Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence?

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Sexual segregation by micro- or macrohabitat is common in birds, and usually attributed to size-mediated dominance and exclusion of females by larger males, trophic niche divergence or reproductive role specialization. Our study of black-browed albatrosses, *Thalassarche melanophrys*, and grey-headed albatrosses, *T. chrysostoma*, revealed an exceptional degree of sexual segregation during incubation, with largely mutually exclusive core foraging ranges for each sex in both species. Spatial segregation was not apparent during brood-guard or post-guard chick rearing, when adults are constrained to feed close to colonies, providing no evidence for dominance-related competitive exclusion at the macrohabitat level. A comprehensive morphometric comparison indicated considerable species and sexual dimorphism in wing area and wing loading that corresponded, both within and between species, to broad-scale habitat preferences relating to wind strength. We suggest that seasonal sexual segregation in these two species is attributable to niche divergence mediated by differences in flight performance. Such sexual segregation may also have implications for conservation in relation to sex-specific overlap with commercial fisheries.

Keywords: sexual segregation; niche divergence; seabird; size dimorphism; foraging habitat preference

1. INTRODUCTION

Sexual segregation by foraging habitat is a relatively common characteristic of birds, and occurs at varying temporal and spatial scales (Catry *et al.* 2005). In many wildfowl, waders, passerines and raptors, the females winter in areas that are considerably further from the breeding grounds than those of males, or (less frequently) exhibit a macrohabitat preference unrelated to differential migration (Cristol *et al.* 1999; Catry *et al.* 2005). Sexual segregation during reproduction is also common, and typically includes a microhabitat preference, for example for particular vegetation characteristics by woodland birds, or water depth by diving species (see Selander 1966; Petit *et al.* 1990; Kato *et al.* 2000).

Sexual segregation is generally considered to result from either social dominance and competitive exclusion (usually of females by larger males), or niche specialization arising from differences in morphology or reproductive role (Peters & Grubb 1983; Morton 1990; Petit *et al.* 1990; Marra 2000). Most studies have been of species in which males and females can be distinguished visually, hence a historical emphasis on taxa that are terrestrial, show obvious sexual dimorphism in bill size or shape, or possess sexually dichromatic plumage. Research on wandering albatrosses, *Diomedea exulans*, provided a novel example of sexual segregation in the marine environment. Differences in foraging habitat between males and females were first proposed on the basis of latitudinal variation in at-sea distributions of birds sexed by plumage (Weimerskirch & Jouventin 1987), and confirmed by the pioneering use of satellite-telemetry in the early 1990s (Prince *et al.* 1992; Weimerskirch *et al.* 1993).

With recent advances in miniaturization of transmitters and loggers, and the advent of molecular sexing, it has since become possible to examine individual foraging behaviour and habitat specialization of other seabirds, including those that are apparently monomorphic. In several taxa (particularly penguins), males and females differ in species or size class of prey (Volkman *et al.* 1980; Quinn 1990; Williams 1991; Wagner 1997), or in stable isotope signatures (Forero *et al.* 2002; Nisbet *et al.* 2002), providing tantalizing evidence of potential variation, at least in microhabitat selection. Moreover, attachment of time–depth recorders to cormorants, *Phalacrocorax* spp., indicates that dives by males are often deeper and/or of longer duration (Wanless *et al.* 1995; Kato *et al.* 2000). Thus, sexual segregation by water depth in diving birds could be related to size dimorphism (Williams 1991; Kato *et al.* 2000). In addition, satellite tracking has revealed large-scale sex-related differences in foraging areas during the breeding season in some (González-Solís *et al.* 2000; Nel *et al.* 2002), but by no means all, procellariiform seabirds (Anderson *et al.* 1998; Stahl & Sagar 2000*b*; Hedd *et al.* 2001). Detection of such macrohabitat selection is not straightforward, however, as overall foraging ranges of males and females may overlap considerably, and even if there are apparent differences in core areas (e.g. Hyrenbach *et al.* 2002), these could conceivably result from a combination of individual preferences unrelated to gender, given the small sample sizes.

Following the demonstration of sexual segregation in marine habitat use, the next most pertinent questions concern its origin and maintenance. Sexual size dimorphism clearly plays a role in giant petrels, *Macronectes* spp., where males outcompete smaller females for access to penguin and seal carrion, and compel them to forage far out to sea (e.g. González-Solís *et al.* 2000). In the wandering albatross, segregation is especially pronounced during

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brood-guard, when the requirement for one adult to attend the chick constrains the other to forage close to the colony, leading to suggestions that it also results from exclusion of females by the larger dominant males (Weimerskirch *et al.* 1993). However, size-mediated competitive exclusion is not the only possibility. Although this mechanism may partly explain the distribution of southern Buller's albatross, *Thalassarche bulleri*, females probably also have an active preference for waters of a particular depth (Stahl & Sagar 2000b). Recently, Shaffer *et al.* (2001) presented a novel hypothesis suggesting that because female wandering albatrosses not only weigh less, but have lower wing loading than males, they are probably better able to exploit subtropical and tropical waters where winds are lighter. Of course, niche divergence could have arisen secondarily, and it is rather difficult to distinguish proximate from ultimate factors in this situation. This is clearly a complex issue, particularly as a recent study of northern gannets, *Morus bassanus*, found that females were more selective in foraging areas, made longer, deeper dives and spent more time on the sea surface than males; however, this is a species that is sexually monomorphic (Lewis *et al.* 2002).

The aims of our study were to test for sexual segregation in two medium-sized mollymawks (*Thalassarche* spp.), black-browed albatrosses, *T. melanophrys*, and grey-headed albatrosses, *T. chrysostoma*. We tracked individual birds at different stages of the breeding season when parents are subject to different reproductive and foraging constraints, variable potential maximum foraging ranges and levels of intraspecific competition. We also measured differences in body size and wing morphology. This provided a suitable framework in which to examine hypotheses relating potential sexual segregation to the effects either of dominance, foraging habitat partitioning or breeding role specialization.

2. MATERIAL AND METHODS

This study was performed over three consecutive breeding seasons (2000/2001 to 2002/2003) at Bird Island, South Georgia (54°00′ S, 38°03′ W). Timing and duration of breeding differs between the two study species, with grey-headed albatrosses returning, laying and hatching earlier than black-browed albatrosses, but taking much longer to fledge their single chick. Incubation is prolonged, with adults alternating at the nest in shifts of up to three weeks while their partner forages at sea. After hatching, the (initially vulnerable) chick is attended continuously for approximately three weeks. Once brood-guard has ceased, both parents forage simultaneously and independently, returning to feed the chick approximately every 2–4 days. The sex of all birds (or their partners) in this study had either been determined previously for those in the main study colonies from records of observed copulatory position or pre-laying attendance pattern ($n = 113$ individuals), or was identified subsequently ($n = 53$ individuals) using DNA extracted from a blood sample (Fridolfsson & Ellegren 1999).

(a) *Instrumentation*

Information on locations and characteristics of complete foraging trips during incubation, brood-guard and post-guard chick rearing were available for, respectively, 17, 22 and 12 black-browed albatrosses and 24, 17 and eight grey-headed albatrosses

of known sex, with some individuals tracked for multiple trips (figures 1 and 2). Birds were selected at random, and at no stage of the season was there a significant difference between males and females in the mean date or number of days elapsed since laying, when instrumented birds departed on their first foraging trip. All tracking data for black-browed albatrosses were collected in a single breeding season (2001/2002), and for grey-headed albatrosses were collected in two seasons (post-guard data in 2000/2001, and incubation and brood-guard data in 2002/2003). A 20 g or 30 g satellite tag (Platform Terminal Transmitter) set to transmit every *ca.* 90 s was attached to mantle feathers, and in most cases a 9 g saltwater logger or combined global location sensing–saltwater logger and/or a 17 g radio transmitter with a unique transmission frequency was mounted on one or both tarsi. Albatrosses tracked during post-guard were always fitted with radio transmitters, which allowed the recording of trip start and end times using an automatic radio receiver–logger system (Televilt International AB, Sweden). Otherwise, these times were derived from a combination of observations at the nest and assumed from satellite data. Devices were deployed for a single foraging trip (all incubating birds, brooding black-browed albatrosses), one to three consecutive trips (total $n = 28$ trips from 17 brooding grey-headed albatrosses) or 6–29 consecutive trips (total $n = 93$ trips from eight grey-headed albatrosses, and $n = 237$ trips from 12 black-browed albatrosses, both datasets from post-guard). Total device mass always represented less than 2% of adult body mass, and irrespective of deployment duration had no effect on mean foraging trip duration, breeding success or likelihood of returning the following year (Phillips *et al.* 2003).

(b) *Foraging trip characteristics*

All satellite-transmitter locations in ARGOS location class (LC) 3,2,1,0, A and B were filtered using an iterative forward/backward-averaging filter (McConnell *et al.* 1992) to remove any that involved unrealistic flight speeds (filter velocity greater than 80 km h^{-1}). Any unclassified locations (ARGOS LC Z) were excluded. For each trip, we calculated the duration, maximum range (furthest distance reached from the colony), total (cumulative) travel distance along the route, and maximum latitude (furthest north), minimum latitude (furthest south), maximum longitude (furthest east) and minimum longitude (furthest west) reached at any point. Time intervals between successive satellite fixes are highly variable, and therefore we standardized the calculation of trip statistics by using interpolated fixes at 1 h intervals. Between-sex differences in foraging trip characteristics were analysed using *t*-tests. For individuals tracked for multiple trips, between-sex comparisons of trip characteristics used the unweighted mean value per individual, or for maximum and minimum latitudes and longitudes, the extreme value during the entire deployment. In fact, repeating these comparisons considering each trip to be statistically independent made little material difference to the results.

(c) *Morphological comparisons*

A full set of morphological measurements was taken from 32 black-browed and 32 grey-headed albatrosses in December 2002 – January 2003. All were banded birds with prior breeding experience (i.e. fully adult), and were measured by the same observer (R.A.P.). Given that most were non-breeders or had failed much earlier in the season, it was assumed that weights were representative of true mass without any food in the stomach. Head plus bill length, bill length, minimum bill depth, bill
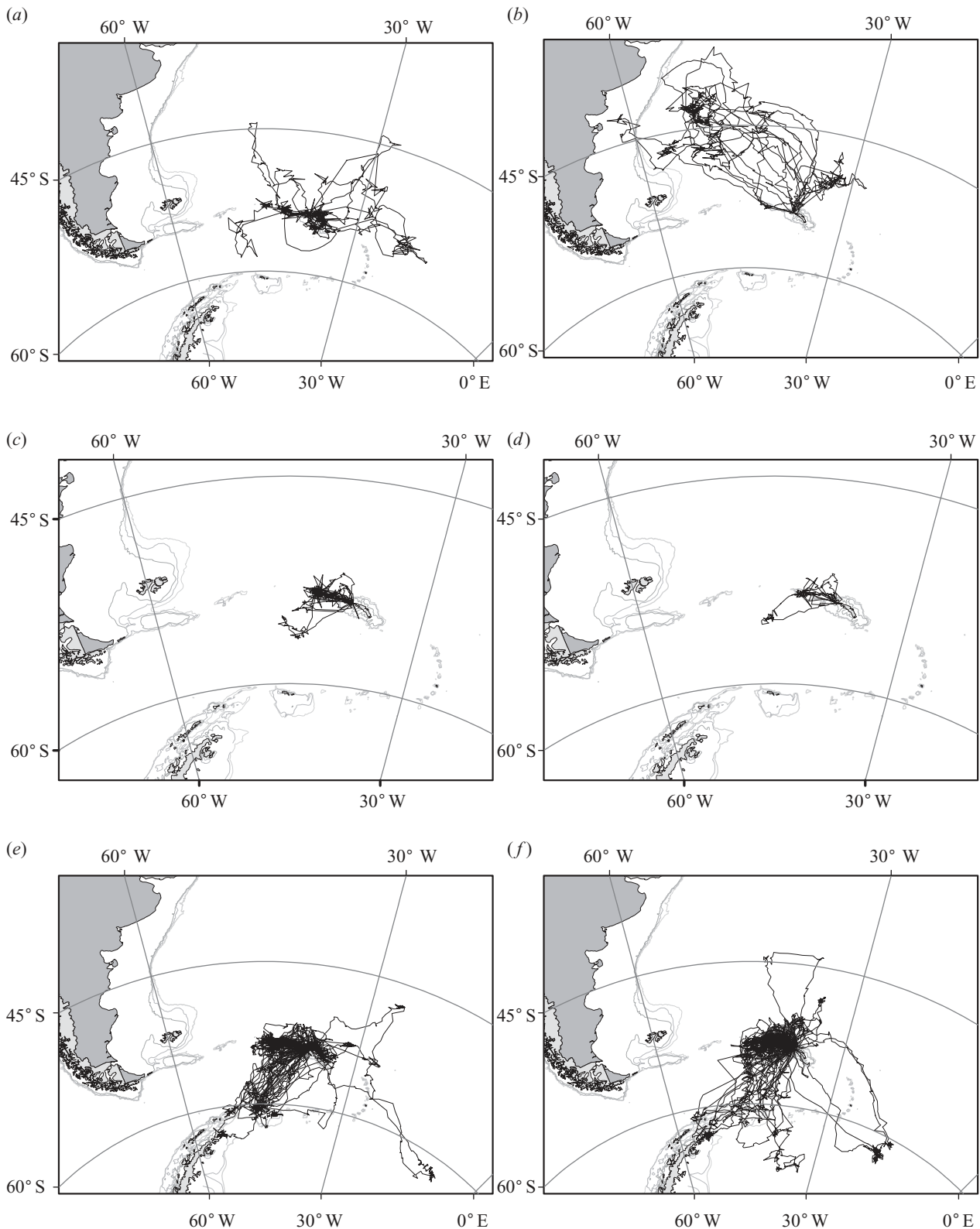
Figure 1. The distribution of male and female black-browed albatrosses tracked from South Georgia during incubation: (*a*) males (*n* = 8 birds, eight trips) and (*b*) females (*n* = 9 birds, nine trips); brood-guard chick rearing: (*c*) males (*n* = 14 birds, 14 trips) and (*d*) females (*n* = 8 birds, eight trips); and post-guard chick rearing: (*e*) males (*n* = 6 birds, 121 trips) and (*f*) females (*n* = 6 birds, 116 trips).

depth at the nail (i.e. perpendicular to the mid-point of the inter-ramicorn) and right tarsus length were measured to the nearest 0.1 mm using vernier callipers. Maximum body circumference and shoulder width were measured using a dressmaker's tape, and the outline of the extended right wing was traced onto a

sheet of parcel paper attached to a flat plywood board (Pennycuick 1989).

Each wing trace was digitized, and the area calculated using ArcMap software (ESRI, California). Total wing area (*S*) was calculated by doubling the area of the digitized wing and adding
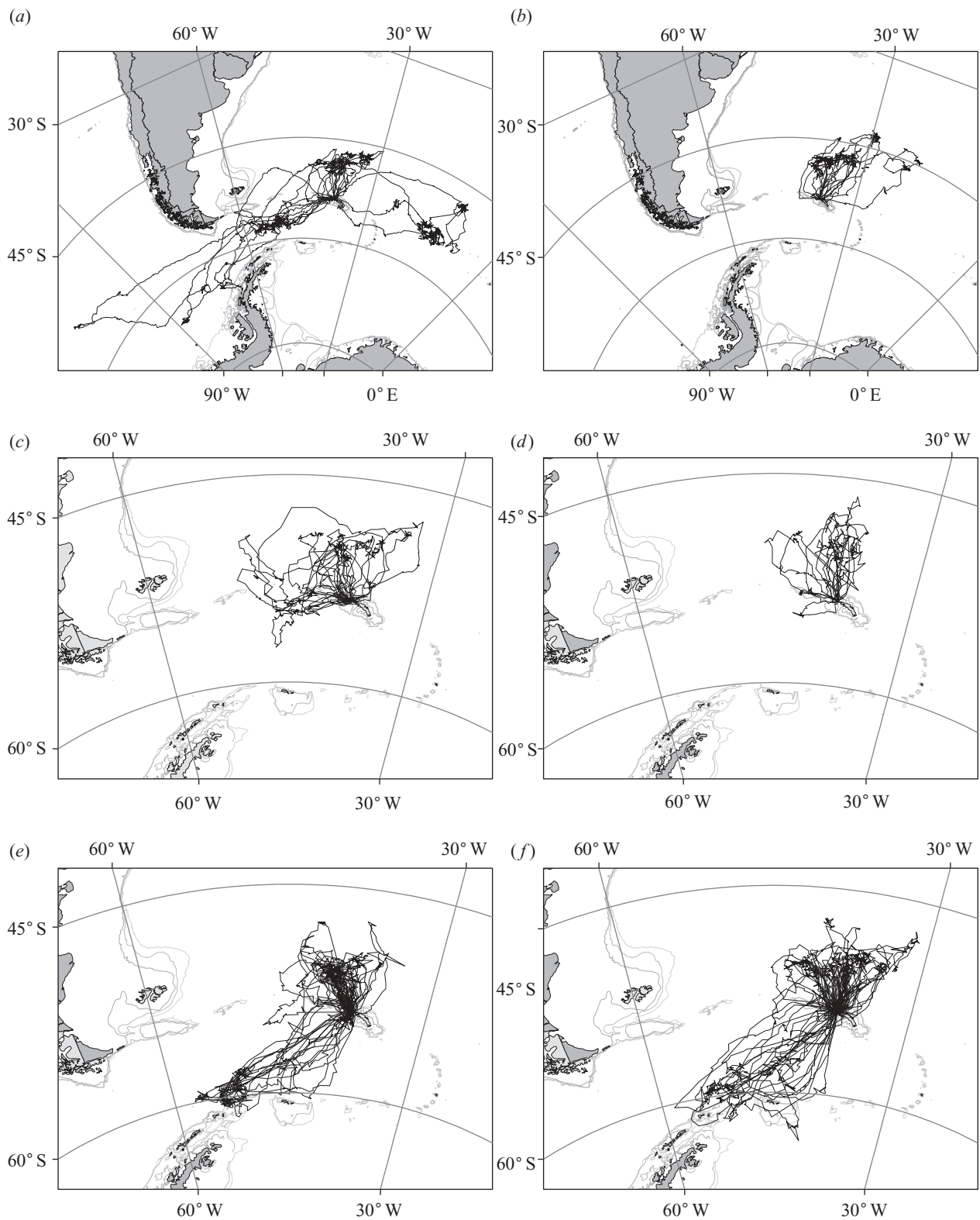
Figure 2. The distribution of male and female grey-headed albatrosses tracked from South Georgia during incubation: (a) males ($n = 14$ birds, 14 trips) and (b) females ($n = 10$ birds, 10 trips); brood-guard chick rearing: (c) males ($n = 11$ birds, 16 trips) and (d) females ($n = 6$ birds, 12 trips); and post-guard chick rearing: (e) males ($n = 4$ birds, 42 trips) and (f) females ($n = 4$ birds, 51 trips).

the area between the wings, the latter equal to the root chord (= wing width at the junction with the body, measured on the trace) × shoulder width. Wing span (b) was calculated by doubling the distance from the tip of the outermost primary to the junction with the body (measured from the wing trace) and adding the shoulder width. Maximum body frontal area (= cross-sectional area at its widest point; S_b), was calculated from maximum body circumference (C) measured in the field, according to $S_b = C^2/4\pi$. Wing chord (= mean wing width; c) was calculated as S/b, wing loading (W) as Newtons (N)/S

Table 1. Foraging trip characteristics of black-browed and grey-headed albatrosses.
(Values are mean ± s.d; *t*-tests comparing trip characteristics of males and females non-significant unless indicated otherwise by *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.)

black-browed albatrosses	incubation		brood-guard		post-guard chick rearing	
	males ($n = 8$)	females ($n = 9$)	males ($n = 14$)	females ($n = 8$)	males ($n = 6$)	females ($n = 6$)
travel distance (km)	5862 ± 2653	7828 ± 1904	1230 ± 424	933 ± 544	1789 ± 613	2072 ± 901
trip duration (h)	262.1 ± 90.9	326.9 ± 49.3	56.7 ± 15.8	44.8 ± 32.1	70.4 ± 22.7	77.1 ± 28.0
maximum range (km)	981 ± 388**	1689 ± 414**	325 ± 101	276 ± 148	429 ± 104	506 ± 226
maximum latitude (°)	−48.8 ± 3.6***	−41.1 ± 3.1***	−52.9 ± 0.5	−52.9 ± 0.6	−51.2 ± 2.0	−49.8 ± 2.9
minimum latitude (°)	−55.7 ± 1.6*	−54.0 ± 0.04*	−54.6 ± 0.7	−54.3 ± 0.6	−61.9 ± 0.9	−61.0 ± 5.1
maximum longitude (°)	−29.8 ± 8.2	−35.1 ± 3.3	−38.0 ± 0.2	−38.0 ± 0.1	−28.7 ± 10.9	−32.9 ± 8.3
minimum longitude (°)	−43.0 ± 4.5**	−53.4 ± 6.6**	−42.8 ± 1.7	−41.9 ± 2.5	−50.8 ± 3.0	−50.9 ± 5.6
grey-headed albatrosses	males ($n = 14$)	females ($n = 10$)	males ($n = 11$)	females ($n = 6$)	males ($n = 4$)	females ($n = 4$)
travel distance (km)	7268 ± 3719*	4539 ± 1480*	2585 ± 1258	1980 ± 627	1960 ± 545	1924 ± 270
trip duration (h)	326.2 ± 155.3	271.3 ± 97.2	83.0 ± 36.9	68.7 ± 19.4	64.0 ± 15.3	64.1 ± 6.0
maximum range (km)	1589 ± 1054	1068 ± 334	592 ± 204	595 ± 146	568 ± 178	574 ± 76
maximum latitude (°)	−49.0 ± 2.8**	−45.4 ± 2.0**	−49.9 ± 2.0	−48.9 ± 2.4	−49.0 ± 1.2	−48.4 ± 1.2
minimum latitude (°)	−57.9 ± 4.3**	−54.1 ± 0.1**	−54.7 ± 1.0	−54.3 ± 0.5	−59.4 ± 3.4	−60.1 ± 3.7
maximum longitude (°)	−31.8 ± 10.0	−31.1 ± 4.7	−36.5 ± 1.9	−37.0 ± 1.1	−35.9 ± 1.7	−34.5 ± 2.7
minimum longitude (°)	−55.0 ± 21.3*	−39.8 ± 1.6*	−44.1 ± 3.6	−42.7 ± 2.1	−53.2 ± 6.1	−52.9 ± 5.5

assuming $g = 9.81 \text{ ms}^{-2}$, and aspect ratio (*A*), which is an index of wing shape, as b^2/S. For details, see Pennycuick (1989) and Shaffer *et al.* (2001).

Principal component analysis (PCA) was used to produce single factor scores for the first principal component axis (PC1) from the morphometric data, representing a composite index of body size (Rising & Somers 1989). Separate PCAs were performed for each species, as this is more likely to account for differences in body shape. Between-sex differences in morphology, and relationships with body mass were examined using *t*-tests and linear regression, and general linear models (GLMs) using sequential sums of squares.

3. RESULTS

(a) *Foraging areas and trip characteristics*

During incubation, although there was some overlap, many female but no male black-browed albatrosses foraged north and northeast of the Falkland Islands (52° S, 60° W), whereas several males but no females foraged far to the east of South Georgia (figure 1). On average, females had significantly greater maximum foraging ranges (by 72%), and reached areas significantly further north and further west than males (table 1). Females also tended to be away for considerably longer (by 25%) and travel further (by 34%) than males, although given the large between-individual variation, these differences were not statistically significant. By contrast, during brood-guard and post-guard chick rearing, although one female black-browed albatross travelled rather far north (to *ca.* 42° S), there was little or no indication of any large-scale sexual segregation in foraging areas (figure 1).

Substantial segregation in foraging areas was also apparent for male and female grey-headed albatrosses during incubation. Only males travelled south and west towards the Antarctic Peninsula, Drake Passage and southern Pacific, whereas females foraged exclusively within a fairly

limited area to the north of South Georgia (figure 2). On average, males travelled significantly further (by 60%) and reached areas significantly further south and further west (table 1). Males were also away for longer (by 20%) and had greater foraging ranges (by 49%), but given the large between-individual variation, these differences were not significant. By contrast, during brood-guard, although some male grey-headed albatrosses foraged in areas further west and further east than any female, these differences were relatively slight and there were no significant differences between the sexes in mean trip characteristics in that period or in subsequent post-guard chick rearing (table 1).

(b) *Sexual size dimorphism in body size, wing morphology and flight performance*

Both mollymawks showed a strong degree of sexual size dimorphism in all morphological characters with the exception of aspect ratio (table 2). Dimorphism was greater in black-browed albatrosses: males were on average 20.2% heavier, and had an overall wing area and wing loading 6.6% and 13.0% greater, respectively, than females. In grey-headed albatrosses, males were on average 14.7% heavier, with overall wing area and wing loading 4.7% and 9.6% greater, respectively, than females.

In PCAs incorporating wing span, tarsus length, bill length and bill depth (at the nail), all variables had high positive factor loadings (0.713–0.878) on the PC1, and a high proportion (70.7% and 65.6%) of the total variance was captured by the respective component for black-browed and grey-headed albatrosses. In linear regression, much of the variation in mass was explained by PC1 score (black-browed albatrosses: $F_{1,30} = 96.1$, $p < 0.001$, $r^2 = 0.75$; grey-headed albatrosses: $F_{1,30} = 67.9$, $p < 0.001$, $r^2 = 0.68$; figure 3). Similarly, much of the variation in wing area was related to these composite indices of body size (linear regression results; black-browed albatrosses:

Table 2. Sexual size dimorphism in body measurements and flight morphology of black-browed and grey-headed albatrosses.
(Values are mean ± s.d., with sample sizes in parentheses. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.)

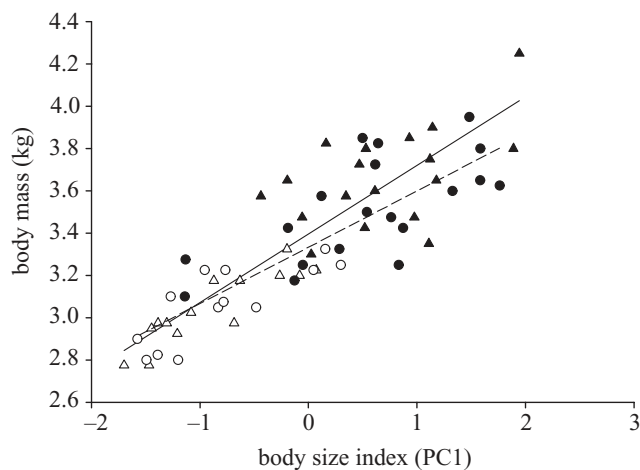|	black-browed albatrosses			grey-headed albatrosses		
	males ($n = 18$)	females ($n = 14$)	*t*-statistic	males ($n = 19$)	females ($n = 13$)	*t*-statistic
mass (g)	3665 ± 229	3048 ± 170	$8.4***$	3516 ± 248	3065 ± 184	$5.6***$
bill length (mm)	118.3 ± 3.6	113.3 ± 2.8	$4.3***$	112.3 ± 2.1	107.9 ± 3.7	$4.3***$
bill depth at the nail (mm)	32.1 ± 1.8	29.5 ± 1.2	$4.6***$	30.2 ± 1.1	28.7 ± 1.1	$4.0***$
bill depth minimum (mm)	29.0 ± 0.8	27.1 ± 1.2	$5.6***$	27.4 ± 1.2	26.2 ± 1.2	$2.9**$
maximum girth (cm)	57.1 ± 1.5	54.3 ± 1.1	$5.8***$	55.8 ± 1.4	54.1 ± 1.2	$3.6***$
tarsus length	92.5 ± 2.0	88.7 ± 2.6	$4.7***$	90.2 ± 2.0	88.0 ± 1.5	$3.4**$
body size index (PC1)	0.68 ± 0.69	-0.87 ± 0.55	$6.9***$	0.56 ± 0.76	-0.83 ± 0.69	$5.3***$
maximum frontal area (cm^2)	259 ± 14	234 ± 10	$5.8***$	248 ± 12	233 ± 10	$3.6***$
wing span (cm)	228.8 ± 5.3	221.8 ± 3.4	$4.3***$	221.2 ± 4.0	216.0 ± 5.5	$3.0**$
wing area (cm^2)	3900 ± 150	3660 ± 90	$5.1***$	3555 ± 130	3395 ± 135	$3.3**$
wind chord (cm)	17.0 ± 0.4	16.5 ± 0.3	$4.3***$	16.1 ± 0.4	15.7 ± 0.5	$2.3*$
wing loading (N m^{-2})	92.3 ± 5.3	81.7 ± 4.0	$6.1***$	97.1 ± 7.0	88.6 ± 5.9	$3.5***$
aspect ratio	13.4 ± 0.3	13.4 ± 0.3	0.1	13.8 ± 0.3	13.8 ± 0.5	0.1

Figure 3. Body mass in relation to body size index (PC1 scores) of male and female black-browed (solid line: filled triangles, males; open triangles, females) and grey-headed (dotted line: filled circles, males; open circles, females) albatrosses.
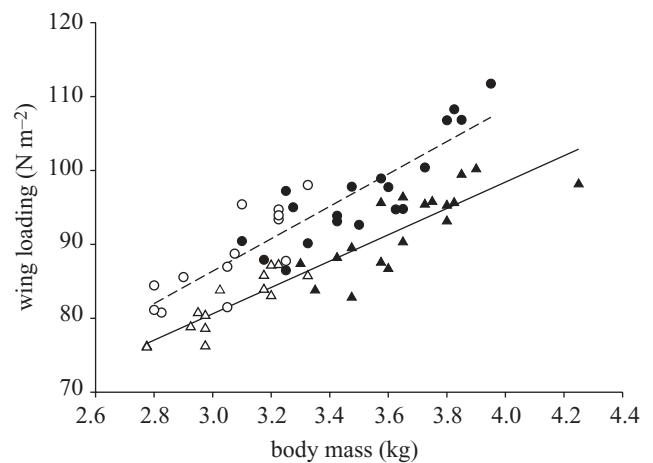

Figure 4. Wing loading in relation to body mass of male and female black-browed (solid line: filled triangles, males; open triangles, females) and grey-headed (dotted line: filled circles, males; open circles, females) albatrosses.

$F_{1,30} = 42.3$, $p < 0.001$, $r^2 = 0.57$; grey-headed albatrosses: $F_{1,30} = 24.3$, $p < 0.001$, $r^2 = 0.43$).

In a GLM, log of wing area showed a significant overall linear relationship with log body mass ($F_{1,59} = 52.0$, $p < 0.001$), and, after accounting for body mass, there was a significant effect of species ($F_{1,59} = 82.8$, $p < 0.001$), a borderline effect of sex ($F_{1,59} = 3.5$, $p = 0.067$), but no interaction between species and sex ($F_{1,59} = 0.25$, n.s.). Wing loading in both species showed a significant linear relationship with body mass (black-browed albatrosses: $F_{1,30} = 173.8$, $p < 0.001$, $r^2 = 0.85$; grey-headed albatrosses: $F_{1,30} = 114.1$, $p < 0.001$, $r^2 = 0.79$; figure 4). Note that these r^2 values are inflated because of the problem of part–whole correlation (Sokal & Rohlf 1995), where the dependent variable (in this case, wing loading) is a composite of the independent variable (body mass).

4. DISCUSSION

This study revealed an unexpected degree of sexual segregation in foraging areas of black-browed and grey-

headed albatrosses during incubation. This segregation is even more marked than in breeding wandering, Amsterdam, *D. amsterdamensis*, or southern royal albatrosses, *D. epomophora* (Weimerskirch 1995; Prince *et al.* 1998; Waugh & Weimerskirch 2003). In comparison, there was little or no evidence of sexual segregation during broodguard or post-guard chick rearing in the two mollymawks, nor has this ever been apparent in any previous tracking study at Bird Island (Prince *et al.* 1998). Our results are not unprecedented, as sexual segregation has been clearly demonstrated for southern Buller's albatross at the Snares Islands (48°02′ S, 166°36′ E; Stahl & Sagar 2000b), and there is weak evidence that it exists for southern Buller's and grey-headed albatrosses breeding at other sites (Nel *et al.* 2000; Stahl & Sagar 2000a). Ours is, to our knowledge, the first study, however, to indicate such an unusual seasonal pattern.

Macro-scale differences between sexes in foraging habitat preferences during breeding are usually size-mediated, and associated with dominance and competition, or feeding specialization and efficiency (see § 1), with the former generally hypothesized to account for latitudinal

segregation of male and female wandering albatrosses (Weimerskirch *et al.* 1993). In seabirds, adult foraging ranges are most constrained after hatching, particularly during brood-guard when one parent must always be in attendance at the nest, and the limited stomach capacity and body reserves of the chick necessitate frequent feeds to prevent starvation (Ricklefs 1983). Our results show incontrovertibly that there is no large-scale exclusion of females by male black-browed and grey-headed albatrosses from areas close to the colony during brood-guard or post-guard chick rearing. This is despite a degree of sexual dimorphism in body mass in both species (15–20%; table 2), broadly comparable to that in wandering albatrosses (20%; Shaffer *et al.* 2001). In addition, during incubation (when sexual segregation was apparent), it is difficult to see how despotic exclusion could result in male grey-headed albatrosses travelling further than females.

So, what mechanism does lead to sexual segregation during incubation? The answer may be, as Shaffer *et al.* (2001) hypothesized for wandering albatrosses, that dimorphism in body mass and wing morphology has a functional role in flight performance and is an important determinant of at-sea distribution, at least during part of the year. Our morphometric comparison indicated a degree of dimorphism in wing area (4.7–6.6%) and wing loading (9.6–13.0%) in both species comparable to that found in wandering albatrosses (6.8% and 12.1%, respectively; Shaffer *et al.* 2001). Out of the four species-sex groups in our study, only those with the highest wing loading (male grey-headed albatrosses; table 2) travelled far south during incubation, to windy Antarctic waters (figure 2). By contrast, only the group with the lowest wing loading (female black-browed albatrosses; table 2) travelled far to the north, to the region with the lightest winds (figure 1).

This partitioning of habitat reflects the benefits of differential flight morphology and performance. Albatrosses seem to have little leeway to increase their airspeed much above their predicted minimum power speed, and proceed predominantly using gliding flight (Pennycuick 1997). They therefore exploit the wind to minimize travel costs, and are able to forage more economically in windy areas where the number of energetically expensive take-offs and landings may be reduced (Weimerskirch *et al.* 2000*b*; Murray *et al.* 2002). Birds have to increase airspeed when flying into headwinds, and reduce it when flying with tailwinds (Pennycuick 1978). In addition, the higher the wing loading, the faster the required flight speed (Pennycuick 1989), and also the higher the stall speed, making it more difficult to fly in light wind conditions (Shaffer *et al.* 2001). Therefore, male grey-headed albatrosses are more likely to feed in Antarctic and sub-Antarctic waters because there they encounter sufficient wind strength to provide the increased lift dictated by their higher wing loading, allowing them to sustain rapid flight over long distances. By contrast, because female black-browed albatrosses have low wing loading, they are better adapted for exploitation of the less windy northerly regions. Similarly, in a recent interspecific comparison of variation in habitat preferences of great albatrosses (*Diomedea* spp.), Waugh & Weimerskirch (2003) suggested that the longer wings relative to body mass of Amsterdam albatrosses facilitated their foraging in tropical waters.

If differences in flight performance are responsible for large-scale sexual segregation in grey-headed and black-browed albatrosses, the obvious question is why is this apparent only during incubation? Part of the answer may relate to time constraints, and/or spatio-temporal variation in environmental conditions. It seems reasonable to assume that the ocean domains to the northeast of the Falkland Islands visited by female black-browed albatrosses, and to the north and west of the Antarctic peninsula visited by male grey-headed albatrosses, contain prey resources that are abundant or predictable, at least when birds at South Georgia are incubating, otherwise why would any albatross travel so far? In fact, we know the latter is a rich feeding ground from satellite-tracking of local breeding grey-headed albatrosses from Diego Ramirez Islands (56°31′ S, 68°44′ W; G. Robertson and J. Arata, personal communication). Moreover, these areas are visited by non-breeding grey-headed albatrosses from South Georgia in the weeks before they arrive back at the colony, and also by adults that fail during incubation (British Antarctic Survey, unpublished data).

During incubation, foraging trips are far longer than in chick rearing (by four to five times on average; table 1), and the fasting capabilities of a partner at the nest is high. There is therefore the greatest scope for an adult of either sex to visit a distant site. During chick rearing, a higher or more predictable level of food abundance closer to the colony presumably makes it unnecessary, and/or the requirement to maximize provisioning rates to offspring makes it undesirable, to routinely travel so far. That only female black-browed albatrosses travel so far north and west early in the season could be, as we suggested, because they are better able to exploit lighter winds (and see Shaffer *et al.* 2001). Of course, this does not explain why females of both species tend to avoid Antarctic waters during incubation but not chick rearing. Either it is less efficient for them to do so, there is simply no need, or weather or feeding conditions change as the season progresses. Alternatively, females might have a greater demand for some scarce nutrient or mineral (such as calcium) that induces them to target a particular type of prey found in one area (as suggested for Northern gannets; Lewis *et al.* 2002). This is possible, but very hard to test given the difficulty of obtaining sufficient data on diet composition at this time of year (birds usually return to incubate with empty stomachs), although the question might be addressed by using a forensic approach (e.g. Nisbet *et al.* 2002).

Large-scale sexual segregation in foraging areas has also been linked to breeding role specialization. In the marginally sexually size dimorphic Adélie penguin, *Pygoscelis adeliae*, Clarke *et al.* (1998) suggested that there may be an advantage for the more aggressive males to spend longer with the chick during the guard period, and consequently they have less time than females to travel to the most productive areas at sea. In brown boobies, *Sula leucogaster*, males feed closer to the colony, possibly to maximize time spent defending the territory or to increase the number of opportunities for extra-pair copulations (Gilardi 1992). Although males usually, but not always, undertake a greater share of chick provisioning (Huin *et al.* 2000; Weimerskirch *et al.* 2000*a*), there is little obvious differentiation in the reproductive role of male and female

albatrosses during incubation. Males do arrive earlier and spend much more time than females at the colony before egg laying (Tickell & Pinder 1975), and it is conceivable that they have a different incubation foraging strategy to females that somehow allows them to more readily replenish reserves lost during this time. However, it is difficult to see how this, or indeed any other constraint or restraint related to reproductive role specialization, could explain why in grey-headed albatross, males travel further than females, but the opposite is true for black-browed albatrosses; such hypotheses can probably, therefore, be discounted.

Sexual segregation in these two species has conservation implications. Their breeding populations, along with those of many other albatrosses and petrels in the Southern Ocean, have declined dramatically as a consequence of incidental mortality in long-line and trawl fisheries (Weimerskirch & Jouventin 1987; Croxall *et al.* 1998; Nel *et al.* 2002). There are often sex (and age) biases in by-catch rates, frequently, but not always, towards males (Murray *et al.* 1993; Gales *et al.* 1998; Ryan & Boix-Hinzen 1999). Sexual segregation of black-browed or grey-headed albatrosses might therefore lead to greater exposure of one sex to fisheries interactions. This could explain why male black-browed albatrosses have a much lower (by 2%) survival rate than females at South Georgia (Croxall *et al.* 1998). The link to fisheries was not made in that study, largely because there was little evidence for sex differences in foraging areas during chick rearing (Prince *et al.* 1999). However, until 1997, black-browed albatrosses were taken as by-catch in high numbers during the summer in the South Georgia area (Dalziell & de Poorter 1993), and there are substantial long-line fisheries operating in regions where these birds winter (Prince *et al.* 1998; Tuck *et al.* 2003). Sexual segregation could therefore be implicated in their decline, although whether this might result from large-scale microhabitat differences during incubation or on migration, or from microhabitat differences such as the competitive exclusion of females from around fishing vessels (see e.g. Ryan & Boix-Hinzen 1999), requires further investigation.

In conclusion, our results indicated substantial sexual segregation in foraging areas at large spatial scales in incubating, but not chick-rearing, grey-headed and black-browed albatrosses. This appears to be mediated by foraging niche divergence rather than by either competitive exclusion of females from areas close to the colony or reproductive role specialization. More detailed analyses might reveal some level of habitat segregation during chick rearing (e.g. Stahl & Sagar 2000*b*; Hyrenbach *et al.* 2002), but this would not affect our conclusion. Although we suggest that differences in flight performance could be the proximate determinant of at-sea foraging distributions during at least part of the year, the ultimate cause of size dimorphism remains obscure. It may very well have arisen from sexual selection for larger, dominant males related to some other aspect of role division during reproduction. It is also possible that foraging niche specialization could exaggerate such a trait (Shine 1989), and this is clearly a topic that merits further study.

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