

SUMMER DISTRIBUTION AND MIGRATION OF NONBREEDING ALBATROSSES: INDIVIDUAL CONSISTENCIES AND IMPLICATIONS FOR CONSERVATION

RICHARD A. PHILLIPS,¹ JANET R. D. SILK, JOHN P. CROXALL, VSEVOLOD AFANASYEV,
AND VICTORIA J. BENNETT

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

Abstract. Many birds show a surprising degree of intraspecific variability in migratory tendency and choice of wintering site. In this study, we tracked the seasonal movements of 35 nonbreeding Black-browed Albatrosses *Thalassarche melanophrys* from South Georgia, including 24 birds followed in two consecutive years. This revealed consistent patterns of status-related, sex-specific, and individual variation in wintering strategies, and provided the first description of the summer distribution of failed/deferring breeders. Individuals exhibited a striking degree of site fidelity, returning to the same region (southwest Africa or Australia) and showing correlated centers of distribution, as well as remarkable consistency in the chronology of their movements, in consecutive years. Nonetheless, a degree of behavioral flexibility remained, and particularly on the return migration, birds moved between, or bypassed, alternative intermediate staging sites depending on local circumstances. Initiation of the outward migration varied according to breeding status, timing of failure, and sex: deferring breeders and those that failed early departed two months before successful birds, and successful females departed 1–2 weeks earlier than males. Sex-related latitudinal variation in distribution was also apparent, with females wintering farther north within the Benguela system. Moreover, the only migrant to Australia was a male, supporting an apparent tendency for male-biased breeding dispersal inferred from genetic analyses. Distribution and timing of movements appeared in general to relate to avoidance of competition from congeners and conspecifics from other populations. From a conservation perspective, the study indicated that, for the declining Black-browed Albatross population at South Georgia, the primary focus should be toward improving the management (especially reducing bycatch levels) of fisheries in the central and eastern South Atlantic.

Key words: conservation; differential migration; interspecific competition; sexual segregation; winter philopatry.

INTRODUCTION

There is a remarkable diversity of migration strategies within as well as between bird species: different populations can be either wholly sedentary or highly migratory, may have greatly dispersed wintering grounds yet breed in comparative geographical proximity, or may winter in the same area yet breed hundreds of kilometers apart (Robertson and Cooke 1999, Berthold 2001). Within a population, differential migration by birds of different age, breeding status or sex can lead to segregation at local to regional scales, although some overlap always remains (Cristol et al. 1999, Catry et al. 2005). In addition, although several studies show that individuals are highly faithful to wintering sites (Percival 1991, Gunnarsson et al. 2004, Iverson et al. 2004), this is not universal (Mehl et al. 2004), and it cannot be assumed that migration strategies are necessarily fixed from one year to the next.

Current knowledge of avian migration patterns has been gleaned primarily from band recovery analyses (Berthold 2001). However, spatiotemporal variation in reporting rates can lead to unforeseen and unquantifiable biases (Robertson and Cooke 1999, Mehl et al. 2004), and an alternative approach is to actively track the movements of individuals of known provenance, status, and sex. The latter is particularly effective for revealing the fine detail of migration routes, and for elucidating the role of individual flexibility and constraint in the evolution of alternative strategies. Large seabirds are ideal for this type of study, given their ability to carry devices with long battery lives with negligible detrimental effects (Phillips et al. 2003). They also have the advantage of long being the target of intensive banding programs, whereby the primary wintering grounds of the main populations have already been inferred.

Although there has been a recent surge of interest in tracking of nonbreeding seabirds (Grémillet et al. 2000, Ristow et al. 2000, Stahl and Sagar 2000, Weimerskirch and Wilson 2000, Nicholls et al. 2002, Hyrenbach and Dotson 2003), only one published study has included

Manuscript received 13 December 2004; revised 1 February 2005; accepted 15 February 2005. Corresponding Editor: M. Wikelski.

¹ E-mail address: raphil@bas.ac.uk

more than a few birds followed throughout the migration period (Croxall et al. 2005). By comparison, foraging ranges are much better described during the breeding season. This has revealed various degrees of spatial structuring: inter-specific segregation by location or habitat type (Hyrenbach et al. 2002, Waugh and Weimerskirch 2003, Birdlife International 2004, Phillips et al. 2005); limited overlap between adjacent colonies in some (Weimerskirch et al. 1988, Huin 2002, Grémillet et al. 2004) but not all cases (Stahl and Sagar 2000); sexual segregation during part or all of the reproductive cycle (Weimerskirch et al. 1993, Phillips et al. 2004b) although again, this is not universal (Hedd et al. 2001); in some species, consistent individual preferences for specific foraging areas or departure directions (Weimerskirch et al. 1993, Irons 1998, Hamer et al. 2001). Increasingly, researchers have begun to explore the potential mechanisms underlying such variation, with the aim of relating resource partitioning to competitive exclusion or niche specialization arising from inequalities in body size, foraging efficiency, flight capability, manoeuvrability, or nutritional requirements (Weimerskirch and Lys 2000, Shaffer et al. 2001, Lewis et al. 2002, Phillips et al. 2004b, 2005).

The purpose of the current study was to determine whether these same factors and processes also characterise the distribution of a nonbreeding seabird, the Black-browed Albatross *Thalassarche melanophrys*. On the basis of band recoveries (mainly of juveniles), Black-browed Albatrosses from South Georgia appear to winter predominantly in shelf and shelf-slope waters of the Benguela upwelling system, and less commonly off South America and southern Australia (Tickell 1967, Prince et al. 1998). Until now, the proportion of birds of breeding age wintering in each region, and detailed information on individual route choice was unavailable. Our main aims were, therefore, (1) to compare the foraging range and key feeding areas of nonbreeding with breeding adults to assess the extent of the central-place foraging constraint imposed by incubation and chick-provisioning duties; (2) to characterize in detail the timing, routes, staging, and destination areas of migrating black-browed albatrosses; (3) to investigate differences in migration strategies in relation to sex and recent reproductive performance; (4) to assess individual and within-pair consistency in timing of movements and site selection in successive years; (5) to determine the degree of segregation or overlap between this population and conspecifics and congeners during migration; and (6) to identify those foraging areas where conservation and management actions are most urgently needed to improve the status of this endangered species. Annual monitoring of Black-browed Albatrosses at South Georgia indicates marked reductions in adult and juvenile survival rates, and an overall population decline of >4% per annum since the mid 1970s, attributable largely to incidental mortality in long-line fisheries (Croxall et al. 1998).

MATERIALS AND METHODS

Fieldwork was carried out on Black-browed Albatrosses in three consecutive breeding seasons (October to May each year, beginning in October 2001 and ending in May 2004; hereafter referred to as summer 2002, 2003, and 2004) at a single colony of 199–258 pairs on Bird Island, South Georgia (54°00' S, 38°03' W). In February–April 2002 (mid to late chick-rearing), combined immersion and Global Location Sensors (GLS loggers: Afanasyev 2004) weighing 9 g were deployed on the tarsus of 58 breeding adults. Black-browed Albatrosses typically breed annually, and devices were retrieved the following season (October 2002–January 2003), then redeployed on 27 birds tracked successfully over the first winter. These were retrieved in November 2003, thereby potentially providing data for two consecutive winters.

During chick-rearing in the first summer (2002), some birds were also equipped with a 17 g radio transmitter and in some cases an additional 30 g satellite transmitter. Even with all three devices, instrument mass corresponded to <2% of adult mass, and had no significant effect on mean foraging trip duration, breeding success, or probability of returning in the following season (Phillips et al. 2003). The effect of GLS deployment during the winter was therefore likely to be negligible. The sex of all birds (or their partner) was known from behavioral observations (copulatory position and pre-laying attendance pattern), or analysis of DNA extracted from a blood sample (Fridolfsson and Ellegren 1999).

Light data from the GLS loggers were processed subsequently according to Phillips et al. (2004a). Sunset and sunrise times were estimated from thresholds in the light curves, latitude derived from day length, and longitude from the time of local midday with respect to Greenwich Mean Time and Julian day, providing two locations per day. During processing, locations derived from light curves with apparent interruptions around sunset and sunrise, or that required unrealistic flight speeds (>35 km/h sustained over a 48-h period) were identified and later excluded, if appropriate. Data were subsequently smoothed twice. Concurrent deployment of these loggers along with satellite transmitters during breeding indicates a mean accuracy (\pm SD) of 186 ± 114 km, which is more than adequate for tracking migration and breeding-season foraging ranges of pelagic species (Phillips et al. 2004a). Accuracy in the current study was likely to be somewhat lower, as the albatrosses wintered at lower latitudes (Hill 1994). In addition, locations were unavailable for variable periods around the equinoxes when it is difficult or impossible to estimate latitude (Wilson et al. 1992, Hill 1994). Although this will have a minor impact on the maps, neither issue will have any appreciable effect on our results or conclusions. A partially automated approach was used to identify periods of transit, based

on consistent movement in an easterly or westerly direction at velocities of 20 km/h and 12 km/h, respectively (values chosen after initial data inspection). The foraging range of Black-browed Albatrosses from South Georgia during the breeding season is already well established (Prince et al. 1998, Wood et al. 2000, Phillips et al. 2004b), and therefore only results from nonbreeding birds during the summer breeding season, or the winter migration, are presented here. The volume of data generated was large (14 937 bird-days) and detailed analyses of distribution and timing were restricted mainly to the 24 individuals tracked in both winters. Kernel density maps were generated in a Lambert equal-area azimuthal (South Pole) projection using the ESRI ArcGIS spatial analyst density tool with a cell size of 50 km and a search radius of 200 km. Examination of possible sex effects (*t* tests assuming equal or unequal variances, as appropriate) were restricted to comparisons with adequate sample sizes.

RESULTS

Loggers were deployed on 58 breeding Black-browed Albatrosses in summer 2002, of which 52 (90%) returned, all with devices, of which 35 (67%) downloaded successfully, at the start of summer 2003. Loggers were redeployed on 27 of these 35 birds, of which 26 (96%) returned in early summer 2004 (one without the logger). Twenty-four (96%) of these 25 devices downloaded successfully.

Overall wintering distribution

Of the 35 Black-browed Albatrosses (17 females, 18 males) tracked in the first winter (2002), all females spent the core winter months in the Benguela region off southwest Africa. Sixteen males (89%) wintered in the Benguela, one (6%) traveled east to southeastern Australia, and one (6%) remained in the southwest Atlantic, mainly on the Patagonian shelf. The following winter (2003), the 23 birds that traveled to the Benguela, and the male that flew to Australia, all did so again. The male that had wintered on the Patagonian shelf was not tracked a second time.

The wintering distributions of the study birds indicate little change between years in the extent of the core area off southern Africa, but more variation elsewhere, with an apparent extension of the range west of 20° W in the mid South Atlantic in the second year (Fig. 1). During the summer, deferring breeders and those that failed early used very similar sites, including the South Georgia region, the Antarctic Peninsula, and waters in the vicinity of the South Sandwich fracture zone (mostly >3000 m deep) centered around 61° S, 17° W (Fig. 2). Birds that traveled to the Benguela exploited a number of areas on the return migration back to the breeding colony, in particular an extensive region on the mid-Atlantic ridge around Tristan da Cunha (37° S, 14° W) from mid July to early September. Occasional return trips of 5–38 d duration were also

undertaken to this area during the mid-winter (total $n = 16$ trips from 10 individuals over the two winters). Birds that left the Benguela relatively late traveled back slowly at higher latitudes (50° S), with the only obvious staging area situated just to the east of South Georgia around 26° W. Only one bird commuted directly back to South Georgia (at the end of its second winter only). During their pre-laying exodus (the time spent at sea between copulation and egg laying), which lasted around 9 d, females stayed relatively near to the colony (usually within 700 km).

The single male that spent 84 d around the Bass Strait and elsewhere off southeast Australia in winter 2002, stopped in shelf waters at the Crozet archipelago during its outward journey, and around the Kerguelen and Crozet archipelagos on its return (see Fig. 1). The next summer, following failure during early incubation, it spent 113 d in the South Atlantic around 59° S, 18° W, before making a rapid, direct journey of over 9000 km in just 17 d across the Indian Ocean to reach Australia. In comparison with the previous winter, it stayed for less time (66 d) in waters further to the west (Spencer Gulf and south of the Great Australian Bight), and on the return journey, staged to the north of the Kerguelen shelf, but by-passed Crozet and instead stopped in the mid South Atlantic before finally returning to South Georgia.

Influence of reproductive status on outward migration

Timing of movements and the use of different regions were closely linked to reproductive status (Fig. 3). Of the 24 birds tracked in consecutive winters, in the first breeding season, 11 fledged their chick successfully, two failed early (before mid February), and 11 failed late in chick rearing. The following year, eight did not breed, and of the 16 that did, none was successful: 13 failed in incubation or early chick rearing, and three in late chick rearing. This low success mirrored that in the study colony as a whole (British Antarctic Survey, *unpublished data*), and was unrelated to device deployment.

The most common departure pattern for a successful breeder (summer 2002) was to leave the South Georgia area about a week before the chick fledged, and either fly directly and rapidly (in 3–6 d) to the Benguela ($n = 7$), or initially travel west for a brief (5–13 d) visit to the Patagonian shelf ($n = 4$), before traveling eastwards. In both summers, birds that failed late (total $n = 13$) departed slightly earlier, but otherwise showed a similar movement pattern to successful breeders, although none visited the Patagonian shelf. In contrast, those that failed early departed from the South Georgia area much sooner. There was a highly significant negative correlation between fail date and the subsequent number of days before departure (which varied from 1 to 127 d) in summer 2003 ($r_{11} = -0.94$, $P < 0.001$) indicating that departure date was related to the time

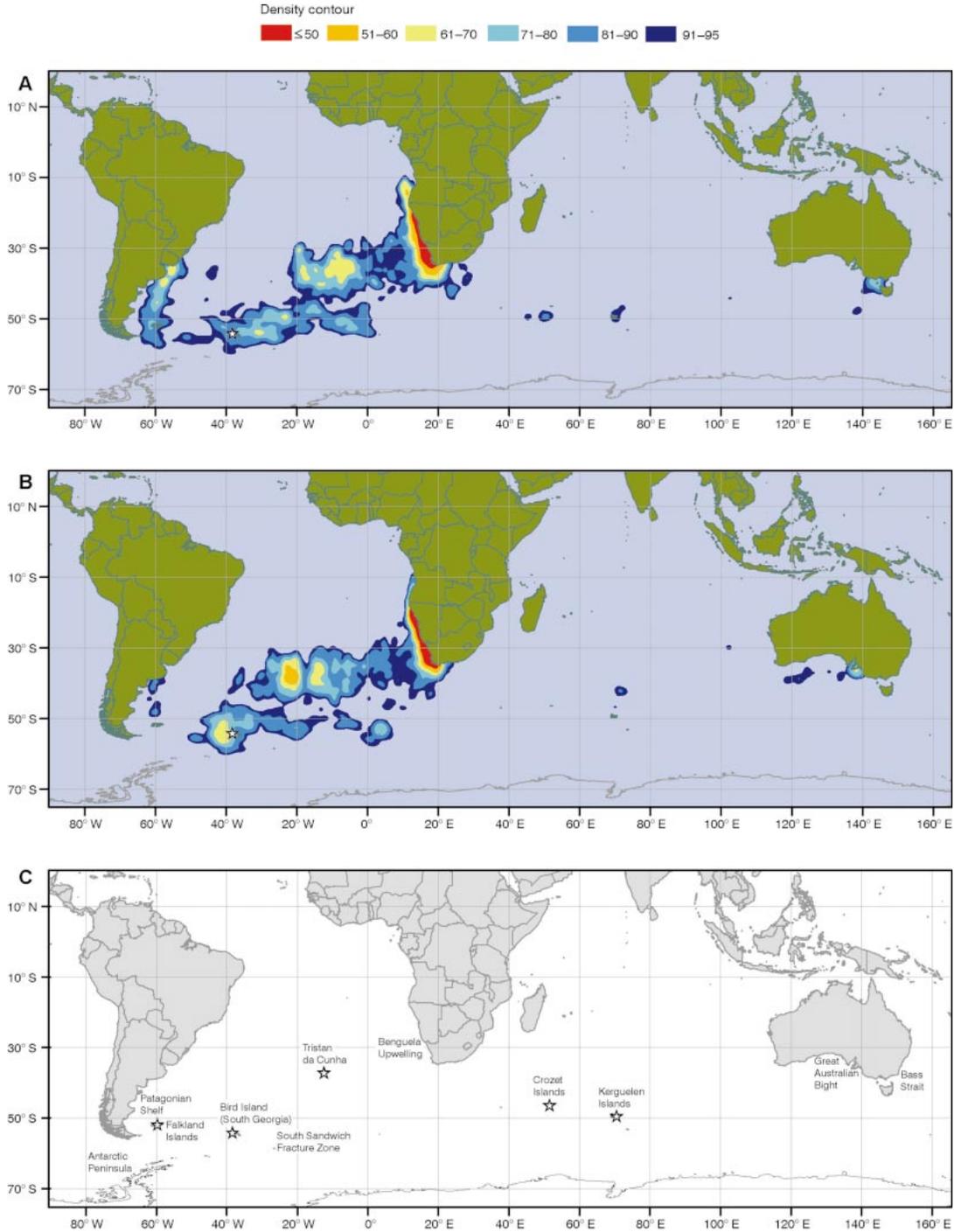


FIG. 1. Density distribution of nonbreeding Black-browed Albatrosses from South Georgia during the winter (May–September) in (A) 2002 ($n = 25$ birds) and (B) 2003 ($n = 24$ birds). Each contour encompasses a specific proportion (50–95%) of the total kernel density surface. Note that one bird that wintered exclusively in the southwest Atlantic was tracked in 2002 only. Map (C) indicates the location of places mentioned in the text.

of year and not the period elapsed since egg or chick loss. There was no significant difference between the mean departure date from South Georgia of birds that failed early and those that deferred breeding in summer

2003 (means of 10 February and 20 February, $n = 13$ and $n = 8$, respectively; $t_{19} = 1.5$, $P = 0.14$).

Year effects.—Given the higher rates of failure and breeding deferral in the second season, the same in-

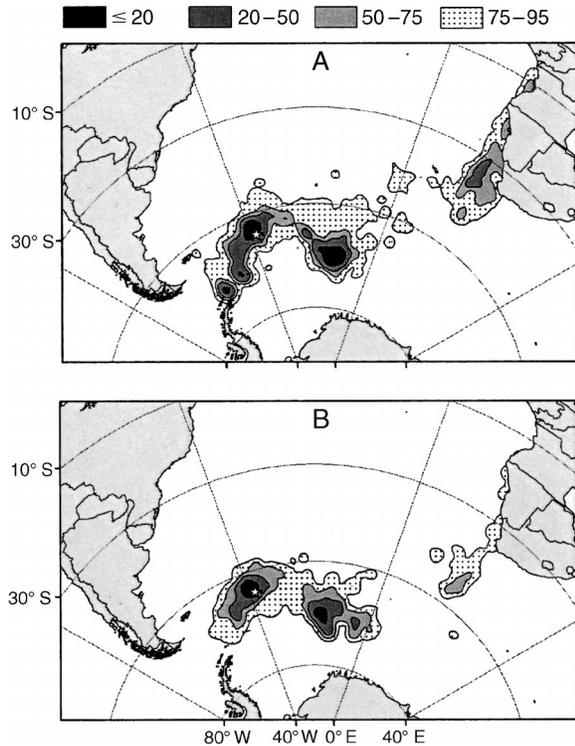


FIG. 2. Density distribution of nonbreeding Black-browed Albatrosses from South Georgia during the summer: (A) early failed breeders in summer 2003 ($n = 13$ birds) and (B) deferring breeders in summer 2003 ($n = 8$ birds). The density contours indicated in the legend encompass 20–95% of the total distribution. Bird Island, South Georgia, is represented by a small white star.

dividuals arrived on average significantly earlier (by about a month) in the Benguela in their second winter (paired t test, $t_{22} = 5.1$, $P < 0.001$). Less predictably, birds on average departed earlier (by 17 d) from the Benguela in 2003 (paired t test, $t_{22} = 3.4$, $P < 0.005$), and arrived earlier (by 12 d) in the southwest Atlantic (paired t test, $t_{22} = 3.2$, $P < 0.005$). Arrival in the proximity of the breeding colony at Bird Island was also slightly earlier, but the difference was only 3 d and not quite significant (paired t test, $t_{22} = 1.9$, $P = 0.07$).

Sex effects.—Sexual segregation in distribution was apparent during the period corresponding to the pre-laying exodus of females (when they traveled further from the breeding colony), and in that the two birds that wintered in Australia or the southwest Atlantic were both males. In addition, in the Benguela during both winters, the centers of distribution of the females were on average 4.4–4.8° further north ($t_{9,6} = 3.4$, $P < 0.01$ in 2002, and $t_{21} = 3.3$, $P < 0.005$ in 2003), and 1.4–2.0° further west than those of males ($t_{9,8} = 3.1$, $P < 0.05$ in 2002, and $t_{21} = 2.5$, $P < 0.05$, in 2003).

There were also clear differences in timing of movements (Fig. 3). At the end of the 2002 summer, although there was no significant difference in mean chick fledged dates ($t_9 = 1.4$, $P = 0.20$), successful females departed earlier from South Georgia ($t_{8,9} = 3.0$, $P < 0.02$) and arrived earlier at the Benguela than successful males ($t_9 = 2.8$, $P < 0.05$), with no difference in travel time between the regions ($t_9 = 0.6$, $P = 0.6$). The following season, among birds that failed early or deferred breeding, although there was no significant difference between males and females in departure date ($t_{18} = 0.8$, $P = 0.41$), females arrived one month earlier in the Benguela ($t_{18} = 2.5$, $P < 0.05$).

Males and females did not differ significantly in mean residency time, or date of departure from the Benguela, in winter 2002 ($t_{20,5} = 0.4$, $P = 0.72$, and $t_{21} = 0.7$, $P = 0.50$, respectively) or 2003 ($t_{21} = 1.6$, $P = 0.12$ and $t_{21} = 0.5$, $P = 0.66$, respectively). Although there was no significant difference in winter 2002 in mean arrival date of each sex in the southwest Atlantic ($t_{21} = 0.1$, $P = 0.94$), males arrived in the proximity of Bird Island on average 5 d earlier than females, which was marginally nonsignificant ($t_{21} = 1.9$, $P = 0.067$). In 2003, differences were clearer: males arrived in the southwest Atlantic 15 d earlier than females (marginally nonsignificant, with $t_{17,8} = 2.0$, $P = 0.065$), and significantly earlier (by 4 d) in the proximity of Bird Island ($t_{21} = 2.1$, $P < 0.05$).

Individual effects.—The 24 individuals not only maintained their preference for the Benguela or Australia, but while in the Benguela also showed correlations in the mean latitude ($r_{21} = 0.73$, $P < 0.001$) and mean longitude ($r_{21} = 0.74$, $P < 0.001$) of the centers of their winter distribution from one year to the next. There was however no evidence of preferred staging areas: many used the Patagonian Shelf, Antarctic Peninsula, South Sandwich Fracture Zone, and Tristan da Cunha regions in only one of the two years. Given the changes in breeding status and fail date, there was no significant correlation between 2002 and 2003 in date of departure from South Georgia ($r_{22} = -0.07$, $P = 0.76$), or arrival in the Benguela ($r_{21} = 0.28$, $P = 0.19$). However, individuals were highly consistent in the timing and duration of every phase thereafter, with significant correlations between winter 2002 and 2003 in time spent off southwest Africa ($r_{21} = 0.53$, $P < 0.01$), departure date ($r_{21} = 0.54$, $P < 0.01$), arrival date in the southwest Atlantic ($r_{22} = 0.55$, $P = 0.005$), arrival date near to Bird Island ($r_{22} = 0.50$, $P < 0.02$), and laying date ($r_{14} = 0.52$, $P < 0.05$). Moreover, intervals between these events were also consistent in individuals between years ($r_{21} = 0.51$, $P < 0.02$, $r_{22} = 0.45$, $P < 0.05$ and $r_{14} = 0.53$, $P < 0.05$, respectively). This also applied to the albatross that wintered in Australia: dates of departure from Australia and arrival in the southwest Atlantic were 10 August and 13 October in 2002, and 12 August and 9 October in 2003, respectively.

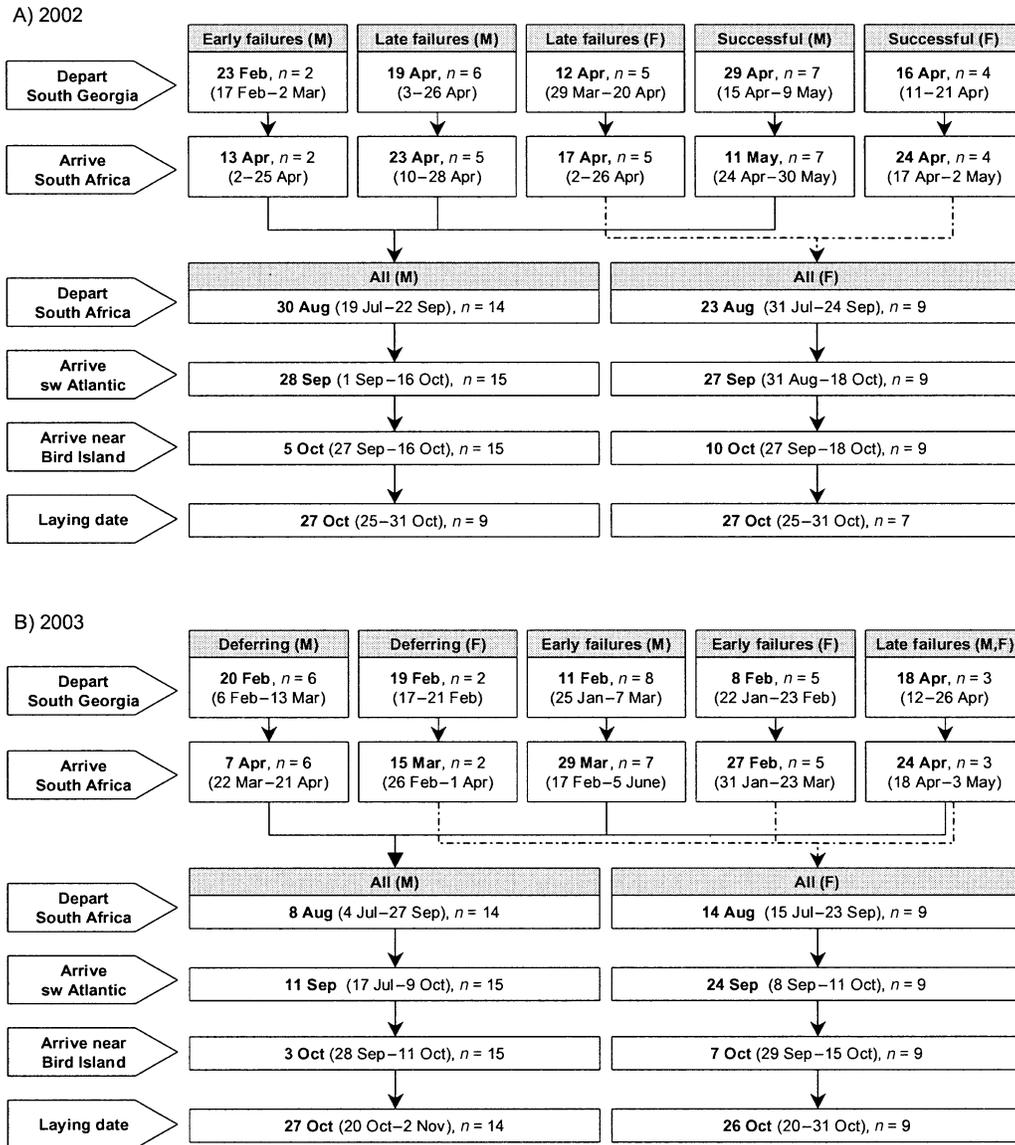


FIG. 3. Timing of movement between different regions for Black-browed Albatrosses of different status and sex in 2002 and 2003. Mean dates are in boldface, with range in parentheses. M, males; F, females.

Both members of, respectively, six and five pairs were tracked in the first and second winters. There was no evidence that pair members actively associated with each other at sea: the partners of the males that wintered off Australia and in the southwest Atlantic both migrated to the Benguela. Nor did pair members depart on similar dates from South Georgia, or South Africa. However, at the end of winter 2002 (with the slightly larger sample), pair members arrived near to the breeding colony at relatively similar times, indicated by the significant variation within, compared to among pairs in arrival date in the proximity of Bird Island ($F_{5,11} = 5.9, P = 0.026$).

DISCUSSION

This study of 35 birds, of which 24 were tracked over two consecutive seasons, is the most comprehensive to date of nonbreeding distribution in a migratory seabird. The extensive detail on timing of movements and utilization of different oceanographic regions confirmed the existence of three distinct primary wintering destinations (the Benguela upwelling system, Patagonian shelf, and southern Australia, used by 94%, 3%, and 3% of birds, respectively), as well as complex variation in smaller-scale habitat preferences during the outward and return journeys from South Georgia. The study also revealed consistent patterns of status-related,

sex-specific, and individual variation in wintering strategies, as well as the first description of the distribution of nonbreeding Black-browed Albatrosses during the summer.

Individual site fidelity

One particularly striking result was the high degree of regional site fidelity. Not only did individuals visit the same region (i.e., the Benguela or Australia), but those that returned to the Benguela also showed correlated centers of distribution in consecutive years. To our knowledge, this is the first time that wintering site philopatry has been confirmed in an annually breeding seabird, although it might actually be a common characteristic of albatrosses. In the biennial Grey-headed Albatross *Thalassarche chrysostoma*, adults have a much more diverse range of migration strategies, and most (although not all) adopt the same tactics in consecutive winters (Croxall et al. 2005). There have also been serial recaptures of some wandering albatrosses *Diomedea exulans* in a small area off New South Wales (Nicholls et al. 1995), although potentially these birds could migrate to other areas in intervening seasons, and others that are captured infrequently or winter elsewhere might not be as site faithful.

Fidelity to intermediate staging sites was, by contrast, rather less pronounced. The overall distribution differed to some extent between years, with an apparent extension west of 20° W in the mid South Atlantic in the second winter. More importantly, on the return migrations from the Benguela, individuals usually stopped in a particular area only once, and sometimes traveled back at high, and sometimes at low latitudes. The Australian migrant also varied its staging areas (combinations of the Crozet and Kerguelen archipelagos, the mid South Atlantic, or no stop at all, depending on year and direction), and terminus (southeast Australia in the first year and south of the Great Australian Bight in the second).

Endogenous control of timing of movements and site selection

In addition to high site fidelity, there was a remarkable degree of year-to-year consistency in the chronology of individual movements. This of course excludes date of departure from South Georgia and arrival in the Benguela, which were dictated by reproductive status, breeding outcome, and timing of failure, but refers to the timing and duration of every phase thereafter, from the start of the return migration to the date of egg laying some one to three months later. This is one of the very few studies of any bird to show significant individual consistency in timing or duration of migration that was not confounded by potential cultural transmission (also see Potti 1998, Møller 2001, Bêty et al. 2004).

In Black-browed Albatrosses, there appears to be little incentive to arrive very early at the breeding col-

ony, as there is no relationship between laying date and hatching or breeding success (British Antarctic Survey, unpublished data). Nor is there selection against rarer choices of wintering destination. Despite the extra distance involved, the Australian migrant (a male) arrived back at Bird Island in sufficient time for his partner to lay among the first 7%, 24%, and 2% of pairs in the colony in summer 2001, 2002, and 2003, respectively. In other species with disjunct wintering ranges, remaining close to the breeding site may confer a slight reproductive advantage (Mehl et al. 2004). Indeed, a hypothesis based on arrival times is often invoked to explain differential migration, where classes differ in timing or intensity of competition for breeding opportunities (Cristol et al. 1999). However, this is clearly not the case for Black-browed Albatrosses, for which there is no reason to consider the minority destinations in any way suboptimal. Individual migration characteristics (specifically, timing and choice of destination), may therefore have a major genetic component, a conclusion that is also supported by selection experiments in passerines (Berthold and Helbig 1992).

Although it was not possible to determine the precise cues that triggered movements, albatrosses must possess an endogenous timer similar to that of other long-distance migrants (Gwinner 1996). This is likely to be synchronized in response to an external environmental stimulus such as photoperiod. Albatrosses and petrels have exceptional homing abilities, and are capable of true navigation rather than path integration, although details of their large-scale bi-coordinate map and solar or magnetic compass system are uncertain (Åkesson et al. 2001, Benhamou et al. 2003). Being long lived, they should also have accumulated extensive knowledge of the range of alternative foraging areas available in different regions. These attributes clearly provide them with the flexibility to select alternative sites at any juncture, depending on local environmental conditions, with such decisions probably mediated by physiological status, experience of recent, and memory of past, feeding success.

This operational flexibility was also apparent in the strategies of failed and deferring breeders, which for most of the summer had very similar foraging ranges (Fig. 2). Active breeders also use the same areas, but because of central-place foraging constraints imposed by the need to return regularly to feed chicks, tend to be rather less widely dispersed. In particular, trips by chick-rearing birds to as far as the South Sandwich Fracture Zone are rare (Prince et al. 1998, Phillips et al. 2004b). Deferring breeders and those that failed early commenced migration in February (Fig. 3), presumably because conditions were by then more favorable elsewhere. This was much earlier than successful birds, which are forced to remain at South Georgia to complete chick-rearing duties. This resulted in large variation in arrival date in the Benguela but thereafter, recent breeding status ceased to be important.

Although a fair degree of behavioral plasticity was evident on the return migration in terms of departure date from the Benguela, arrival date in the southwest Atlantic, and choice of staging area, this did not apply to timing of arrival in the proximity of the breeding colony, which was far more tightly constrained (Fig. 3). This presumably reflects the disadvantages of arriving too soon, resulting in a protracted and energetically costly (given the marked decline in body condition that takes place even under normal circumstances; Huin et al. 2000) period of pre-laying attendance, or too late, which would not allow sufficient time for egg formation or replacement of a missing partner. Arrival dates of pair members tended to coincide, despite no evidence for any association at sea during the winter. Although Gunnarson et al. (2004) suggest a variety of reasons why Black-tailed Godwit *Limosa limosa* pair members that winter far apart should nonetheless show synchronized arrival, the most parsimonious explanation is simply a higher probability of pair formation between partners that arrive relatively early or late in the season, which, according to our results, is a more or less fixed characteristic.

Sex differences in timing and distribution

Recent empirical work has demonstrated a degree of gender-specific variation in various aspects of foraging behavior in seabirds, including albatrosses (Weimerskirch and Lys 2000, Lewis et al. 2002, Phillips et al. 2004b). In this study, there were clear between-sex differences in regional distribution and timing of movements. Successful females departed earlier from South Georgia, and successful, failed and deferring females all arrived earlier in the Benguela. A more extensive dataset on attendance of birds fitted with radio-transmitters confirms that females usually depart a few days before males and are much less likely to visit the nest after fledging (British Antarctic Survey, unpublished data).

In contrast, at the start of the breeding season, males arrived 4–5 d earlier in the proximity of Bird Island. Sightings of banded birds indicate, similarly, that males arrive around 4 d earlier and spend more time at the colony than females prior to egg laying (Tickell 2000). This presumably reflects their greater role in nest acquisition and defense. Why females should depart before males is less clear. Male albatrosses usually, but not always, undertake a greater share of chick provisioning (Huin et al. 2000, Weimerskirch and Lys 2000), and one possibility is that being larger, they can expend greater overall reproductive effort. Hence the earlier departure of females could reflect a more equitable investment relative to body size. In Buller's Albatross *Thalassarche bulleri*, males apparently desert the chick 1–2 mo before fledging, which Stahl and Sagar (2000) attributed to reduced body condition as a consequence of their far greater provisioning effort earlier in chick rearing. Note that it was once thought that female Wan-

dering Albatrosses also deserted the offspring earlier than males, but this now appears to be a misinterpretation resulting from the much reduced feeding frequency of females late in chick rearing (Weimerskirch and Lys 2000). However, an explanation based on reproductive costs does not explain why failed and deferring female black-browed albatrosses also arrived in southern African waters sooner than males. One alternative is that females, with their lower wing loading (Phillips et al. 2004b), are better adapted for meteorological conditions in the Benguela during the late summer. Niche specialization might also explain the pronounced latitudinal segregation of the sexes in this region throughout the winter, but more detailed analyses of sex-specific habitat preferences are clearly required.

There was also a larger-scale, between-sex difference in distribution: the only two birds that did not winter in the Benguela were both males. This could be dismissed as a sampling artifact were it not for evidence in other albatrosses for gender differences in migration tactics or distribution (Weimerskirch and Wilson 2000, Croxall et al. 2005; N. Huin, unpublished data). Furthermore, in the small population of *T. melanophrys* at Campbell Island, which has probably been established within the last century, there is a strong male bias (Moore et al. 2001). In addition, the degree of genetic isolation of black-browed albatross populations, when assessed using mitochondrial DNA (limited to female lineages), is considerably higher than when assessed using microsatellites (inherited biparentally), which is suggestive of male-biased dispersal (Burg and Croxall 2001). Gene flow may therefore be effected by the immigration of small numbers of errant males such as those detected here. This would also explain the presence of marker genes typical of South Georgia Black-browed Albatrosses in the Falklands and New Zealand populations (Burg and Croxall 2001).

Intra- and interspecific segregation and competition

Although Black-browed Albatrosses tend to concentrate in shelf and shelf-slope waters, they and the closely related Campbell Albatross *Thalassarche impavida*, will also feed over much deeper water (Prince et al. 1998, Waugh et al. 1999, Huin 2002). Not surprisingly, given this variety of foraging habitat, Black-browed Albatrosses have catholic dietary tastes: depending on the site, they generally take fish, krill, or squid in shelf and shelf-break areas, and squid at frontal zones or in deeper oceanic water (Waugh et al. 1999, Chérel et al. 2000, Xavier et al. 2003). As such, they potentially compete with a number of other large, opportunistic, highly pelagic predators in the same ecological guild. Indeed, there is strong evidence for inter-specific resource partitioning among sympatric albatrosses during the breeding season, mediated by variation in habitat preferences and behavior (Hyrenbach et al. 2002, Phillips et al. 2005).

Much less is known about ecological segregation while on migration, although two separate studies have recorded substantial spatial or habitat segregation between congeneric *Diomedea* and *Thalassarche* albatrosses in their respective wintering grounds off South America (Nicholls et al. 2002, Spear et al. 2003). The benefits of minimizing competition from other taxa with overlapping prey preferences, as well as conspecifics from other populations, may explain some movements of the tracked birds. The Falkland Islands hold 75% of the world population of Black-browed Albatrosses; these birds forage on the Patagonian Shelf throughout the year, and intensively around the Falklands during chick rearing (Grémillet et al. 2000, Huin 2002). Despite the relative geographical proximity, failed and deferring breeders from South Georgia avoided the area entirely during the summer, successful birds only visited for brief periods after mid April when Falklands chicks have fledged, and only one bird wintered there. Similarly, waters around Tristan da Cunha that were exploited occasionally during the winter and at the start of the return migration, were vacated by early September when the endemic Atlantic yellow-nosed albatross *Thalassarche chlororhynchos* returns to its breeding colonies (Tickell 2000). Some Atlantic Yellow-nosed and adult White-capped Albatrosses *Thalassarche [cauta] steadi* also migrate to African coastal waters, but the former are less abundant and tend to winter further north (Morant et al. 1983), and the latter usually feed closer inshore; moreover, successful breeders are unlikely to reach the area in large numbers until well after chick fledging at the Auckland Islands in mid August (Tickell 2000), by which time the South Georgia black-browed albatrosses have mostly departed (Fig. 3).

Implications for conservation

The winter distribution of the tracked birds overlapped with a number of major fisheries, including trawlers targeting hake *Merluccius* spp. or blue whiting *Micromesistius australis* in the South African Exclusive Economic Zone (EEZ) and the Patagonian Shelf, and longliners targeting tuna *Thunnus* spp., Patagonian toothfish *Dissostichus eleginoides*, or (less commonly) swordfish *Xiphias gladius* or hake throughout much of the South Atlantic, the southern Indian Ocean, and the Australian Fishing Zone (Klaer and Polacheck 1997, Grémillet et al. 2000, Ryan et al. 2002, Favero et al. 2003, Tuck et al. 2003). In several of these areas, including the Australian Fishing Zone and South African EEZ, levels of incidental mortality of Black-browed Albatrosses were at one time very high, in the order of hundreds or thousands of birds each year (Brothers 1991, Ryan et al. 2002), which was undoubtedly a major factor contributing to the decline of the South Georgia population (Croxall et al. 1998).

Most of those killed in South African waters are immatures, which remain in the area and are potentially

vulnerable to bycatch throughout the year (Ryan et al. 2002). There was also a sharp increase in the proportion of banded birds from South Georgia recovered in Australian waters from the mid 1960s onwards (Prince et al. 1998). Assuming this reflects more than spatiotemporal variability in reporting rates, this could partly explain the higher mortality (by 2%) of males compared with females in the South Georgia study colonies (Croxall et al. 1998), as males seem to have a higher probability of visiting Australian waters. Alternatively, males may compete more vigorously for longline bait or there may be some other aspect of the spatial or temporal sexual segregation in South African waters that increases their overlap with particular fisheries or vulnerability to incidental mortality (Ryan and Boix-Hinzen 1999).

On the basis of the tracking results, which indicate that it is rare for birds of breeding age to migrate to Australian waters, it is reasonable to conclude that bycatch there is not the priority concern for the South Georgia population. In any event, bird capture rates in that region have gradually declined with the introduction of better observer coverage and improved mitigation (Klaer and Polacheck 1997). The same is true for some of the longline fisheries on the Patagonian Shelf, although a recent increase in trawl-associated mortality is having a serious detrimental effect on the Falklands black-browed albatross population, which has declined by 25% in the last 20 years (Tuck et al. 2003). During the breeding season, when the South Georgia birds forage mainly in waters whose fisheries are well-regulated under the jurisdiction of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), bycatch levels are minimal (CCAMLR 2003). A small proportion might be vulnerable as they travel through the Indian Ocean, although on the Kerguelen Shelf at least, winter fishing effort by licensed vessels is low to avoid bad sea conditions (Weimerskirch et al. 2000).

Therefore, attention should be focused on fisheries interactions primarily in the central and eastern South Atlantic during the austral winter. Although there is little evidence that the domestic South African longline fishery for hake is a problem (Barnes et al. 1997), that is not true of their hake trawlers and tuna longliners. Of greater concern are the extensive fisheries by Japanese, Taiwanese, and IUU (illegal, unregulated, and unreported) vessels operating in the area regulated by two existing regional fisheries management organizations, the International Commission for the Conservation of Atlantic Tuna (ICCAT) and the Commission for the Conservation of Southern Bluefin Tuna (CCSBT), and the nascent South East Atlantic Fisheries Organisation (SEAFO). Mitigation measures such as the use of streamer (tori) lines, night-setting, retention of offal and used bait on board, line-weighting, and so forth can be extremely effective in reducing the level of incidental mortality of albatrosses (Murray et al.

1993, Brothers et al. 1999). Given the current rate of population decline, if attempts are not made by ICCAT, CCSBT, and SEAFO to minimize IUU fishing effort, to promote the use of mitigation measures, and to introduce an independent observer program to monitor and assist compliance, the future for Black-browed Albatrosses at South Georgia appears bleak.

ACKNOWLEDGMENTS

We are grateful to all fieldworkers (Dafydd Roberts and Ben Phalan in particular), for assistance with instrument deployment and retrieval at Bird Island, to Dirk Briggs for technical support, and to Peter Ryan and Sam Petersen for information on Black-browed Albatross distribution and interactions with fisheries off South Africa. Two anonymous referees provided many helpful comments on the manuscript.

LITERATURE CITED

- Afanasyev, V. 2004. A miniature daylight level and activity data recorder for tracking animals over long periods. *Memories of National Institute of Polar Research, Special Issue* **58**:227–233.
- Åkesson, S., P. Luschi, F. Papi, A. C. Broderick, F. Glen, B. J. Godley, and G. C. Hays. 2001. Oceanic long-distance navigation: do experienced migrants use the Earth's magnetic field? *Journal of Navigation* **54**:419–427.
- Barnes, K. N., P. G. Ryan, and C. Boix-Hinzen. 1997. The impact of the hake *Merluccius* spp. longline fishery off South Africa on Procellariiform seabirds. *Biological Conservation* **82**:227–234.
- Benhamou, S., F. Bonadonna, and P. Jouventin. 2003. Successful homing of magnet-carrying White-chinned Petrels released in the open sea. *Animal Behaviour* **65**:729–734.
- Berthold, P. 2001. Bird migration: a general survey. Second edition. Oxford University Press, Oxford, UK.
- Berthold, P., and A. J. Helbig. 1992. The genetics of bird migration: stimulus, timing and direction. *Ibis* **134**(supplement 1):35–40.
- Bêty, J., J.-P. Giroux, and G. Gauthier. 2004. Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). *Behavioral Ecology and Sociobiology* **57**:1–8.
- Birdlife International. 2004. Tracking ocean wanderers: the global distribution of albatrosses and petrels. Results from the Global Procellariiform Tracking Workshop, 1–5 September, 2003, Gordon's Bay, South Africa. Birdlife International, Cambridge, UK.
- Brothers, N. 1991. Albatross mortality and associated bait loss in the Japanese longline fishery in the Southern Ocean. *Biological Conservation* **55**:255–268.
- Brothers, N., R. Gales, and T. Reid. 1999. The influence of environmental variables and mitigation measures on seabird catch rates in the Japanese tuna longline fishery within the Australian Fishing Zone, 1991–1995. *Biological Conservation* **88**:85–101.
- Burg, T. M., and J. P. Croxall. 2001. Global relationships amongst black-browed and grey-headed albatrosses: analysis of population structure using mitochondrial DNA and microsatellites. *Molecular Ecology* **10**:2647–2660.
- Catry, P., R. A. Phillips, and J. P. Croxall. 2005. Sexual segregation in birds and implications for conservation. In K. E. Ruckstuhl and P. Neuhaus, editors. *Sexual segregation*. Cambridge University Press, Cambridge, UK.
- Cherel, Y., H. Weimerskirch, and C. Trouve. 2000. Food and feeding ecology of the neritic-slope forager Black-browed Albatross and its relationships with commercial fisheries in Kerguelen waters. *Marine Ecology Progress Series* **207**:183–199.
- Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). 2003. Report of the twenty-second meeting of the Scientific Council of the Commission for the Conservation of Antarctic Marine Living Resources. CCAMLR, Hobart, Australia.
- Cristol, D. A., M. B. Baker, and C. Carbone. 1999. Differential migration revisited: latitudinal segregation by age and sex class. Pages 33–88 in V. J. Nolan, E. D. Ketterson, and C. F. Thompson, editors. *Current ornithology*. Kluwer Academic/Plenum Press, New York, New York, USA.
- Croxall, J. P., P. A. Prince, P. Rothery, and A. G. Wood. 1998. Population changes in albatrosses at South Georgia. Pages 69–83 in G. Robertson and R. Gales, editors. *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, UK.
- Croxall, J. P., J. R. D. Silk, R. A. Phillips, V. Afanasyev, and D. R. Briggs. 2005. Global circumnavigations: tracking year-round ranges of non-breeding albatrosses. *Science* **307**:249–250.
- Favero, M., C. E. Khatchikian, A. Arias, P. S. Rodriguez, G. Cañete, and R. Mariano-Jelicich. 2003. Estimates of seabird by-catch along the Patagonian Shelf by Argentine longline fishing vessels, 1999–2001. *Bird Conservation International* **13**:273–281.
- Fridolfsson, A. K., and H. Ellegren. 1999. A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology* **30**:116–121.
- Grémillet, D., G. Dell'Omo, P. G. Ryan, G. Peters, Y. Ropert-Coudert, and S. J. Weeks. 2004. Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of cape gannets from neighbouring colonies. *Marine Ecology Progress Series* **268**:265–279.
- Grémillet, D., R. P. Wilson, S. Wanless, and T. Chater. 2000. Black-browed Albatross, international fisheries and the Patagonian Shelf. *Marine Ecology Progress Series* **195**:269–280.
- Gunnarsson, T. G., J. A. Gill, T. Sigurbjornsson, and W. J. Sutherland. 2004. Pair bonds—arrival synchrony in migratory birds. *Nature* **431**:646.
- Gwinner, E. 1996. Circannual clocks in avian reproduction and migration. *Ibis* **138**:47–63.
- Hamer, K. C., R. A. Phillips, J. K. Hill, S. Wanless, and A. G. Wood. 2001. Contrasting foraging strategies of Gannets *Morus bassanus* at two North Atlantic colonies: foraging trip duration and foraging area fidelity. *Marine Ecology Progress Series* **224**:283–290.
- Hedd, A., R. Gales, and N. Brothers. 2001. Foraging strategies of Shy Albatross *Thalassarche cauta* breeding at Albatross Island, Tasmania, Australia. *Marine Ecology Progress Series* **224**:267–282.
- Hill, R. D. 1994. Theory of geolocation by light levels. Pages 227–236 in B. J. Le Boeuf and R. M. Laws, editors. *Elephant seals: population ecology, behaviour and physiology*. University of California Press, Berkeley, California, USA.
- Huin, N. 2002. Foraging distribution of the Black-browed Albatross, *Thalassarche melanophris*, breeding in the Falkland Islands. *Aquatic Conservation: Marine and Freshwater Ecosystems* **12**:89–99.
- Huin, N., P. A. Prince, and D. R. Briggs. 2000. Chick provisioning rates and growth in Black-browed Albatross *Diomedea melanophris* and Grey-headed Albatross *D. chrysostris* at Bird Island, South Georgia. *Ibis* **142**:550–565.
- Hyrenbach, K. D., and R. C. Dotson. 2003. Assessing the susceptibility of female Black-footed Albatross (*Phoebastria nigripes*) to longline fisheries during their post-breeding dispersal: an integrated approach. *Biological Conservation* **112**:391–404.
- Hyrenbach, K. D., P. Fernández, and D. J. Anderson. 2002. Oceanographic habitats of two sympatric North Pacific Albatrosses during the breeding season. *Marine Ecology Progress Series* **233**:283–301.

- Irons, D. B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology* **79**:647–655.
- Iverson, S. A., D. Esler, and D. J. Rizzolo. 2004. Winter philopatry of harlequin ducks in Prince William Sound, Alaska. *Condor* **106**:711–715.
- Klaer, N., and T. Polacheck. 1997. By-catch of albatrosses and other seabirds by Japanese longline fishing vessels in the Australian Fishing Zone from April 1992 to March 1995. *Emu* **97**:150–167.
- Lewis, S., S. Benvenuti, L. Dall'Antonia, R. Griffiths, L. Money, T. N. Sherratt, S. Wanless, and K. C. Hamer. 2002. Sex-specific foraging behaviour in a monomorphic seabird. *Proceedings of the Royal Society of London, Series B* **269**:1687–1693.
- Mehl, K. R., R. T. Alisauskas, K. A. Hobson, and D. K. Kellett. 2004. To winter east or west? Heterogeneity in winter philopatry in a central-Arctic population of king eiders. *Condor* **106**:241–251.
- Møller, A. 2001. Heritability of arrival date in a migratory bird. *Proceedings of the Royal Society, London B* **268**:203–206.
- Moore, P. J., T. M. Burg, G. A. Taylor, and C. D. Millar. 2001. Provenance and sex ratio of Black-browed Albatross, *Thalassarche melanophrys*, breeding on Campbell Island, New Zealand. *Emu* **101**:329–334.
- Morant, P. D., R. K. Brooke, and R. W. Abrams. 1983. Recoveries in southern Africa of seabirds breeding elsewhere. *Ring and Migration* **4**:257–268.
- Murray, T. E., J. A. Bartle, S. R. Kalish, and P. R. Taylor. 1993. Incidental capture of seabirds by Japanese southern bluefin tuna longline vessels in New Zealand waters, 1988–1992. *Bird Conservation International* **3**:181–210.
- Nicholls, D., D. Murray, H. Battam, G. Robertson, P. Moors, E. Butcher, and M. Hildebrandt. 1995. Satellite tracking of the Wandering Albatross *Diomedea exulans* around Australia and in the Indian Ocean. *Emu* **95**:223–230.
- Nicholls, D. G., C. J. R. Robertson, P. A. Prince, M. D. Murray, K. J. Walker, and G. P. Elliott. 2002. Foraging niches of three *Diomedea* albatrosses. *Marine Ecology Progress Series* **231**:269–277.
- Percival, S. M. 1991. The population structure of Greenland barnacle geese *Branta leucopsis* on the wintering grounds on Islay. *Ibis* **133**:357–364.
- Phillips, R. A., J. R. D. Silk, and J. P. Croxall. 2005. Foraging and provisioning strategies of the light-mantled sooty albatross at South Georgia: competition and co-existence with sympatric pelagic predators. *Marine Ecology Progress Series* **285**:259–270.
- Phillips, R. A., J. R. D. Silk, J. P. Croxall, V. Afanasyev, and D. R. Briggs. 2004a. Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series* **266**:265–272.
- Phillips, R. A., J. R. D. Silk, B. Phalan, P. Catry, and J. P. Croxall. 2004b. Seasonal sexual segregation in two *Thalassarche* albatrosses: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proceedings of the Royal Society of London, Series B* **271**:1283–1291.
- Phillips, R. A., J. C. Xavier, and J. P. Croxall. 2003. Effects of satellite transmitters on albatrosses and petrels. *Auk* **120**:1082–1090.
- Potti, J. 1998. Arrival time from spring migration in male pied flycatchers: individual consistency and familial resemblance. *Condor* **100**:702–708.
- Prince, P. A., J. P. Croxall, P. N. Trathan, and A. G. Wood. 1998. The pelagic distribution of South Georgia albatrosses and their relationships with fisheries. Pages 137–167 in G. Robertson and R. Gales, editors. *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, UK.
- Ristow, D., P. Berthold, D. Hashmi, and U. Querner. 2000. Satellite tracking of Cory's Shearwater migration. *Condor* **102**:696–699.
- Robertson, G. J., and F. Cooke. 1999. Winter philopatry in migratory waterfowl. *Auk* **116**:20–34.
- Ryan, P. G., and C. Boix-Hinzen. 1999. Consistent male-biased seabird mortality in the Patagonian toothfish longline fishery. *Auk* **116**:851–854.
- Ryan, P. G., D. G. Keith, and M. Kroese. 2002. Seabird bycatch by tuna longline fisheries off southern Africa, 1998–2000. *South African Journal of Marine Science* **24**:103–110.
- Shaffer, S. A., H. Weimerskirch, and D. P. Costa. 2001. Functional significance of sexual dimorphism in Wandering Albatrosses, *Diomedea exulans*. *Functional Ecology* **15**:203–210.
- Spear, L., D. G. Ainley, and S. W. Webb. 2003. Distribution, abundance and behaviour of Buller's, Chatham Island and Salvin's albatrosses off Chile and Peru. *Ibis* **145**:253–269.
- Stahl, J. C., and P. M. Sagar. 2000. Foraging strategies and migration of southern Buller's Albatrosses *Diomedea b. bulleri* breeding on the Solander Islands, New Zealand. *Journal of the Royal Society of New Zealand* **30**:319–334.
- Tickell, W. L. N. 1967. Movements of Black-browed and Grey-headed Albatrosses in the South Atlantic. *Emu* **66**:357–367.
- Tickell, W. L. N. 2000. Albatrosses. Pica Press, Sussex, UK.
- Tuck, G. N., T. Polacheck, and C. M. Bulman. 2003. Spatio-temporal trends of longline fishing effort in the Southern Ocean and implications for seabird bycatch. *Biological Conservation* **114**:1–27.
- Waugh, S. M., and H. Weimerskirch. 2003. Environmental heterogeneity and the evolution of foraging behaviour in long-ranging Greater Albatrosses. *Oikos* **103**:374–384.
- Waugh, S. M., H. Weimerskirch, Y. Cherel, U. Shankar, P. A. Prince, and P. M. Sagar. 1999. Exploitation of the marine environment by two sympatric albatrosses in the Pacific Southern Ocean. *Marine Ecology Progress Series* **177**:243–254.
- Weimerskirch, H., J. A. Bartle, P. Jouventin, and J. C. Stahl. 1988. Foraging ranges and partitioning of feeding zones in three species of southern albatrosses. *Condor* **90**:214–219.
- Weimerskirch, H., D. Capdeville, and G. Duhamel. 2000. Factors affecting the number and mortality of seabirds attending trawlers and long-liners in the Kerguelen area. *Polar Biology* **23**:236–249.
- Weimerskirch, H., and P. Lys. 2000. Seasonal changes in the provisioning behaviour and mass of male and female Wandering Albatrosses in relation to the growth of their chick. *Polar Biology* **23**:733–744.
- Weimerskirch, H., M. Salamolard, F. Sarrazin, and P. Jouventin. 1993. Foraging strategy of Wandering Albatrosses through the breeding season: a study using satellite telemetry. *Auk* **110**:325–342.
- Weimerskirch, H., and R. P. Wilson. 2000. Oceanic respite for Wandering Albatrosses. *Nature* **406**:955–956.
- Wilson, R. P., J. J. Ducamp, G. Rees, B. M. Culik, and K. Niekamp. 1992. Estimation of location: global coverage using light intensity. Pages 131–134 in I. M. Priede and S. M. Swift, editors. *Wildlife telemetry: remote monitoring and tracking of animals*. Ellis Horward, Chichester, UK.
- Wood, A. G., B. Naef-Daenzer, P. A. Prince, and J. P. Croxall. 2000. Quantifying habitat use in satellite-tracked pelagic seabirds: application of kernel estimation to albatross locations. *Journal of Avian Biology* **31**:278–286.
- Xavier, J. C., J. P. Croxall, and K. Reid. 2003. Interannual variation in the diets of two albatross species breeding at South Georgia: implications for breeding performance. *Ibis* **145**:593–610.