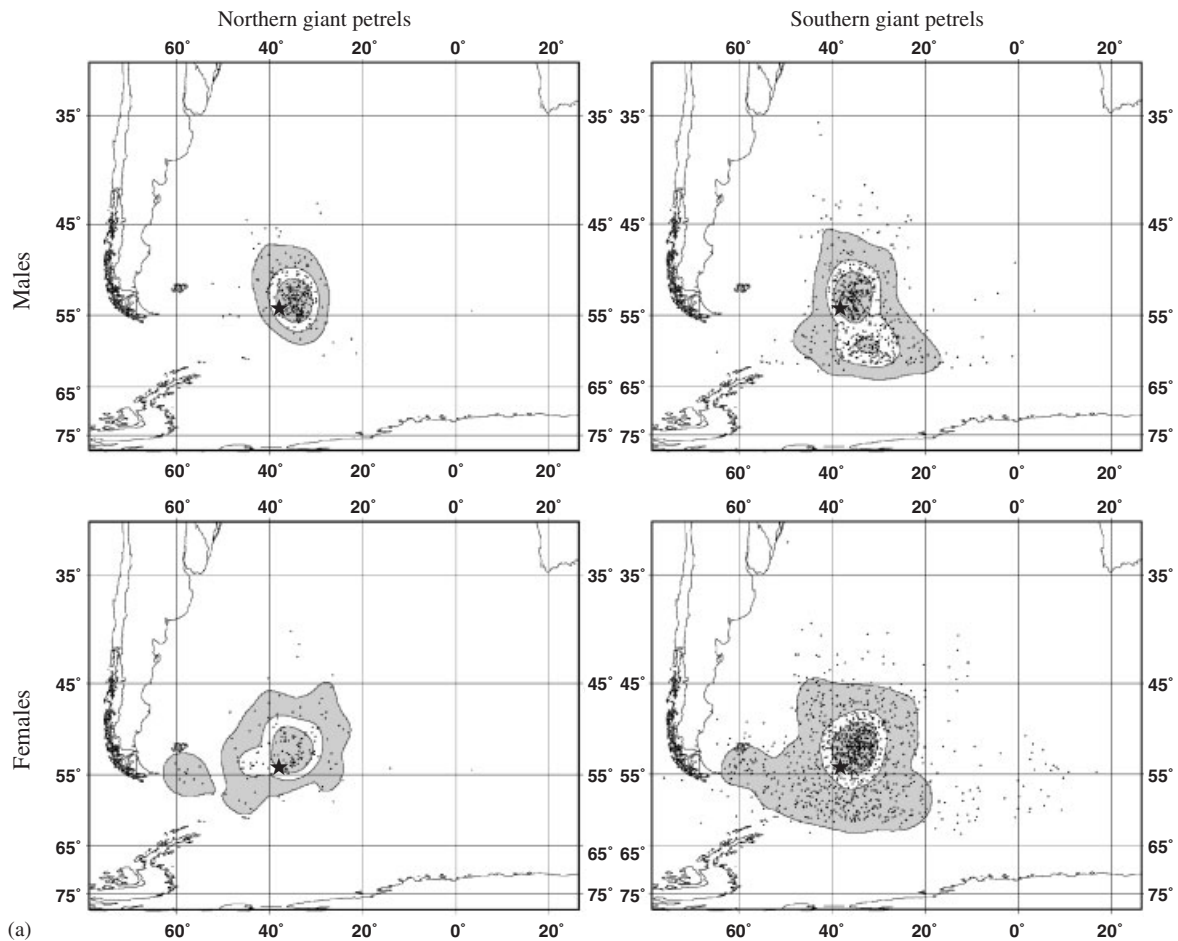
Figure 2. Validated locations for all trips and the respective activity ranges derived from kernel analyses (encompassing 95%, 75%, 50% of locations) in relation to gender and species during the incubation (a), guarding (b), post-guarding (c), and wintering (d) periods, and for failed birds during incubation and/or chick-rearing period (e).

foraging range, some males travelled further away to the Antarctic Peninsula shelf and Cape Horn areas; similarly, southern giant petrel males and females clearly increased their foraging range (Figure 2(e)).

The monthly degree of spatial segregation over one year between male and female northern and southern giant petrels is shown in Figure 3. The degree of spatial segregation between male and female northern giant petrels was lowest at the end of the winter (August), peaked during the incubation period (November), then reduced and stabilized over the chick-rearing period (January to May), dropping again over the wintering period. In contrast, spatial segregation between male and female southern giant petrels was lowest during the incubation and guarding period (November to January), increased over the chick-rearing period, peaking at the end of the breeding season (May) and reduced slightly and stabilized over the wintering period (June to October) (Figure 3(a)). Interspecific spatial segregation was highest at the end of the breeding period, particularly between males of the two species (April and May), and showed a second smaller peak in December. In November, the segregation coefficient between northern and southern giant petrels was lowest for males and highest for females (Figure 3(b)).

Northern giant petrels   Southern giant petrels
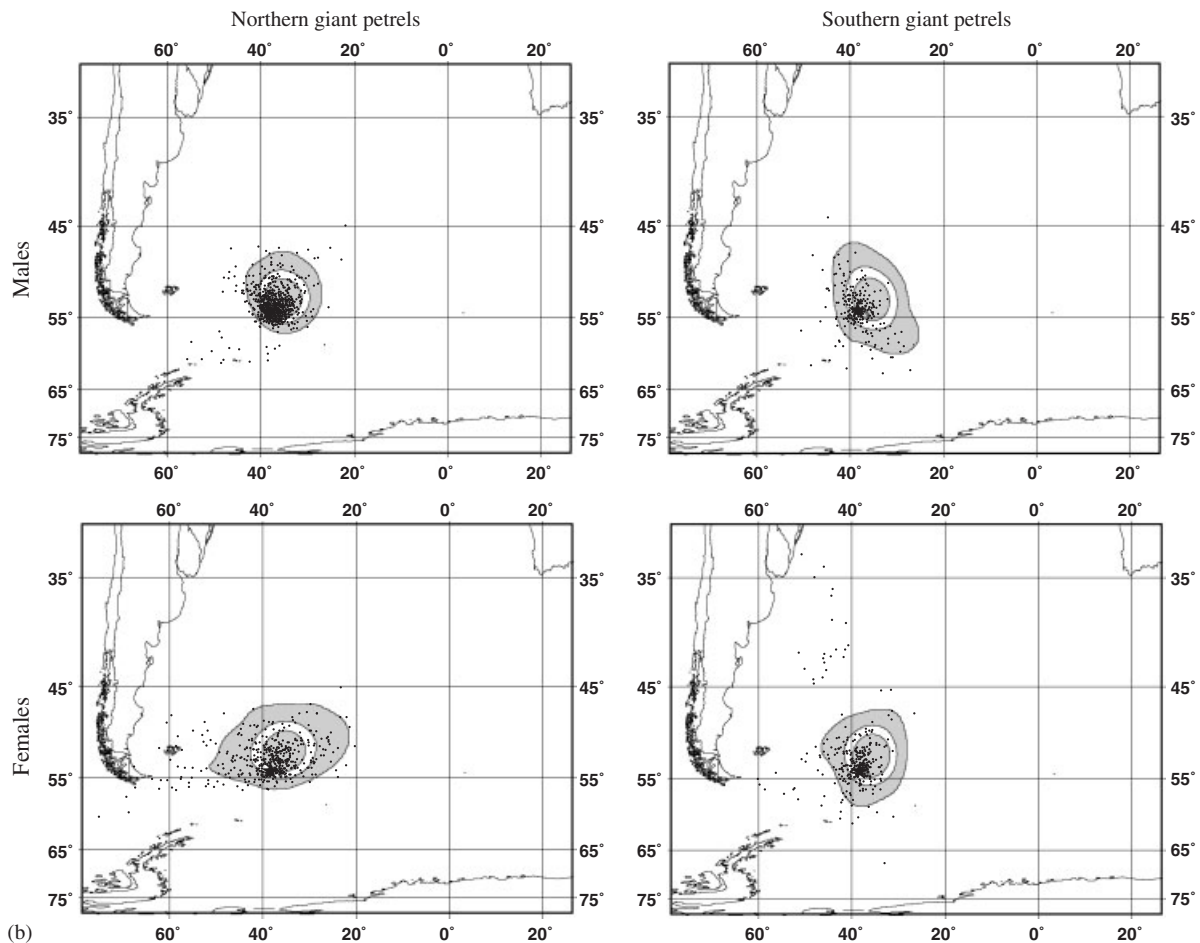
Figure 2. *continued.*

DISCUSSION

This study reports on the most comprehensive investigation to date of species and sex-specific spatial and habitat segregation in a marine system. It provides the first quantitative values for the degree of spatial segregation and comparisons involving all stages of the annual cycle. Generally, giant petrels behaved as typical pelagic seabirds comparable to albatrosses (BirdLife International, 2004), ranging and feeding over huge areas. However, foraging range and spatial segregation showed noticeable changes depending on the stage of the annual cycle, reflecting the different constraints at each period (Figure 2). Changes in foraging habitats, distance to the breeding colony and trip duration in relation to the stage of the annual cycle have been found for a number of albatrosses and petrel species at several breeding sites (Hyrenbach *et al.*, 2002; BirdLife International, 2004; Phillips *et al.*, 2004b). However, none of these studies could compare changes over an entire annual cycle. During the incubation period, male and female giant petrels share duties and alternate foraging trips that can last from 1 to 30 days. At this time, study birds travelled hundreds or thousands of kilometres to feeding areas. As soon as the chick hatches, guarding parents concentrated most foraging on the South Georgia coast, shelf and shelf break, the foraging area during this period being the
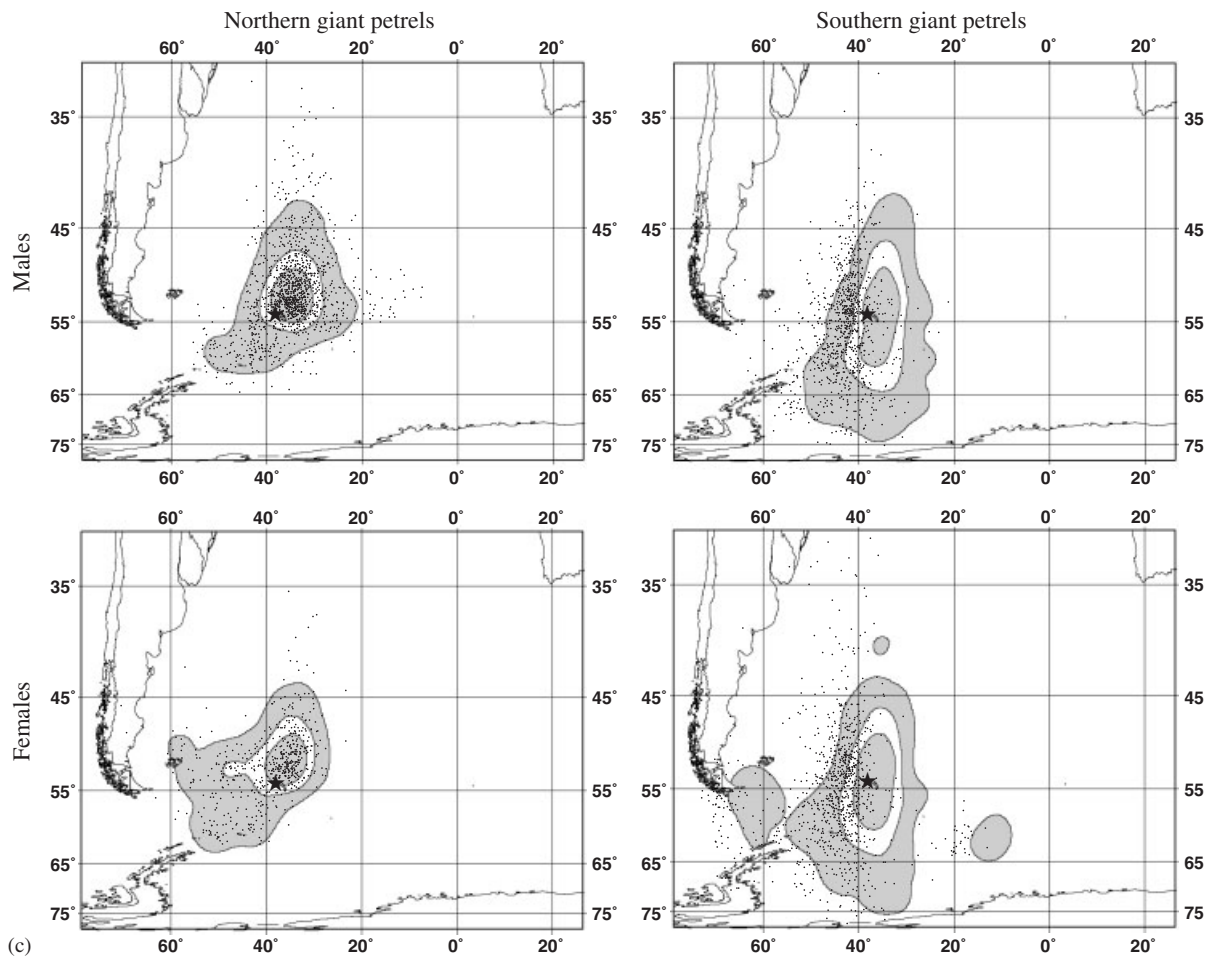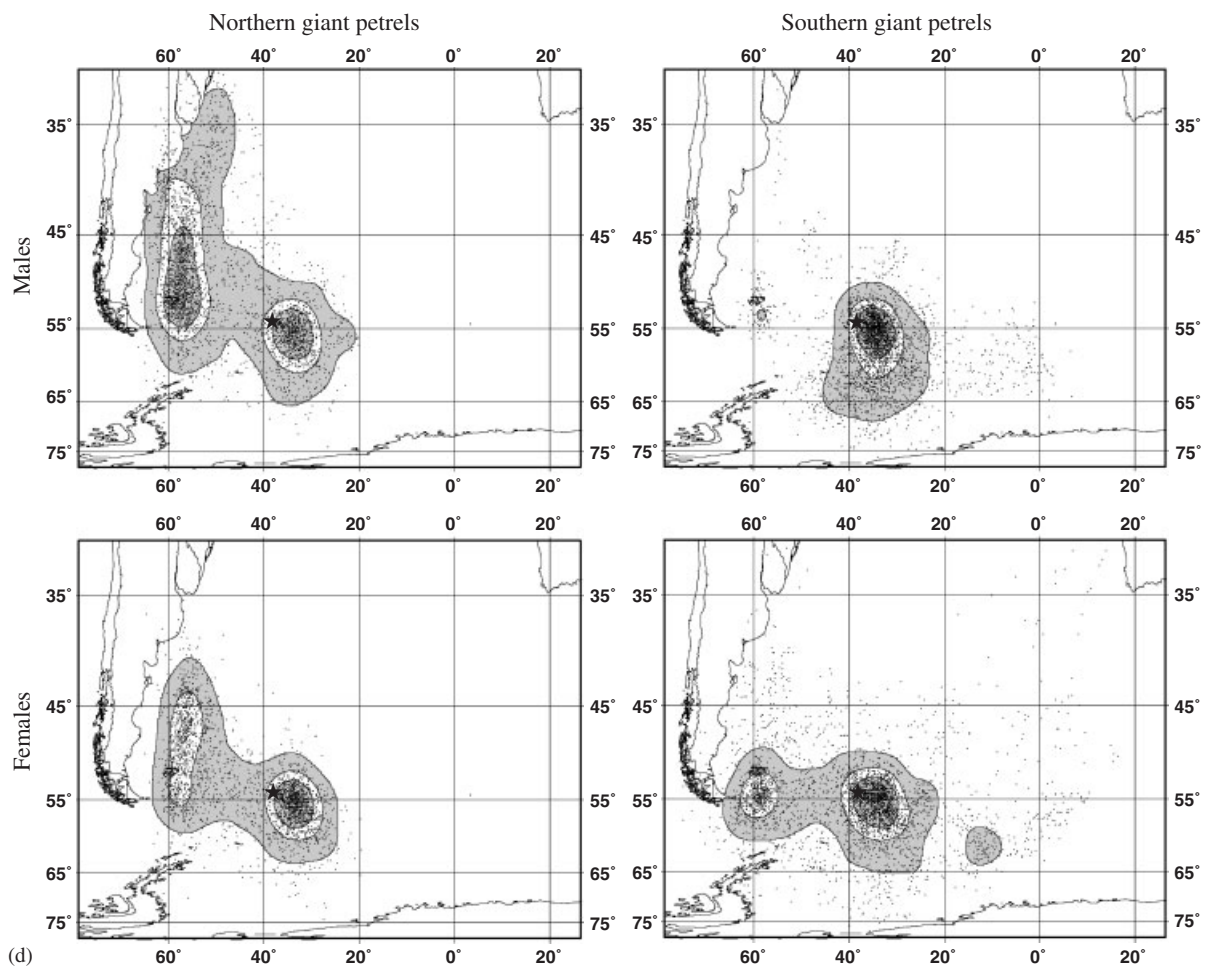
Figure 2. *continued.*

smallest of the annual cycle for all giant petrel groups, as found for a number of albatross species (Hyrenbach *et al.*, 2002; Phillips *et al.*, 2004b). This reflects that near hatching, one parent remains at the nest, and the partner curtails the duration of foraging trips to achieve a higher rate of feeding for the hatchling (Warham, 1990; González-Solís, 2004b). In giant petrels the incubation and guarding periods seem to coincide with the peak in carrion availability. This peak is created by the arrival of penguins as well as by Antarctic fur seal *Arctocephalus gazella* males engaging in territorial conflict and by fur seal females giving birth (Boyd, 1989, 1993). Territorial conflicts result in the death of many fur seal males on the beaches and births result in the refusal of placentas, creating feeding opportunities for scavengers. Similar to albatrosses, in the post-guarding period giant petrel parents forage independently, leaving the chick unattended at the nest and engage in long foraging trips to recover energy reserves lost during incubation and guarding (Weimerskirch *et al.*, 1997; González-Solís *et al.*, 2000b). As in most petrel species, energy requirements increase. At the same time, food availability for giant petrels declines with progress of the season. Fur seal males return to sea, the female pupping season finishes and penguin numbers and the vulnerability of their chicks decrease from January to April. This is reflected in the progressive enlargement of foraging areas at sea (Figure 2). The clearest sign that the increase in pelagic habits over the
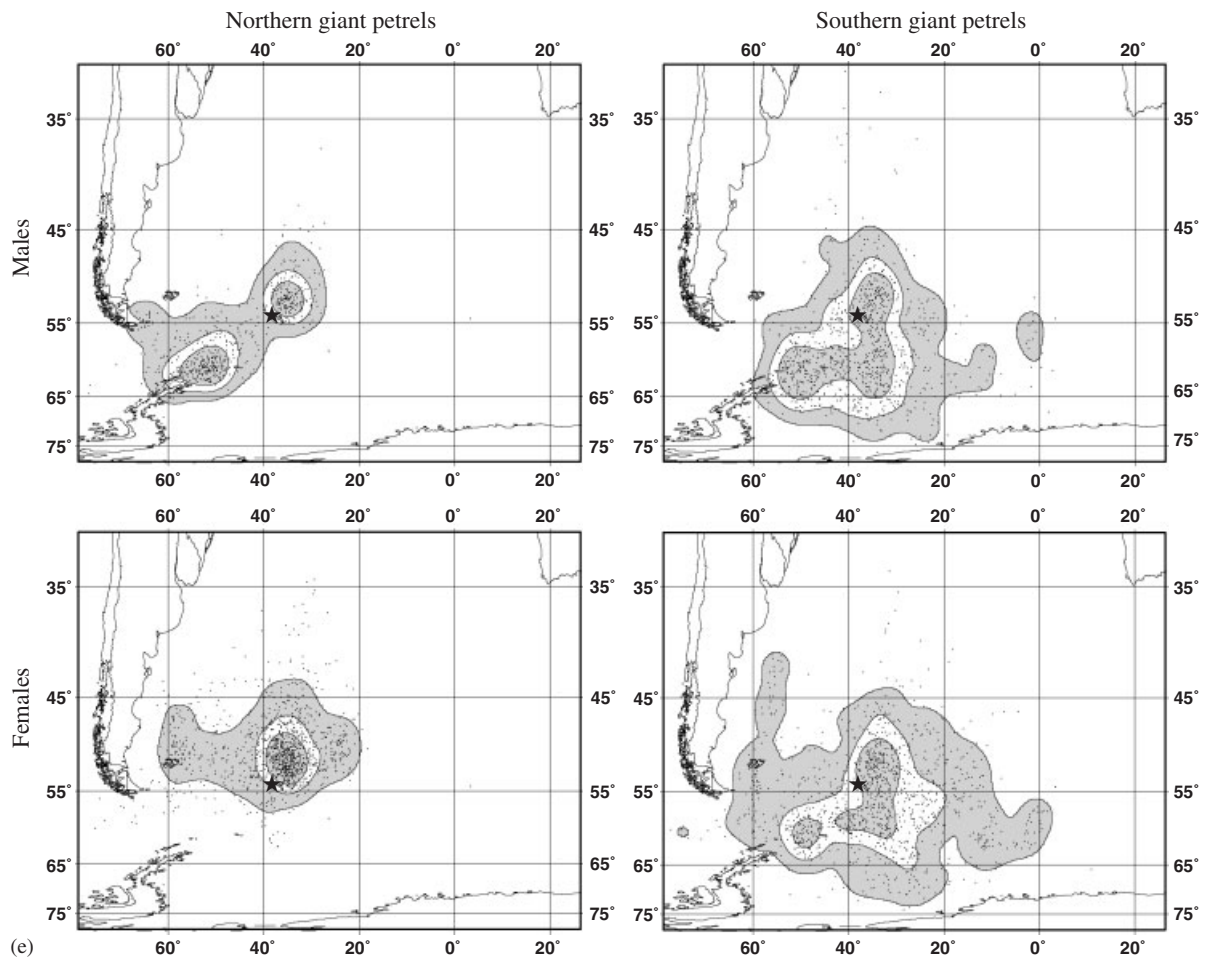
Figure 2. *continued.*

post-guarding period is related to the decrease in carrion availability is provided by the foraging behaviour of failed birds from November to May. In contrast with post-guarding birds, failed birds no longer have breeding duties and can expand their foraging areas, commuting to the Antarctic Peninsula shelf, which is too far from the breeding colony to be visited frequently by incubating or chick-rearing birds (Figure 2(e)). Switching to the Antarctic Peninsula shelf probably allowed them to continue exploiting carrion, taking advantage of the later phenology of Antarctic penguin species (Kooyman, 2002). This behaviour likely reflects the greater rewards of the scavenging strategy compared to pelagic foraging (González-Solís *et al.*, 2000b). Wintering birds did not migrate to new areas but tended to disperse to areas similar to those used during the breeding season (Figure 2(d)). However, being free of parental duties, birds remained in these areas throughout the winter.

Spatial segregation between sexes

Interference competition between males and females while feeding is a common feature in territorial animals, which may lead to spatial segregation in foraging areas mediated by social dominance and

Figure 2. *continued.*

competitive exclusion (Ruckstuhl and Neuhaus, 2005). Spatial segregation in seabirds, however, is more difficult to explain, given that breeding territories only include the nest but not the food resources. Nonetheless, it has been reported in a few seabird species (Stahl and Sagar, 2000; Lewis *et al.*, 2002; BirdLife International, 2004; Phillips *et al.*, 2004b). Reported differences are often restricted to microhabitat use, such as differences in diving depths, or small differences in foraging locations. Thus, foraging differences are usually attributed to niche specialization mediated by some size dimorphic trait, although small foraging differences have occasionally been reported for monomorphic species (Lewis *et al.*, 2002 and references therein). In contrast, giant petrels show extensive and large-scale sexual segregation, as found in some migrating ducks, grouse, owls and passerines (Cristol *et al.*, 1999). During breeding, males of both species generally foraged closer to the colony than females, which mainly engaged in pelagic trips (Figure 2). This is consistent with previous interpretation of sexual differences in foraging ecology as related to the more carrion-based diet of males (González-Solís *et al.*, 2000a, b). Previous research on diet composition showed that males consume more penguin and pinniped carrion than the more pelagic females, which eat more marine prey (Hunter, 1983; Hunter and Brooke, 1992). Direct observation of pinniped carcasses at beaches is also consistent with the detected differences, indicating that carcasses are
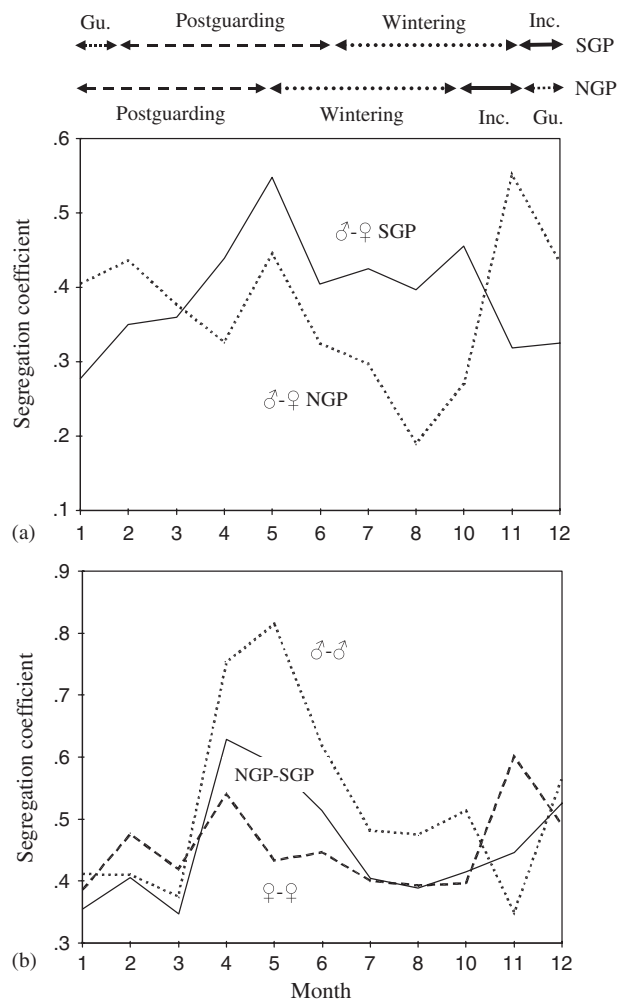
Figure 3. Annual cycle of giant petrels breeding at South Georgia and degree of spatial segregation over one year (a) between males and females of northern (dotted line) and southern giant petrel (solid line) and (b) between northern and southern giant petrel males (dotted line) and females (dashed line) and between the two species (sexes pooled, solid line). Segregation coefficient is based on the frequency of positions in 200×200 km spatial quadrats, for those quadrats with at least two locations and within 2000 km radius of the breeding colony (see methods). Note: September was not included in the graph due to positioning errors near to the autumn equinox (see positioning and filtering procedures section). NGP = Northern giant petrels. SGP = Southern giant petrels. Inc. = Incubation period. Gu. = Guarding period.

mainly attended by males (Johnstone, 1979; Bruyn and Cooper, 2005). Diet segregation has been further confirmed in sexual differences in heavy metal burdens as well as in the isotopic signatures of nitrogen and carbon (González-Solís *et al.*, 2002; Forero *et al.*, 2005; González-Solís and Croxall, 2005).

The noticeable sexual segregation in giant petrels compared to other seabird species is probably related to the intersexual interference competition when exploiting carrion, a particular food resource of giant petrels. Carrion is a clumped resource; birds meet at carcasses and need to fight for access. It is well known that body size is a key attribute for dominating competitors (Kotler *et al.*, 2005). The larger size of males in all body measurements in both giant petrel species clearly contributes to the ability of males to exclude females

from carrion (Johnstone, 1979; Bruyn and Cooper, 2005). In particular, bill size in males probably helps them to outcompete females. The bill is commonly used as the main weapon in agonistic interactions at carcasses, and is disproportionately larger in males (González-Solís, 2004a). Overall, it appears that males outcompete females in coastal areas close to the colony and females are forced to travel further away to find food.

Since carrion availability varies over the year, spatial segregation between males and females varies concurrently (Figure 3). During incubation, segregation seems particularly large in northern giant petrels (Figure 3(a)), mainly because males restricted most foraging to the South Georgia coast (Figure 2(a)). This contraction in range is related to diet towards a specific resource mainly exploited by northern giant petrel males: fur seal carrion ($>90\%$, Hunter, 1983; Cooper et al., 2001). In contrast, sexual segregation during the post-guarding period was relatively low because both males and females show more pelagic habits compared to the rest of the year, although differences in diet have been found at two different localities even during this period (Hunter, 1983; Hunter and Brooke, 1992). The increase in pelagic habits over the post-guarding period, particularly in males, is probably related to the decrease in carrion availability around South Georgia from January onwards. In winter, sexual segregation was not apparent in northern giant petrels, though male foraging range was larger than that of females. In contrast, southern giant petrel males and females showed the greatest spatial segregation, with females foraging to a large extent on the southern Patagonian shelf break whereas males were mostly restricted to South Georgia and southern waters (Figures 2(d) and 3(a)). This difference probably reflects a specialization of southern giant petrel males for predation on king penguin (*Aptenodytes patagonicus*) chicks from South Georgia, a major breeding site for this species. Indeed, at Marion Island predation on king penguin chicks seems mostly restricted to southern giant petrels, though on Crozet both giant petrel species prey extensively on chicks from April to September (Hunter, 1991; Descamps et al., 2005).

Spatial segregation between species

Some studies have reported spatial segregation of foraging areas between closely related seabird species (Hyrenbach et al., 2002; BirdLife International, 2004). The two giant petrel species breeding in South Georgia segregate their foraging areas most of the year by latitude, particularly males. Northern giant petrels foraged on average further north, mostly ranging from $45°$ to $60°$ S, than southern giant petrels, which foraged mostly from $50°$ to $65°$ S (Figure 2). This latitudinal segregation is also reflected in the more negative values of $\delta^{13}C$ in southern (-22.7) than in northern giant petrels (-21.0) (González-Solís and Croxall, 2005). These values agree with the latitudinal gradient in $\delta^{13}C$ isotopic signatures found in Southern Ocean seabirds (Quillfeldt et al., 2005). There is also segregation by longitude, but this varied over the year and between males and females, southern giant petrel males being the group that usually concentrated foraging further east, ranging from $45°$ W to $25°$ W, whereas the rest of the groups foraged mainly from $60°$ W to $25°$ W. In general, northern giant petrels commuted regularly between South Georgia and the Patagonian Shelf, whereas southern giant petrels were more restricted to waters south of South Georgia (Figure 2).

Interference competition can lead to spatial segregation between species. Since most giant petrel interactions occur when exploiting carrion, spatial segregation between northern and southern giant petrels could be expected to be greatest for males and least for females when carrion is abundant. However, in November, the peak of carrion availability, spatial segregation between species was at a minimum, whereas in winter spatial segregation was highest (Figures 2 and 3). That is, in this period, males of both species scavenge on penguin and seal carrion near to the breeding grounds whereas females engage in longer foraging trips at sea, showing latitudinal and longitudinal segregation between the two species. Similar results were found for satellite-tracked birds during the incubation period at the same breeding colony, suggesting that this is a regular strategy (González-Solís et al., 2000a). The lowest segregation between

males in November suggests that carrion is such a profitable resource that the cost of interference competition among males does not affect its exploitation.

CONCLUSIONS

Giant petrel movements obtained from geolocators enabled researchers to explore whether spatial segregation facilitates coexistence of two closely related species in relation to gender throughout the annual cycle. It is shown that each sex chooses different foraging options, males having a more flexible foraging strategy (from scavenging to pelagic habits probably depending on seasonal changes in carrion availability), whereas females showed more pelagic habits all year round. Unlike other seabird species, the seasonal reliance on carrion by giant petrels (whereby males monopolize the most profitable times and places to exploit it) has an important influence on the patterns, with males apparently able to exclude females from the rich resource. Most likely, temporal and spatial variability in carrion availability provides an axis of environmental heterogeneity for sexual segregation but not for coexistence between the two species. Interspecific competition seems mainly relaxed by a latitudinal segregation, particularly from April to June, probably mediated by different competitive abilities and physical tolerances to temperature and winds.

ACKNOWLEDGEMENTS

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