

Habitat preference, accessibility, and competition limit the global distribution of breeding Black-browed Albatrosses

EWAN D. WAKEFIELD,^{1,9} RICHARD A. PHILLIPS,¹ PHILIP N. TRATHAN,¹ JAVIER ARATA,² ROSEMARY GALES,³ NIC HUIN,⁴ GRAHAM ROBERTSON,⁵ SUSAN M. WAUGH,⁶ HENRI WEIMERSKIRCH,⁷ AND JASON MATTHIOPOULOS⁸

¹British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB30ET United Kingdom

²Instituto Antártico Chileno, Plaza Muñoz Gamero 1055 Chile

³Biodiversity Conservation Branch, Department of Primary Industries and Water, P.O. Box 40 Hobart, Tasmania 7001 Australia

⁴Falklands Conservation, P.O. Box 26, Stanley FIQQ 1ZZ Falkland Islands

⁵Australian Antarctic Division, Channel Highway, Kingston, Tasmania 7050 Australia

⁶Sextant Technology Ltd, 116 Wilton Road, Wellington 6012 New Zealand

⁷Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, 79360 Villiers-en-Bois, France

⁸Sea Mammal Research Unit and Centre for Research into Ecological and Environmental Modeling, Scottish Oceans Institute, University of St. Andrews, Fife KY16 8LB United Kingdom

Abstract. Telemetry methods and remote sensing now make it possible to record the spatial usage of wide-ranging marine animals and the biophysical characteristics of their pelagic habitats. Furthermore, recent statistical advances mean that such data can be used to test ecological hypotheses and estimate species' distributions. Black-browed Albatrosses *Thalassarche melanophrys* are highly mobile marine predators with a circumpolar breeding and foraging distribution in the Southern Hemisphere. Although they remain relatively abundant, increased fisheries bycatch has led to their listing as endangered by conservation bodies. We satellite-tracked 163 breeding Black-browed Albatrosses and eight closely related Campbell Albatrosses *T. impavida* from nine colonies. We then quantified habitat usage, and modeled population-level spatial distribution at spatiotemporal scales >50 km and 1 month, as a function of habitat accessibility, habitat preference, and intraspecific competition, using mixed-effects generalized additive models (GAMM). During incubation, birds foraged over a wider area than in the post-brood chick-rearing period, when they are more time constrained. Throughout breeding, the order of habitat preference of Black-browed Albatrosses was for neritic (0–500 m), shelf-break and upper shelf-slope (500–1000 m), and then oceanic (>1000 m) waters. Black-browed Albatrosses also preferred areas with steeper (>3°) bathymetric relief and, in addition, during incubation, warmer sea surface temperatures (peak preference ~16°C). Although this suggests specialization in neritic habitats, incubation-stage Black-browed Albatrosses from South Georgia also foraged extensively in oceanic waters, preferring areas with high eddy kinetic energy (>250 cm²/s²), especially the Brazil-Malvinas Confluence, a region of intense mesoscale turbulence. During chick-rearing, this species had a more southerly distribution, and following the seasonal retreat of sea ice, birds from some populations utilized neritic polar waters. Campbell Albatrosses showed similar bathymetric preferences but also preferred positive sea level anomalies. Black-browed Albatross foraging areas were partially spatially segregated with respect to colony and region, with birds preferring locations distant from neighboring colonies, presumably in order to reduce competition between parapatric conspecifics. At the global scale, the greatest concentrations of breeding Black-browed Albatrosses are in southern South American neritic, shelf-break, and shelf-slope waters. These regions also hold large fisheries and should therefore be a priority for introduction of bycatch mitigation measures.

Key words: Black-browed Albatross; Campbell Albatross; central-place foraging; GAMM; niche specialization; satellite tracking; spatial modeling; spatial segregation; *Thalassarche impavida*; *Thalassarche melanophrys*.

INTRODUCTION

Understanding the factors that influence the distribution of organisms in space is one of the primary aims of ecologists. When this understanding is sufficiently complete it becomes possible to use spatial models to identify habitats and geographical areas necessary for the survival of endangered species (Guisan and Zim-

Manuscript received 4 May 2009; revised 16 February 2010; accepted 7 April 2010. Corresponding Editor: B. J. Danielson.

⁹ Present address: Institute of Integrative and Comparative Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT United Kingdom.

E-mail: E.D.Wakefield@leeds.ac.uk

mermann 2000, Austin 2007). Hence, in order to meet both ecological and conservation objectives it may be necessary to quantify the effects of habitat preference, competition, and habitat accessibility (e.g., Lewis et al. 2001, Adler and Gordon 2003, Matthiopoulos 2003). While the effects of such factors on terrestrial animals, which are relatively straightforward to observe, have received much attention (Begon et al. 2006), there have, until recently, been far fewer attempts to examine their influence on wide-ranging marine animals (fish, cetaceans, pinnipeds, and seabirds; Wakefield et al. 2009a). In the main, this reflects the difficulty of simultaneously measuring the habitat characteristics and spatial usage of animals that range over wide areas of open ocean, remote from human observation. Although distribution and abundance data collected by ship-based surveys can provide insights into the spatial ecology of these animals (e.g., Hunt et al. 1996, Spear et al. 2001, Ballance et al. 2006, Louzao et al. 2006) such Eulerian studies are limited because they tend to provide only partial spatial and temporal coverage of animals' home ranges and may be biased by the behavioral response of target animals to survey vessels (Hyrenbach 2001, Buckland et al. 2004). Furthermore, it is generally difficult or impossible to determine individual characteristics (provenance, breeding status, sex, age, etc.) of animals observed from ships (Burger and Shaffer 2008). These problems are increasingly being circumvented by adopting a Lagrangian approach to the study of wide-ranging marine animals in which the individual movement is measured using miniature animal-attached devices, such as satellite-tracking tags (Turchin 1998, Burger and Shaffer 2008, Tremblay et al. 2009). Data from these devices can be combined with environmental data collected by satellite remote-sensing (Martin 2004) to give a simultaneous view of both the environment and the movement of known individuals throughout the full extent of their potential home range (e.g., Guinet et al. 2001, Hays et al. 2001, Hyrenbach et al. 2002). Furthermore, advances in statistical modeling are increasingly making it possible to test ecological hypotheses using the large volumes of data that these technologies provide (Guisan and Zimmermann 2000, Aarts et al. 2008, Patterson et al. 2008).

Black-browed Albatrosses *Thalassarche melanophrys* (BBA) are among the most mobile and wide-ranging of marine predators, routinely commuting hundreds to thousands of kilometers from their subantarctic colonies to forage (Weimerskirch et al. 1997, Huin 2002, Phillips et al. 2004). Although they are polyphagous, during chick provisioning they show a marked preference for relatively few prey taxa (Croxall and Prince 1980, Cherel and Klages 1998), and spend the majority of their time in productive neritic, shelf-break, and upper shelf-slope waters (Weimerskirch et al. 1997, Gremillet et al. 2000, Wood et al. 2000, Huin 2002, Pinaud and Weimerskirch 2002, Phillips et al. 2004, Terauds et al. 2006b). However, birds from some populations also forage in

oceanic habitats, including the Antarctic Polar Frontal Zone (APFZ; Phillips et al. 2004, Pinaud and Weimerskirch 2007), and nonbreeding birds associate with mesoscale eddies (Petersen et al. 2008). Until recently, the BBA was considered to comprise the nominate subspecies and the Campbell Albatross (formerly *T. melanophrys impavida*). Genetic evidence now suggests that the Campbell Albatross (CBA) should be regarded as a species in its own right, *T. impavida*, a view which has gained wide acceptance (Roberson and Nunn 1998, Burg and Croxall 2001). The entire world population of 21 000 pairs of CBA breed at Campbell Island in the western Pacific (Gales 1998, Moore 2004). Although a small number of BBA breed sympatrically on Campbell Island, it is not clear whether the two species diverged by parapatric or sympatric speciation (Alderman et al. 2005). Tracking data show that in qualitative terms the habitats used by the CBA and BBA are very similar and the two species are often regarded as having the same habitat requirements (Waugh et al. 1999). However, to date, differences in habitat use and preference have not been quantitatively compared so this may be a misleading assumption.

Although BBA are the most abundant of the southern hemisphere albatrosses (current world breeding population ~601 000 pairs), increased incidental mortality since the mid 1980s in longline and trawl fisheries has caused widespread and unsustainable population declines (~8.5% in total over the past 10 years), such that they are now classified as Endangered (IUCN 2008). Hence, we used satellite-tracking and remotely-sensed environmental data to estimate the habitat preferences and global distribution of this species during the breeding season. In so doing, we investigated a number of aspects of the ecology of this wide-ranging marine animal. Firstly, the central-place constraint imposed during the breeding season when such animals must return periodically to their colonies means that the accessibility of points in space is not equal (Orians and Pearson 1979). Therefore, the cost (in time or energy) of accessing different locations increases as a function of distance (Matthiopoulos 2003). In addition, in polar waters the seasonal retreat of sea ice considerably increases the area accessible to foraging albatrosses as the breeding season progresses (Tickell 2000). Secondly, habitat use and requirements may vary with breeding stage (Phillips et al. 2004, Breed et al. 2009). Breeding birds must first incubate their egg, and then provision their chick until it fledges. In seabirds, the change of duties is often marked by a shift in spatial usage (Weimerskirch et al. 1993, Phillips et al. 2004), either because of intrinsic factors, such as differences in the severity of the central-place constraint (Shaffer et al. 2003) or differences in the dietary requirements of adult and chick (Williams et al. 2008), or extrinsic factors, such as seasonal changes in prey availability (Humphreys et al. 2006). Given that some populations of BBA switch foraging areas with breeding stage (Huin 2002,

Phillips et al. 2004), habitat preferences probably also change. Thirdly, competition may modify spatial usage: Because of niche overlap, competition between conspecifics is often more intense than that between species (Simberloff and Dayan 1991). In some central-place foragers this may lead to spatial partitioning of animals from adjacent colonies (parapatric conspecifics; Brown and Gordon 2000, Griffin and Thomas 2000, Adler and Gordon 2003). Unlike many central-place foragers, seabirds do not defend foraging territories, yet partial spatial segregation along colonial lines has been observed in some species (Ainley et al. 2003, 2004, Gremillet et al. 2004). It has been hypothesized that the factor mediating partitioning is direct or indirect competition, the intensity of which varies with conspecific density (Ashmole 1963, Furness and Birkhead 1984, Cairns 1989, Lewis et al. 2001). A degree of spatial partitioning is exhibited by BBA in the Falkland Islands and Kerguelen, but there is some overlap in the foraging areas of birds from adjacent colonies (Weimerskirch et al. 1988, Huin 2002). Therefore, it is not known to what extent intraspecific competition causes spatial segregation of BBA populations during the breeding season.

In this study we aimed to quantify the effects of central-place constraint, habitat preference, and competition on the spatial usage of breeding albatrosses. We then demonstrate that by modeling these effects, individual movement data can be used to quantitatively estimate the population-level global distribution of an endangered wide-ranging marine animal, the BBA. Following Aarts et al. (2008), we used mixed-effects generalized additive models (GAMMs), fitted to environmental and satellite-tracking data from 171 breeding BBA and CBA, from nine colonies located throughout the subantarctic, to model spatial usage as a function of habitat preference and intraspecific competition, while controlling for the effects of unequal habitat accessibility. In so doing, we addressed a number of related hypotheses: (1) that spatial usage decreases at a rate proportional to distance from the colony, (2) that BBA express stage-dependent habitat preferences, (3) that BBA and CBA have measurably different habitat preferences, and (4) that spatial usage decreases with parapatric intraspecific competition (competition between birds from neighboring colonies).

METHODS

Conceptual framework and definitions

We adopted the analytical approach of Aarts et al. (2008), defining a *habitat* as a point or region in environmental space, the coordinates of which are the values of environmental covariates. Note that their definition differs considerably from geographical definitions, such as “the place where an animal lives” (Hall et al. 1997). The probability of a satellite-tracked animal’s location being recorded in the i th habitat is defined by a binomial response variable \hat{u}_i . Locations (Fig. 1a) are assumed to be generated by a heterogeneous, spatial

Poisson process, with a rate proportional to a spatial probability density function $f_1(\mathbf{X}_s)$, where \mathbf{X}_s is a vector of environmental covariates (Fig. 1c–h) at a given point s in geographical space. Adopting a case-control approach, we complemented each animal location recorded by satellite-tracking with three temporally matched, randomly generated pseudo-absence (control) locations, at which \hat{u}_i takes the value 0 (Fig. 1b). This framework permits the selection of control points from a biologically realistic null model. This null model expresses the expectation of where an animal might be if it had movement constraints but not preferences. In the case of central-place foragers, a simple null model of usage assumes that the cost (in time or energy) of visiting a point in space is proportional to distance from the colony d_c , the inverse of which is termed *accessibility* α (Matthiopoulos 2003). Hence, we selected control locations via a spatial Poisson process, at a rate $f_0(\mathbf{X}_s)$ proportional to α . The response variable \hat{u}_i is then approximated by a Bernoulli process, with probability h_i . Aarts et al. (2008) show that, at point s ,

$$h(\mathbf{X}_s) = \frac{k_1 f_1(\mathbf{X}_s)}{k_0 f_0(\mathbf{X}_s) + k_1 f_1(\mathbf{X}_s)} \quad (1)$$

where k_1 is the number of telemetry locations and k_0 is the number of control locations. Rearranging Eq. 1, the probability of spatial usage at location s can be estimated by

$$f_1(\mathbf{X}_s) = \frac{h(\mathbf{X}_s)}{1 - h(\mathbf{X}_s)} r f_0(\mathbf{X}_s) \quad (2)$$

where $r = k_0/k_1$. The quantity h can be estimated empirically from the case-control data. To allow for the possibility of a nonlinear response to environmental covariates, we modeled h_i as a GAMM:

$$h_i = g^{-1}(\eta_i) = \frac{e^{\eta_i}}{1 + e^{\eta_i}} \quad (3)$$

$$\eta_i = b_0 + s_1(x_{i,1}) + \dots + s_j(x_{i,j}) + \dots$$

where g^{-1} is the inverse of the logit link function and η_i is the linear predictor. We structured η_i such that it could include parametric smooths of single covariates, and to allow for the possibility of interactions, tensor product smooths of pairs of covariates (Wood 2006). Because tracked individuals are observed repeatedly, we treated individual birds as a random effect. We then assessed competing models by cross-validation, with forward selection, maximizing log-likelihood. Although cross-validation is a somewhat conservative approach (Burnham and Anderson 1998), we adopted it because tracking data tend to be inherently spatially and serially autocorrelated, which are properties that can lead to overparameterized models if information criteria (e.g., the AIC) are used for model selection. Furthermore, parameters were estimated using penalized quasi-likeli-

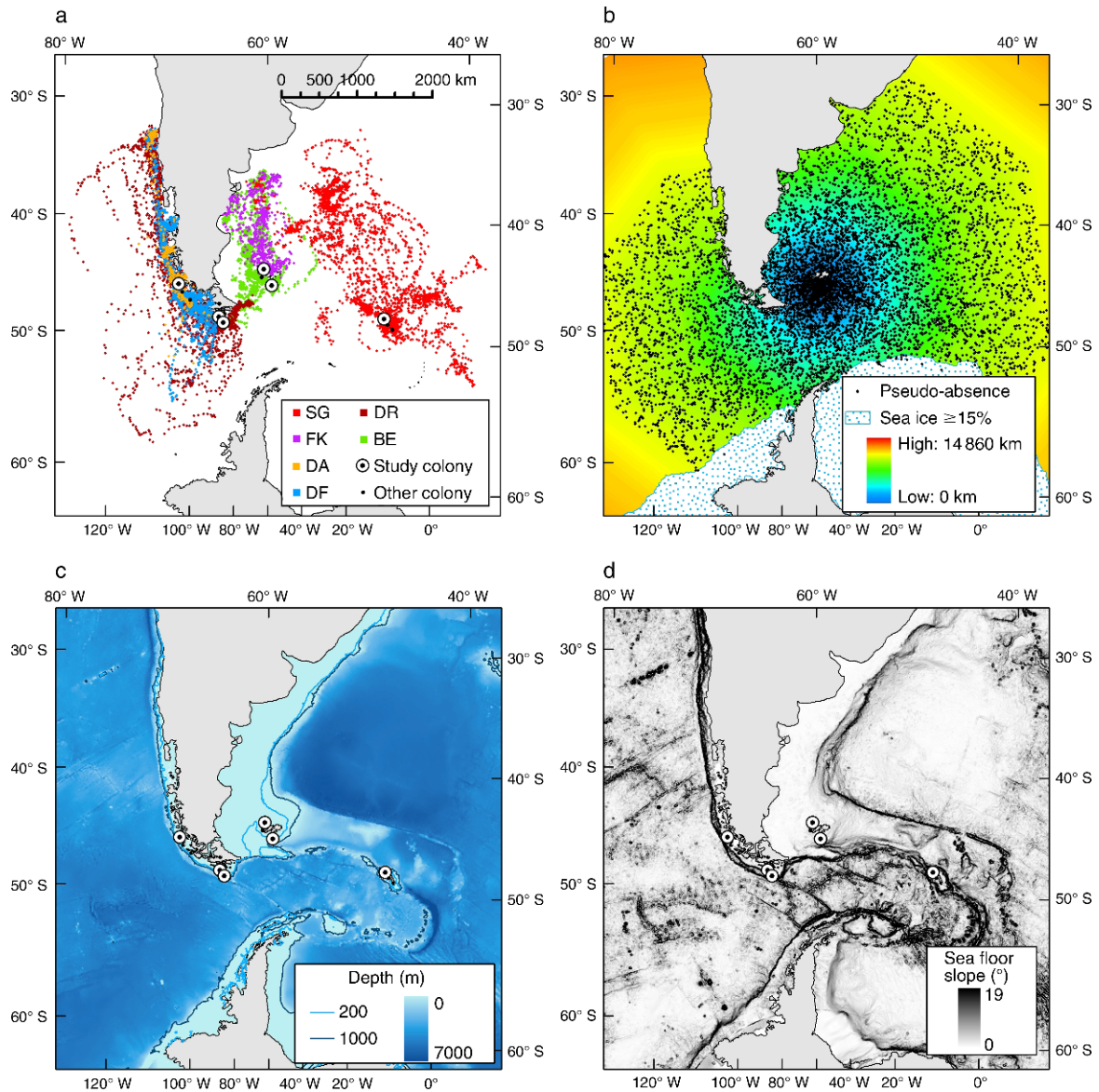


FIG. 1. Examples of the data used to fit the spatial usage models. (a) ARGOS locations of incubation stage Black-browed Albatrosses (*Thalassarche melanophrys*) foraging from six colonies (SG, northwest South Georgia; FK, northwest Falklands Islands; DA, Isla Diego de Almagro; DF, Islas Ildefonso; DR, Islas Diego Ramirez; and BE, Beauchêne Island). (b) Minimum biological distance to all grid cells from the Beauchêne Island super-colony (d_c) and randomly generated control (pseudo-absence) locations, selected by a spatial Poisson process with a rate proportional to d_c^{-1} . (c) Depth, (d) depth slope, (e) mean optimally interpolated sea surface temperature (SST), (f) mean sea level anomaly (SLA), and (g) mean eddy kinetic energy (EKE). (h) Minimum biological distance to the next nearest super-colony to Beauchêne Island (d_n). Values of time-varying covariates in panels (e), (f), and (g) are for November 2000. Mean sea ice extent ($\geq 15\%$ cover) is shown for November.

hood (Wood 2006), which also makes the use of model selection criteria, such as the AIC, inappropriate (Venables and Ripley 2002).

Aarts et al. (2008) define the quantity $h(\mathbf{X}_s)$ as an animal's preference for environmental conditions \mathbf{X}_s at the point s in geographical space. This is the animal's *habitat preference*, which can be defined more generally as *a statistical description of habitat use relative to a particular sample of availability*. The implication in these

definitions is that animals spend more time in habitats that are preferred (Johnson 1980, Manly et al. 2002). However, under certain circumstances this assumption may be invalid (Van Horne 1983, Kennedy and Gray 1993, Pulliam 2000). Firstly, central-place foragers may spend more time in poorer quality habitat patches if these are closer to the central place than more distant but higher quality patches (Matthiopoulos 2003). Following Aarts et al. (2008) we accounted for this

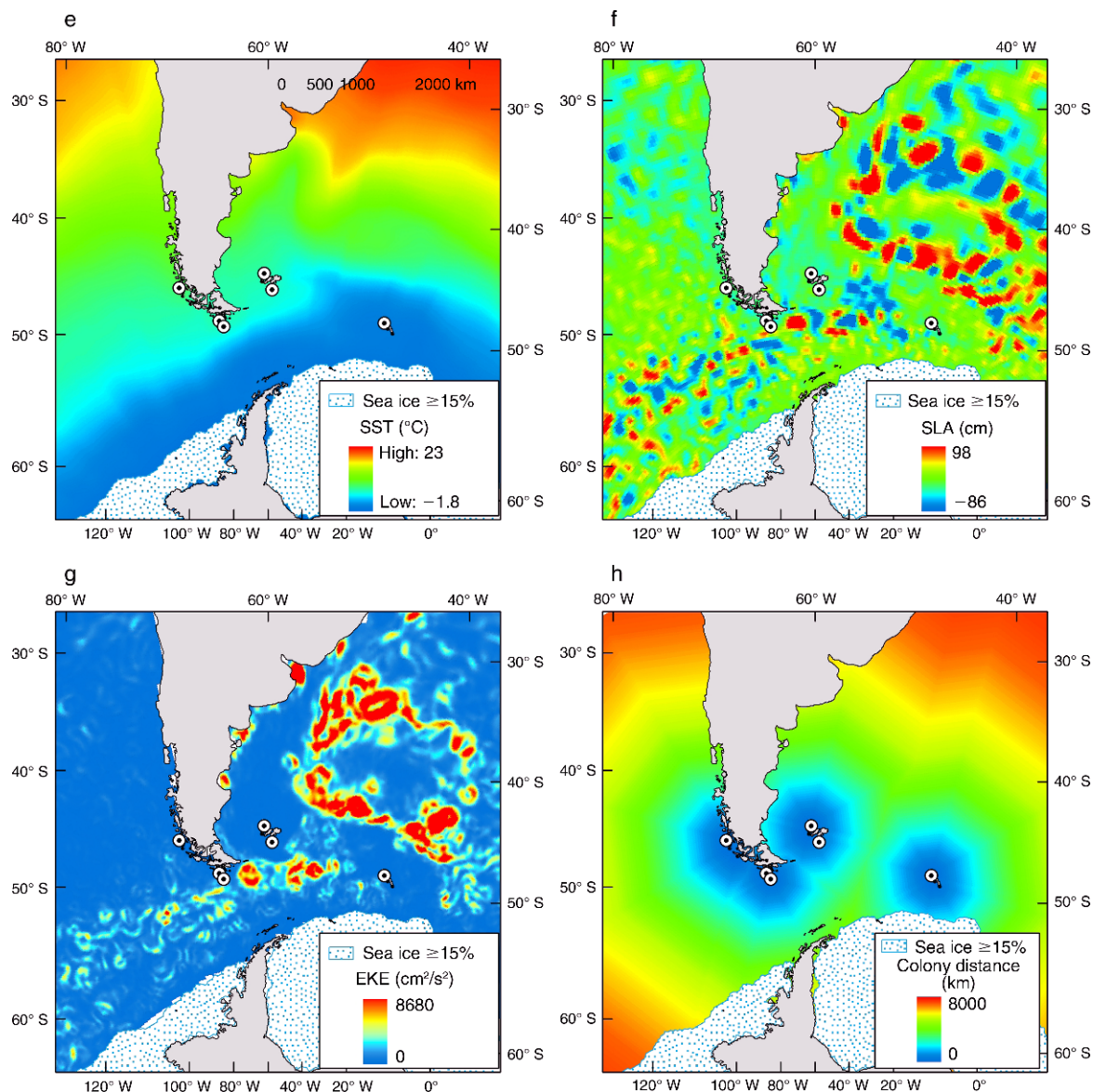


FIG. 1. Continued.

effect by adopting a mechanistic null usage model that assumes that the probability of locations being used declines with distance from the central place (see *Null model and control locations* below). Secondly, animals may be excluded from high-quality habitats by dominant competitors and so spend more time in lower quality habitats. In some species this factor affects habitat choice at the scale of the home range (source-sink dynamics; Lidicker 1975, Van Horne 1983, Pulliam 1988). However, albatrosses are long-lived (60+ years), have low fecundity (maximum one offspring per year), and high philopatry (>95% of juveniles recruit to their natal colonies), so source-sink effects are unlikely to be marked (see also Bock and Jones 2004). However, at the scale of individual foraging trips, intraspecific competi-

tion may exclude birds from high-quality foraging habitats in the vicinity of neighboring colonies that would otherwise have been selected (Gremillet et al. 2004). We estimated this effect by considering parapatric intraspecific competition as an explanatory covariate (we had insufficient a priori information to include its effects in the null model), in effect, treating this term as an additional environmental covariate. Hence, having accounted for unequal accessibility, we made the assumption that birds spend more time in high-quality, low-competition habitats. However, we hereafter use the term habitat preference advisedly, recognizing that other factors, not quantified in our study may also affect spatial usage (Kennedy and Gray 1993).

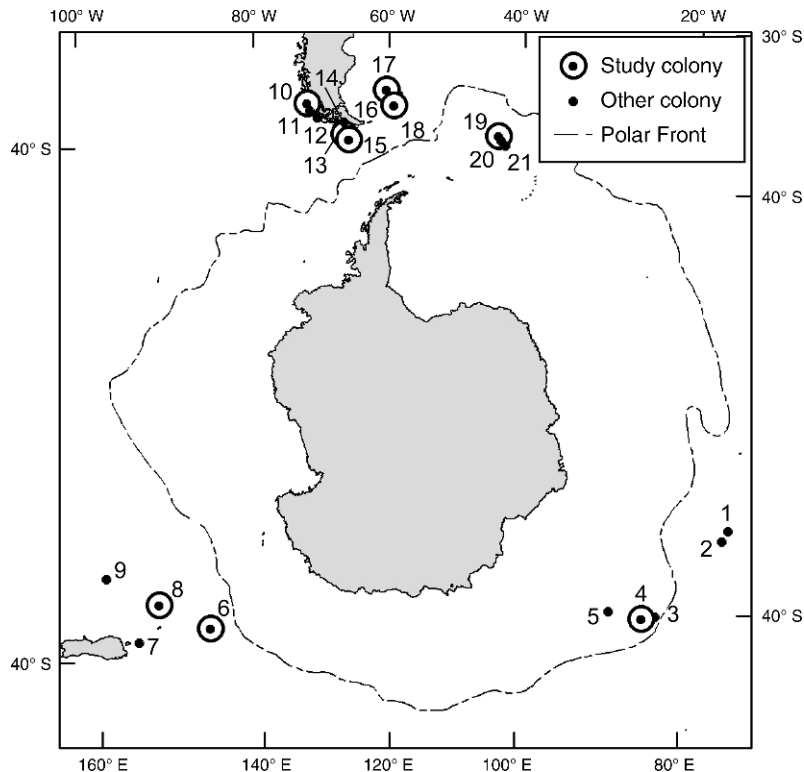


FIG. 2. Breeding locations of Black-browed and Campbell (*T. impavida*) Albatrosses, indicating colonies from which birds were satellite-tracked. Numbers for super-colonies refer to Table 1 and Appendix A. The mean location of the Antarctic Polar Front is from Moore et al. (1999).

Tracking data

Between 1994 and 2003, we used Platform Terminal Transmitters (PTTs) to record the spatial usage of foraging BBA breeding at eight colonies, located in southern Chile (Isla Diego de Almagro, Islas Ildefonso, Islas Diego Ramirez), the Falkland Islands (Beauchene Island, Saunders Island), South Georgia (Bird Island), which together hold 96% of the world population, as well as Île Kerguelen in the southern Indian Ocean and Macquarie Island in the southwest Pacific (Fig. 2, Table 1, Appendix A; for further details see Weimerskirch et al. 1997, Phillips et al. 2004, Terauds et al. 2006a, Pinaud and Weimerskirch 2007). In addition, CBA were tracked from Campbell Island (Waugh et al. 1999). Birds were tracked during the incubation or the post-brood chick-rearing stage (hereafter “chick-rearing”). During the former (late October–early January), parents incubate a single egg, taking turns to make long (~1 week) foraging trips. Once the chick hatches, it is brooded and/or guarded continuously for ~3 weeks. During the chick-rearing stage (late January–mid May), when the chick can be left alone, parents forage simultaneously, returning to provision it after short (~2 d) or sometimes long trips. We captured birds at the nest, either by hand or using a 1.5-m pole fitted with a wire crook and equipped them with a PTT (Microwave Telemetry PTT100 [Columbia, Maryland, USA], Telonics ST10

[Mesa, Arizona, USA], Toyocom T2038 [Tokyo, Japan], or Sirtrack 101 [Havelock North, New Zealand]; mass 20–55 g) attached to mantle feathers using Tesa tape. PTT transmission rate was set to every 60 or 90 sec, providing ARGOS class 3, 2, 1, 0, A, or B locations on average every 2.1 h. We recaptured birds after one or more foraging trips and recovered the devices. Total instrument mass, including attachment materials and in some cases, an additional, small (5–10 g) logger, was <2% of birds’ body mass, which did not result in injury in any cases, and was well below the threshold likely to cause measureable changes in behavior (Phillips et al. 2003). As errors associated with PTT locations are variable and sometimes large (Vincent et al. 2002), we filtered tracking data (McConnell et al. 2002), removing those locations that gave rise to unrealistically high average speeds (>80 m/s). In order to get a more balanced sample across individuals, we used data from only one trip per bird, selecting trips randomly when multiple trips had been recorded.

Null model and control locations

To reduce computing time, we amalgamated colonies <50 km apart into 21 super-colonies, comprising all known BBA and CBA breeding sites (Appendix A). However, we excluded two of these from our analysis because they held <100 breeding pairs (i.e., <0.01% of

TABLE 1. Spatial usage by Black-browed (*Thalassarche melanophrys*) and Campbell Albatrosses (*T. impavida*) satellite-tracked during this study.

| Population and abbreviation | Annual breeding population (pairs) | Area encompassing 75% kernel density ($\text{km}^2 \times 10^3$)† | | Season(s) tracked (chick-rearing year) | Area within 800 km of colony ($\text{km}^2 \times 10^3$)‡ | |
|----------------------------------|------------------------------------|---------------------------------------------------------------------|--------------------------|----------------------------------------|-------------------------------------------------------------|--------------|
| | | Incubation | Post-brood chick-rearing | | <200 m deep | <1000 m deep |
| 4) SE Kerguelen (KG) | 1350 | 2.1 (8) | 1.3 (19) | 1994, 1995, 2000 | 16.4 | 275.8 |
| 6) Macquarie Island (MQ) | 180 | 5.1 (6) | ... | 2000, 2001 | <0.1 | 58.5 |
| 8) Campbell Island (CB)§ | 21 000 | ... | 13.2 (8) | 1997 | 8.4 | 408.6 |
| 10) Isla Diego de Almagro (DA) | 15 594 | 1.6 (10) | ... | 2002 | 36.7 | 154.5 |
| 13) Islas Ildefonso (DF) | 47 000 | 4.6 (25) | ... | 2002 | 32.0 | 325.1 |
| 15) Islas Diego Ramirez (DR) | 55 000 | 6.4 (28) | 2.7 (12) | 1997, 2000, 2001, 2002 | 26.8 | 315.3 |
| 17) Northwest Falklands (FK) | 272 810 | 4.8 (11) | 0.8 (7) | 1999 | 67.0 | 754.5 |
| 18) South Falklands (BE) | 103 341 | 4.2 (4) | 0.6 (4) | 2000, 2001 | 27.3 | 646.0 |
| 19) Northwest South Georgia (SG) | 47 294 | 16.8 (17) | 4.8 (12) | 2002 | 13.2 | 50.0 |

Sources: Gales (1998), Arata et al. (2003), Moore (2004), Huin and Reid (2006), Poncet et al. (2006), Robertson et al. (2007, 2008); H. Weimerskirch (unpublished data).

† The area encompassing 75% of the kernel density of tracking locations; values in parentheses are the numbers of birds tracked, n .

‡ Area of neritic (<200 m deep) and neritic and upper shelf-slope waters (<1000 m deep) within 800 km of the colony.

§ Campbell Albatross, *Thalassarche impavida*.

the world population). For each month we then used the ArcGIS 9.2 spatial analyst package (ESRI 2006) to calculate the minimum biological distance d_c (Matthiopoulos 2003) from each super-colony to all points on a 10-km polar stereographic grid, assuming that albatrosses would not cross extensive land barriers or sea ice (Tickell 2000). We defined areas of sea ice ($\geq 15\%$ coverage) using monthly passive microwave data (Fetterer et al. 2002, updated 2008). We assumed birds would not travel beyond 3300 km (1.1 times the maximum d_c reached by any bird during our study). Within this range, we then calculated accessibility α , as $\alpha = d_c^{-1}$ (cf. Matthiopoulos 2003). Finally, we selected three control locations matched temporally to each tracking location, quasi-randomly, via a spatial Poisson process, with a rate proportional to α for the appropriate month (Fig. 1b). However, as the true relationship between α and d_c was unknown (the null model may over- or under-predict accessibility), following Aarts et al. (2008), we also included d_c as a candidate covariate in the spatial usage models.

Environmental covariates

In a case-control spatial model of the type employed in this study, locations with missing environmental data are effectively treated as inaccessible. Hence, any systematic pattern in the occurrence of missing values results in a spurious null model. In consequence, we were unable to consider remotely-sensed chlorophyll-*a* or conventional sea surface temperature (SST) as candidate environmental covariates because cloud cover causes a systematic reduction in satellite acquisition of these data at high latitudes (Woodward and Gregg 1998). Furthermore, as the first tracking data set was collected in 1994 (Table 1), the only contemporaneous cloud-free SST data set available (NOAA_OI_SST_V2) had a relatively low spatial resolution (1°). Bearing in mind these restrictions, we selected environmental

covariates because, firstly, we had an a priori reason for supposing that they, or a phenomenon for which they are a proxy, would influence albatross spatial usage at our scale of interest (>50 km, months; Austin 2007), and secondly, because their spatial coverage was uniform across our study area. The covariates we considered were: (1) Depth, which we obtained on a 0.1° grid from the GEBCO digital atlas (IOC 2003). We hypothesized that spatial usage varies with bathymetric regime because these regimes are characterized by different levels of productivity (e.g., neritic mesotrophic vs. oceanic oligotrophic waters). (2) Depth slope, which we calculated as the maximum rate of change of depth (resampled on a 10-km Cartesian grid, in polar stereographic projection) between each cell and its neighboring eight cells. We hypothesized that spatial usage varies with slope, ultimately because of the occurrence of productive fronts associated with the steeper slopes and especially with the shelf-break that occurs at the edge of peri-insular and continental shelves. (3) Monthly mean optimally interpolated sea surface temperature (SST), which was supplied on a 1° grid from NOAA/OAR/ESRL PSD, Boulder, Colorado, USA (available online).¹⁰ This data set (NOAA_OI_SST_V2) combines satellite and in-situ observations to provide an estimate of SST in both cloud free and cloud obscured areas (Reynolds et al. 2002). We hypothesized that spatial usage varies with water mass (including macroscale frontal zones) for which SST is a proxy, for two reasons: firstly, because the distribution of prey species may be limited (either directly or indirectly) by temperature and secondly, because productivity varies with water mass. (4) Seven-day mean sea level anomaly (SLA), which can be used to identify mesoscale phenomena such as eddies and meanders, were obtained on a 0.3° Mercator grid, and then averaged by month. We hypothesized that spatial

¹⁰ <http://www.cdc.noaa.gov/>

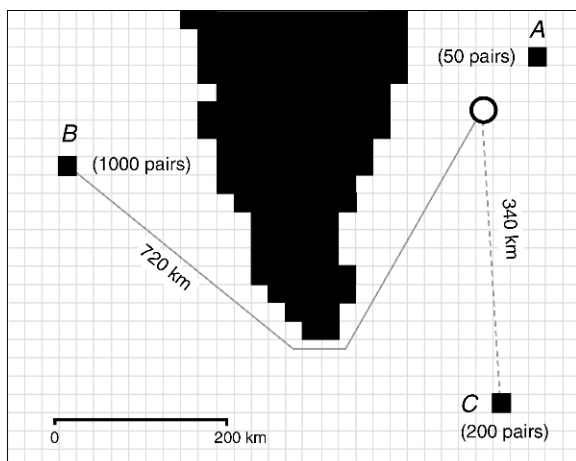


FIG. 3. Calculation of the two indices of parapatric intraspecific competition considered in this study. In this hypothetical example, there are three super-colonies (*A*, *B*, and *C*); the size of breeding populations is shown in parentheses). Black grid squares indicate land, and open squares are sea. Consider a bird from super-colony *A* foraging at the location shown by the open circle. The first index is d_n , the minimum biological distance to the next nearest super-colony, which is colony *C* (distance 340 km, dashed line). This index is a measure of the competition from birds from the nearest neighboring super-colony. The second index ρ is a measure of the total null density of birds from all neighboring super-colonies (see Eq. 4). In this example, $\rho = (1000/720^2) + (200/340^2) = 0.004$ pairs/km² (the distance from colony *A* to colony *B* is 720 km, as shown by the solid line). This index reaches local maxima in the vicinity of neighboring colonies. Note that albatrosses do not routinely cross high land barriers. Hence, the minimum “biological distance” between the albatrosses and colony *B* is 720 km (solid line).

usage may vary with SLA because large SLAs are indicative of warm (+ve) or cold (–ve) mesoscale eddies, which may exhibit higher production than surrounding waters. Such eddies are associated with macroscale fronts and currents. (5) Eddy kinetic energy (EKE) is another index of mesoscale activity, where $EKE = 1/2(u_a^2 + v_a^2)$ and u_a and v_a are the eastward and northward geostrophic current anomalies (Ducet et al. 2000). We obtained seven day mean values of u_a and v_a on a 0.3° Mercator grid, calculated EKE, and then averaged these values by month. Both u_a and v_a and SLA were produced by Ssalto/Duacs and distributed by Aviso, with support from CNES (*available online*).¹¹ We hypothesized that spatial usage may vary with the intensity of mesoscale activity for which EKE is an index because productivity tends to increase with EKE.

Parapatric intraspecific competition

To test hypothesis 4, we calculated two indices of parapatric intraspecific competition (see Fig. 3 for worked examples), which we considered as candidate explanatory covariates of spatial usage: (1) The mini-

mum biological distance to the next nearest super-colony (d_n), assuming that the accessibility of a point in space to parapatric intraspecifics was $\propto 1/d_n$. We calculated d_n for each month and super-colony, in a similar manner to d_c . (2) Relative parapatric conspecific density (ρ_c), assuming that absolute parapatric conspecific density is proportional not only to the distance-squared from the i th super-colony, but also to the size of its breeding population (P_i). Hence, at the j th location,

$$\rho_{cj} = \sum \frac{P_i}{d_{ni,j}^2}. \quad (4)$$

For each super-colony, we calculated grids of d_n for all other super-colonies, and then used estimates of the breeding population at those locations (Appendix A) to calculate ρ_c . These density covariates formalize the notion of opportunity to use a location. Hence, if habitat preferences are captured by all the other covariates in the model, they offer the location in question to one colony or another.

Model fitting and selection

We modeled probability h_i as a function of the covariates outlined above using GAMMs, implemented within the mgcv package (Wood 2004) in R (R Development Core Team 2007). Hypothesis 2 could not be tested directly in a single model, because the mgcv package does not allow GAMMs containing interactions between categorical covariates (breeding stage) and smooths to be specified (Wood 2004). Hence, we fitted a separate model for each breeding stage (incubation were models I and II; chick-rearing, models III and IV). If the covariates retained in these models differed, we concluded that habitat preferences differed between breeding stages. Furthermore, because of the prohibitively large amount of computing time and memory required, it is currently unfeasible to fit GAMMs to very large data sets using desktop computers (Wood 2006). In our case, models could only be fit successfully to be less than ~10 000 tracking and control locations. Given this constraint, we used only every fourth tracking location to model spatial usage.

Habitat preference models fitted to data from one geographic area may perform poorly when applied to another geographical area because of differences in the availability of habitats may lead to behavioral changes (Mysterud and Ims 1998, Boyce et al. 2002). Hence, we tested the ability of global models to explain the spatial usage of individual populations. If the global model (models I and III) explained spatial usage of a population poorly, we also fitted a separate model (models II and IV) for that population. We structured candidate covariates either as parametric variables or smooths of single variables. In order to improve the spread of the data, we double square root-transformed depth slope and log-transformed EKE and ρ_c (Wood 2006). As the shelf-break is often located close to deep-water trenches, our models initially predicted spuriously

¹¹ <http://atoll-motu.aviso.oceanobs.com/>

high spatial usage in distant abyssal areas. To avoid this issue, and with the justification that bathymetric variability does not directly give rise to surface biological variability in these areas, we truncated depth at 4000 m. To allow for plausible, biologically interpretable interactions between terms, we considered tensor product smooths of the following pairs of variables: depth and depth slope, depth and SLA, depth and EKE, SST and EKE, and d_c and d_n . We determined minimum adequate models by forward selection, using K -fold cross-validation, where K is the number of colonies, maximizing the log-likelihood L ,

$$L = \frac{\ln \sum_{i=1}^n h_i^{\hat{u}_{m,i}} (1 - h_i)^{(1 - \hat{u}_{m,i})}}{n} \quad (5)$$

where $\hat{u}_{m,i}$ is the i th observation from the m th colony, and n is the number of locations from that colony (cf. Aarts et al. 2008). We proceeded with model selection as follows: Firstly, we fitted all possible models containing either a single covariate or a single tensor product smooth and ranked them according to L . We next selected the highest ranked model, to which we added each of the remaining terms in turn, retaining the resulting model if L increased. We continued this process until no further increase in L occurred. To reduce the chances of overfitting, we replaced smooths with parametric terms at each stage and, again, retained the resultant model if L increased. As an additional measure against overparameterization, smooths were produced using cubic regression splines with shrinkage, allowing covariates to be penalized out of the model entirely during fitting (Wood 2006).

Estimating spatial usage

Spatial predictions were made using the models' fixed effects. Following Eq. 2, for each super-colony, we calculated the probability density $f_i(\mathbf{X}_s)$ across a regular 0.1° grid centered on each super-colony. We then normalized this to one and multiplied the resulting values by P_i (Appendix A), assuming that during incubation only half the breeding population would be at sea, while during chick-rearing, birds would spend a negligible amount of time at the nest.

RESULTS

Observed spatial distribution and habitat use

We satellite-tracked 109 birds, from eight colonies, and a further 62 birds, from six colonies, during incubation and chick-rearing, respectively (Table 1). During incubation, BBA tended to forage in areas either near or to the north of their colonies, ranging throughout neritic, shelf-break, upper shelf-slope, and, to a lesser extent, adjacent oceanic waters. This included the Chilean coastal waters and the Humboldt Current Upwelling south of 34° S, the Patagonian Shelf south of 40° S, the eastern Bass Strait, and the peri-insular shelves

of South Georgia, Kerguelen, and Macquarie Island (Fig. 4). In addition, birds from northwest South Georgia foraged in the deep oceanic waters of the APFZ and the Brazil Malvinas Confluence during incubation and during both incubation and chick-rearing, birds from the Chilean colonies entered coastal fjords and channels. During chick-rearing, BBA similarly spent the majority of their time in neritic, shelf-break, and upper shelf-slope waters, but tended to have a more southerly distribution, with birds from northwest South Georgia and the Islas Diego Ramirez foraging in ice-free neritic areas around the Antarctic Peninsula and South Orkney Islands. CBA spent the majority of their time on and at the margins of the Campbell Plateau, especially in the vicinity of the Subantarctic Front, but they also ranged widely in oceanic waters between 37° S and 68° S, especially in the APFZ. Segregation of BBA foraging areas occurred at two scales. At the super-colony level, birds from the south and northwest Falkland Islands tended to be absent from the immediate vicinity of the neighboring super-colony, especially during chick-rearing (Fig. 4). In contrast, the foraging zones utilized by BBA from adjacent Chilean colonies overlapped considerably. At the regional scale, birds from Chile, the Falkland Islands, and South Georgia foraged in mutually exclusive areas. There was no correlation between foraging area, as defined by the size of the 75% kernel density contour (Table 1), and colony size (incubation $r^2 = 0.17$, $F_{1,6} < 0.01$, $P = 0.98$; chick-rearing $r^2 = -0.02$, $F_{1,6} = 0.92$, $P = 0.39$).

Spatial usage decreased with d_c , the rate of decrease being greater during chick-rearing than incubation (Fig. 5). During incubation, albatrosses made long trips, with a median duration of 8.3 days (range 0.9–24.2 d), reaching a median maximum d_c of 987 km (20–3039 km). Birds from some populations (e.g., northwest South Georgia and Macquarie Island) visited one or more discrete, distant areas, giving rise to multimodal distributions of d_c , whereas the spatial usage of birds from the Falkland Islands tended to decline more uniformly with d_c . Large areas of oceanic waters were accessible to all populations, but the amount of accessible neritic and upper shelf-slope waters (<1000 m deep) differed (Fig. 6a, Table 1), being greatest for the population at the Falkland Islands, and least for that at Macquarie. Typically, foraging BBA spent a disproportionately large amount of time in neritic waters, compared to the amount of such habitat available. The exception was birds from northwest South Georgia, which, during incubation, spent more time in the deep (more than ~ 4500 m) oceanic waters of the Brazil-Malvinas Confluence. During chick-rearing, BBA made shorter trips (median 2.0 d, range 0.4–23.8 d), closer to their colonies (median maximum d_c 298, range 10–2949 km). Birds from the Falklands and southeast Kerguelen remained in neritic and slope waters, adjacent to their colonies ($d_c < \sim 1000$ km), and those from Islas Diego Ramirez and northwest South Georgia also traveled to

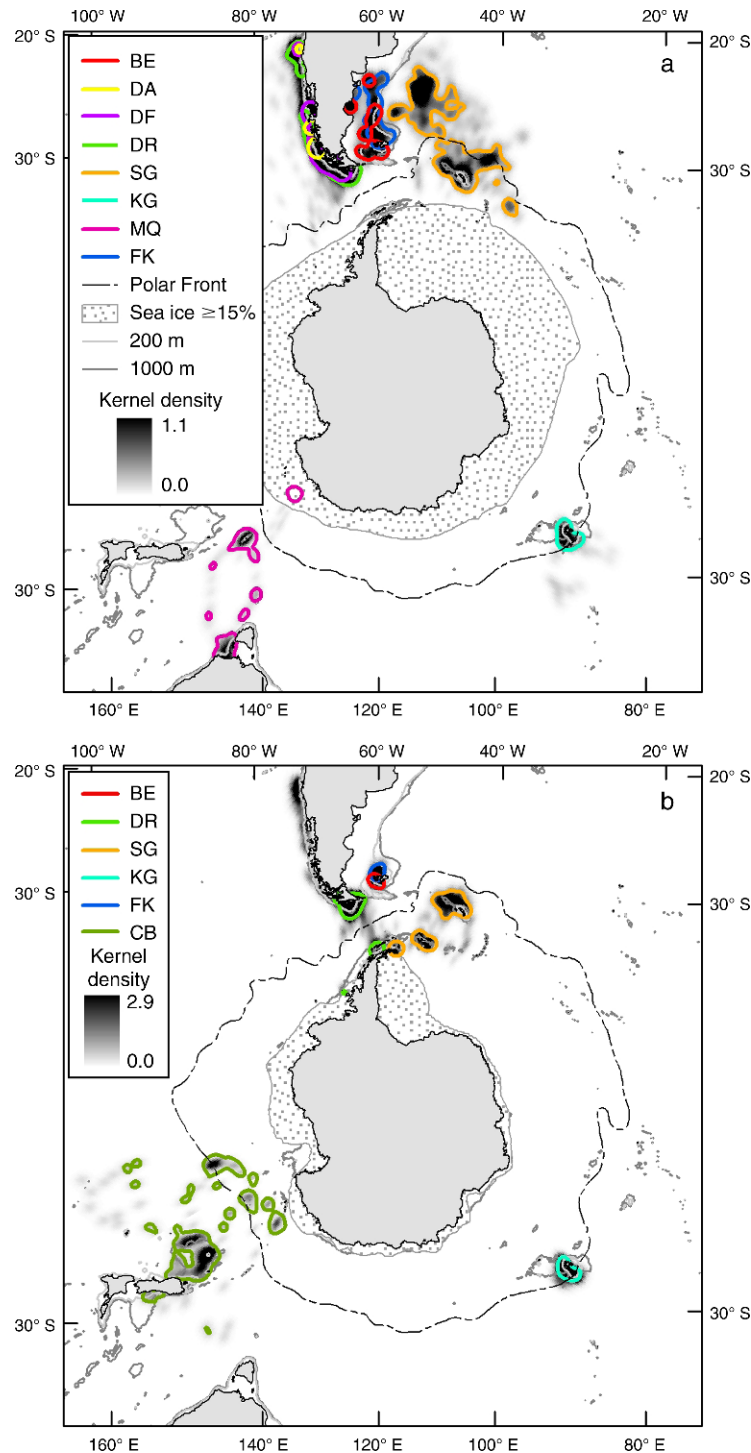


FIG. 4. Kernel density of Black-browed and Campbell Albatross satellite-tracking locations recorded during (a) incubation ($n = 109$), and (b) post-brood chick-rearing ($n = 62$). Colored lines represent 75% kernel density contours for each population tracked: BE, south Falklands; DA, Isla Diego de Almagro; DF, Isla Ildefonso; DR, Isla Diego Ramirez; SG, northwest South Georgia; KG, southeast Kerguelen; MQ, Macquarie Island; FK, northwest Falklands; and CB, Campbell Island). Kernel density was estimated following Phillips et al. (2005) with a cell size of 20 km and a search radius of 100 km. Mean location of the Antarctic Polar Front is after Moore et al. (1999); mean sea ice extent ($\geq 15\%$ cover) is shown for November and February; 200 m and 1000 m depth contours are from the GEBCO digital atlas (IOC 2003).

distant oceanic, neritic, shelf-break, and shelf-slope areas.

The availability of different bathymetric slope habitats was very similar between colonies (Fig. 3b). During both incubation and chick-rearing, birds from the northwest Falklands spent most time in areas of shallow slopes ($\sim 0.1^\circ$), typical of the continental shelf, whereas birds from other populations utilized both shallow ($\sim 0.3^\circ$) and, in some cases, steep ($\sim 4^\circ$) slopes, the latter typically around the shelf-break. The SST regime in accessible waters depended on whether colonies were either south (southeast Kerguelen and northwest South Georgia), or north of the Polar Front (all other colonies; Fig. 6c). During incubation, birds from the latter group spent the majority of time in waters with SSTs of 5–15°C, which in oceanic areas are classified as subtropical (Mann and Lazier 2006). Birds from the southerly colonies also foraged in warm water areas, but spent some (southeast Kerguelen) or much (northwest South Georgia) time in polar ($< 5^\circ\text{C}$) waters. During chick-rearing, BBA foraged in waters with a more restricted range of SSTs. All populations, with the exception of those from the Falklands, spent some time in oceanic areas with high mesoscale turbulence (and therefore variability in SLA), including the APFZ (SST $\sim 5^\circ\text{C}$). However, only BBA from northwest South Georgia and CBA exploited these areas extensively, so EKE values at tracking locations were generally low (Fig. 3d, h).

Model selection and validation

During the preliminary stages of model selection we fitted 13 models, each containing only one explanatory covariate (d_c , depth, depth slope, EKE, SLA, SST, d_n , and p_c) or tensor product smooth (see *Methods* for combinations considered). Log-likelihood values indicated that the model containing depth best described both the incubation and chick-rearing data. Including further covariates, the most parsimonious model fitted to data from incubation (model I) contained four covariates, with no interactions: depth, d_c , SST, and depth slope (Table 2, Fig. 7a). With the addition of further covariates, population specific variations in L indicated that the habitat preferences of the northwest South Georgia population differed from all others (Fig. 7a). A second model (II), fitted to incubation data from this population alone, included an additional covariate, EKE. The minimum adequate model fitted to the chick-rearing data (III) had four covariates, with no interactions: depth, d_c , d_n , and depth slope (Fig. 6b). The habitat preferences of CBA differed from those of BBA (Fig. 7b). A separate model (IV), fitted to the CBA data included the covariates depth, d_c , d_n , and SLA. All terms retained in all models were highly significant ($P \leq 0.001$), except SLA in model IV ($P = 0.002$). Spatial predictions show that both global models (I and III) performed well, reproducing most of the large-scale features of observed spatial usage (cf. Figs. 4 and 8). For example, predicted usage decreased with d_c around the

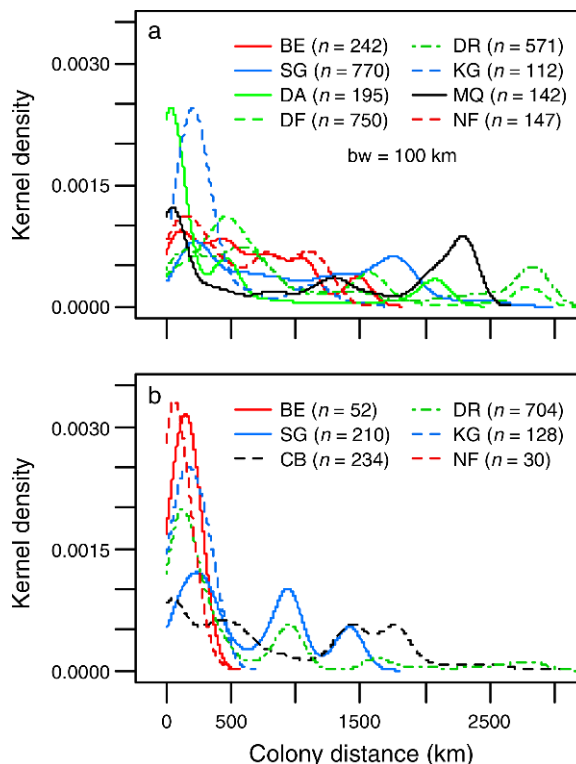


FIG. 5. Kernel density of colony distance (d_c) to Black-browed and Campbell Albatross satellite-tracking locations recorded during (a) incubation ($n = 109$) and (b) post-brood ($n = 62$), from the south Falklands (BE), Isla Diego de Almagro (DA), Islas Ildefonso (DF), Islas Diego Ramirez (DR), northwest South Georgia (SG), southeast Kerguelen (KG); Macquarie Island (MQ), the northwest Falklands (FK), and Campbell Island (CB). The n values in parentheses represent the number of locations; bw is bandwidth.

study colonies, was greatest in neritic, shelf-break, and shelf-slope waters, and became more southerly during the chick-rearing stage. However, model I under-predicted spatial usage in the Humboldt Upwelling region and Chilean coastal waters between $\sim 36^\circ\text{S}$ and 42°S and in the Brazil-Malvinas Confluence, and over-predicted it on the northern Patagonian Shelf between $\sim 38^\circ\text{S}$ and 42°S , in subtropical waters to the north of Kerguelen and on the eastern side of the Campbell Plateau. Model II reproduced the spatial usage of birds from South Georgia more satisfactorily, predicting high usage in both peri-insular shelf waters and the Brazil-Malvinas Confluence (Appendix B). Model III (global chick-rearing), captured the shift to foraging in more southerly waters, especially around the Antarctic Peninsula, and the partial spatial segregation of birds from neighboring populations. However, it under-predicted usage on the central Chilean coast and Humboldt Upwelling (at $36\text{--}46^\circ\text{S}$) and over-predicted it on the Patagonian Shelf in areas distant from the Falklands. Model III did not predict the oceanic spatial usage of CBA as well as model IV (not illustrated).

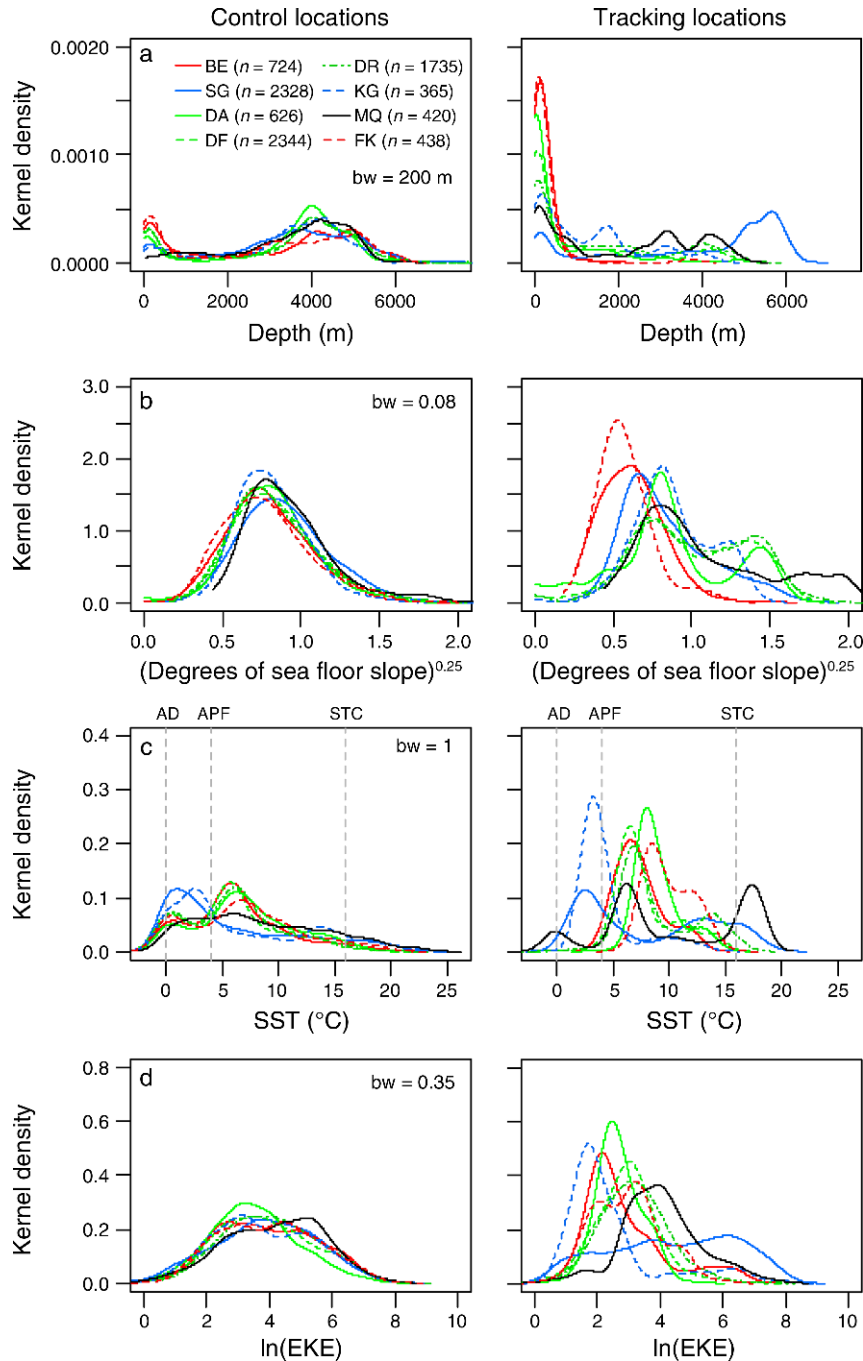


FIG. 6. Kernel density of environmental covariates at Black-browed and Campbell Albatross control locations and satellite-tracking locations during (a–d) incubation and (e–h) post-brood chick-rearing. Birds were tracked from the south Falklands (BE), Isla Diego de Almagro (DA), Islas Ildefonso (DF), Islas Diego Ramirez (DR), northwest South Georgia (SG), southeast Kerguelen (KG); Macquarie Island (MQ), the northwest Falklands (FK), and Campbell Island (CB). Approximate summertime values of sea surface temperature (SST) are marked for the Antarctic Divergence (AD), Antarctic Polar Front (APF), and the Subtropical Convergence (STC). Other abbreviations are: EKE, eddy kinetic energy (originally measured in cm^2/s^2); n , number of control locations (number of tracking locations = $n/3$); and bw, bandwidth used during kernel estimation.

Habitat preference

All covariates included in the two global spatial usage models (I and III) were retained as smooths, except

colony distance, d_c , which was retained as a linear term (Fig. 9). In both cases, d_c had a negative slope, implying that, counter to hypothesis 1, spatial usage decreases at a greater rate than $1/d_c$. On the scale of the linear

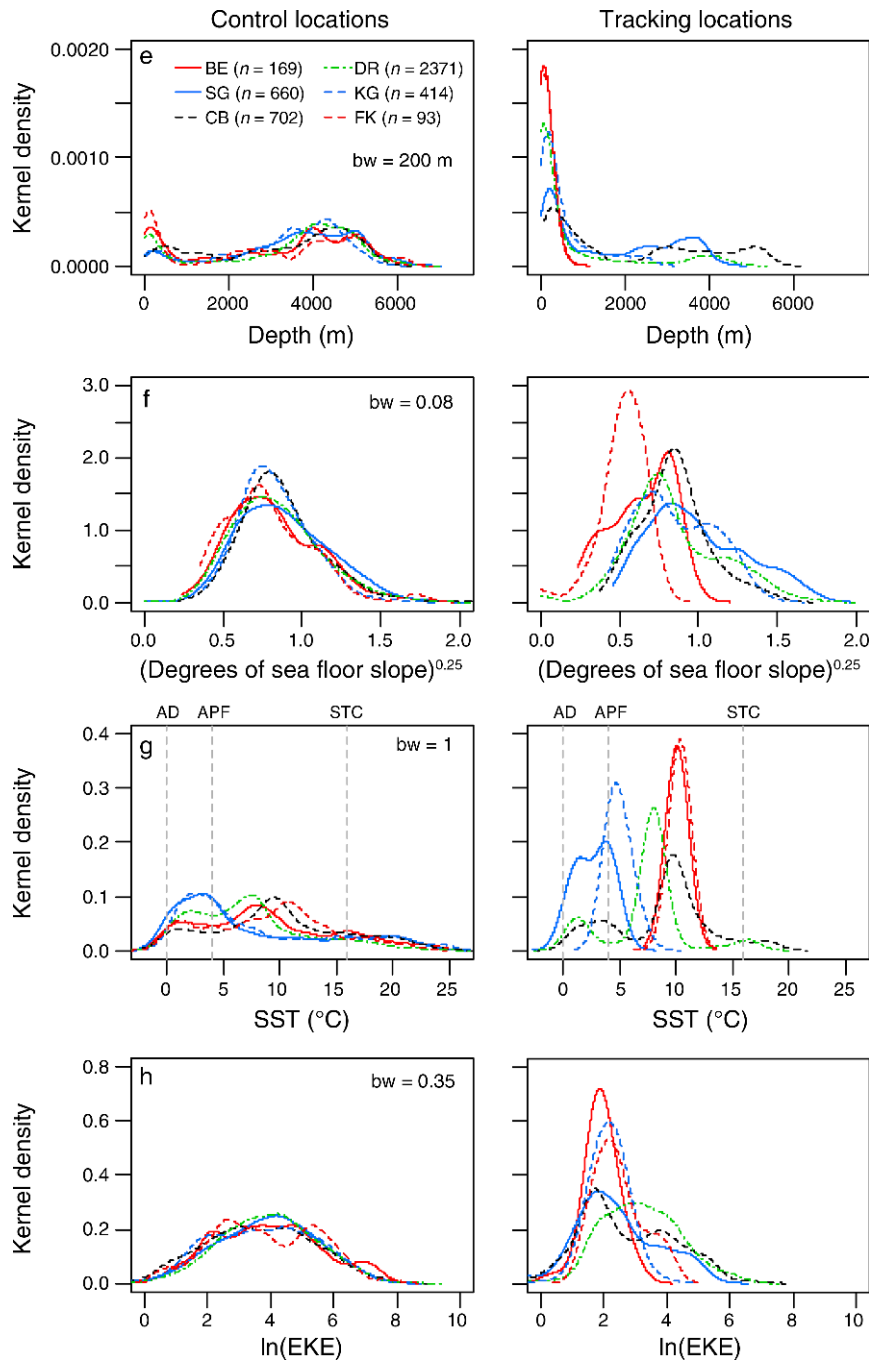


FIG. 6. Continued.

predictor, the gradient of d_c vs. the response was greater for model III ($-2.07 \times 10^{-3} \pm 0.25 \times 10^{-3}$; mean \pm SE) than model I ($-1.61 \times 10^{-3} \pm 0.14 \times 10^{-3}$), confirming that spatial usage declined more sharply with d_c during chick-rearing than incubation. Model I shows that during the latter stage, BBA habitat preference peaks in shallow, neritic habitats. Habitat preference decreases with depth to ~ 500 m (encompassing South American

continental and most peri-insular shelf waters), is similar from ~ 500 – 1600 m (further encompassing deeper peri-insular waters, such as those around Kerguelen) and decreases thereafter. Furthermore, habitat preference was highest for steeper ($>3^\circ$) sea floor slopes and decreased for slopes shallower than this value. Habitat preference with respect to SST peaked at $\sim 16^\circ\text{C}$, this temperature being indicative in oceanic areas of the

TABLE 2. Summary of covariates retained in the most parsimonious models of spatial usage of Black-browed and Campbell Albatrosses.

| Model | Stage | Population | Covariates retained | | | | | | |
|-------|---------------|------------------|---------------------|-------|-------|-----|-----|-----|-------|
| | | | d_c | Depth | Slope | SST | EKE | SLA | d_n |
| I | incubation | all | x | x | x | x | | | |
| II | incubation | NW South Georgia | x | x | x | x | x | | |
| III | chick-rearing | all | x | x | x | | | | x |
| IV | chick-rearing | Campbell Island | x | x | | | | x | x |

Notes: Abbreviations are: d_c , the minimum biological distance to the super-colony, assuming that albatrosses do not cross extensive land barriers or sea ice; SST, sea surface temperature; EKE, eddy kinetic energy; SLA, sea level anomaly; and d_n , the minimum biological distance to the next nearest super-colony, which is a proxy for parapatric intra-specific competition.

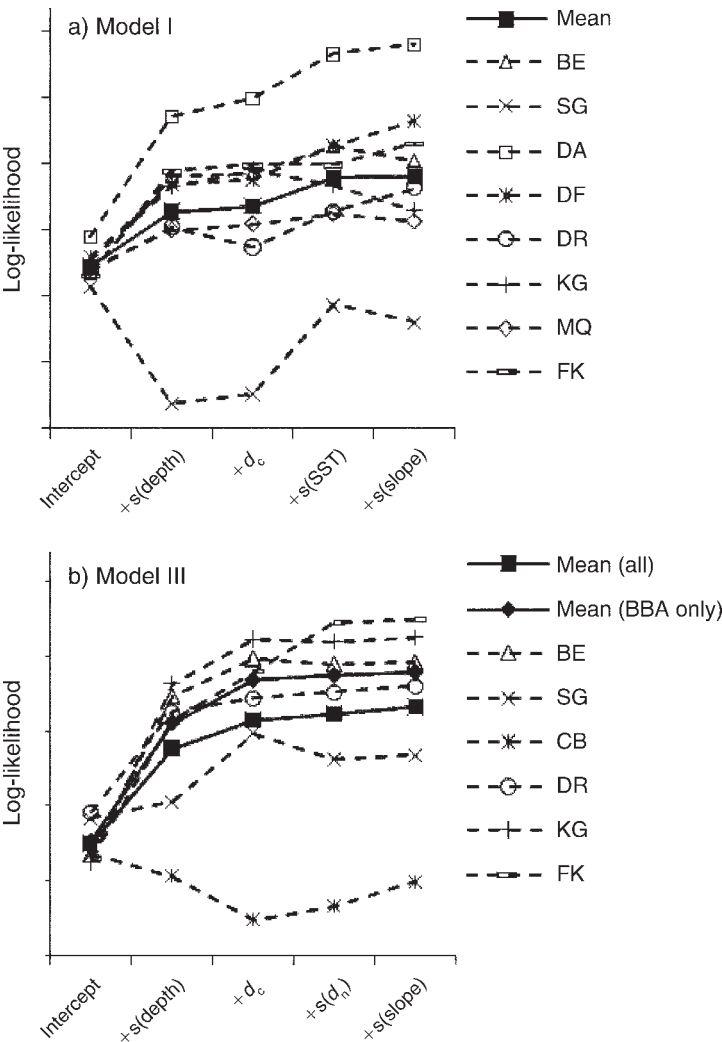


FIG. 7. Results of model selection using K -fold cross-validation where the test data set comprised data from one super-colony (either BE, south Falklands; DA, Isla Diego de Almagro; DF, Islas Ildefonso; DR, Islas Diego Ramirez; SG, northwest South Georgia; KG, southeast Kerguelen; MQ, Macquarie Island; FK, northwest Falklands; or CB, Campbell Island) and the training data sets were data from all remaining colonies. The log-likelihood indicates how well a model fitted to the training data set predicted the test data. Models were selected such that log-likelihood was maximized. (a) Model I, fitted to data from Black-browed Albatrosses tracked during incubation. The solid line indicates the mean log-likelihood for all populations tracked during this stage. (b) Model III fitted to data from Black-browed and Campbell Albatrosses tracked during post-brood chick-rearing. In this instance the solid lines indicate the mean log-likelihood either for all populations tracked or for Black-browed Albatross (BBA) populations only. Covariates smoothed using cubic regression splines are represented by $s()$ (Wood 2006). See Table 2 for explanation of abbreviations.

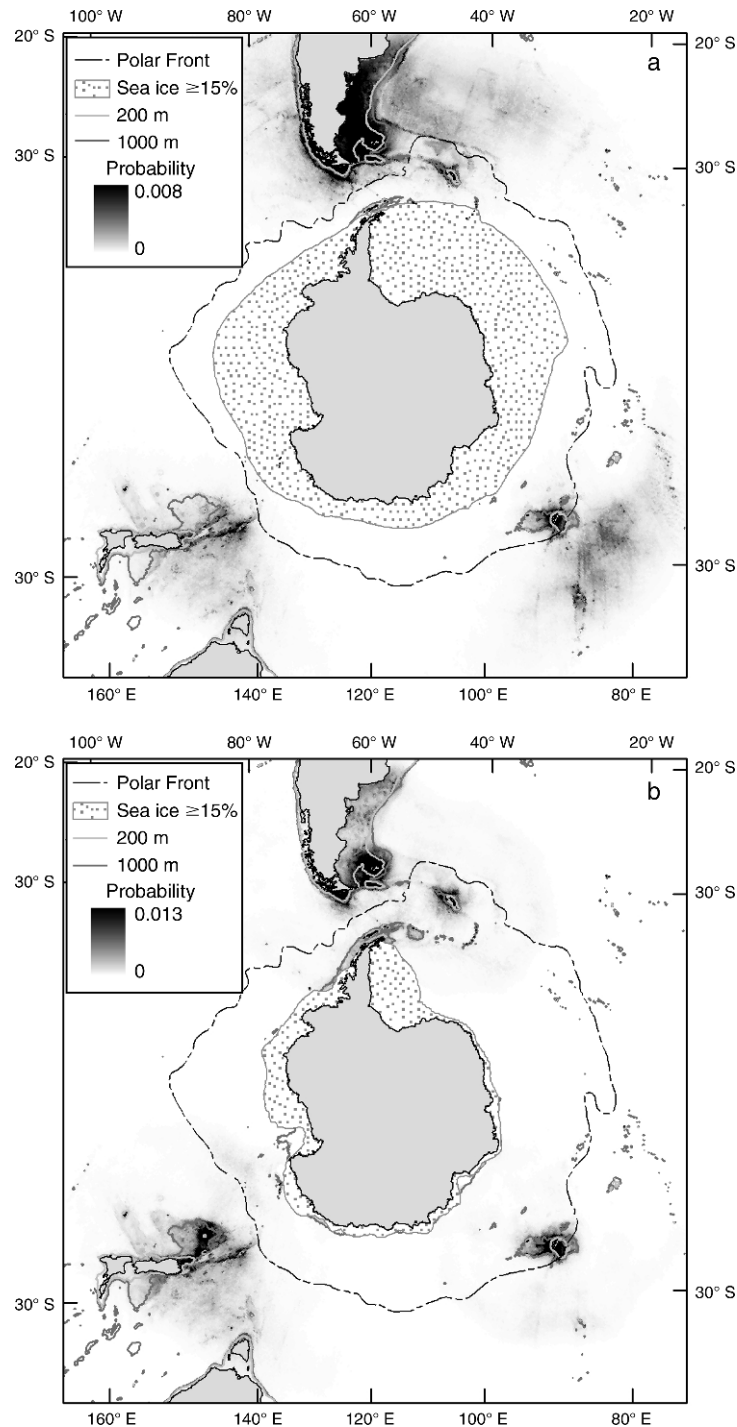


FIG. 8. Probability of the presence of satellite-tracked Black-browed Albatrosses predicted using the fixed-effects part of (a) model I, fitted to all data from incubation, and (b) model III, fitted to all data from post-brood chick-rearing. Mean sea ice extent ($\geq 15\%$ cover) is shown for November and February; 200 m and 1000 m depth contours are from the GEBCO digital atlas (IOC 2003).

Subtropical Convergence Zone (STCZ). Above and below this value, it decreases, but was constant from $\sim 3\text{--}5^\circ\text{C}$ (i.e., in the southern part of the APFZ). Model II indicated that the habitat preference of birds from northwest South Georgia were similar to the global

mean, but also showed an increase in habitat preference with EKE above values of $\sim 250\text{ cm}^2/\text{s}^2$ (Fig. 10a, Appendix C: Fig. C1a). Although there was no variation in habitat preference with SST for chick-rearing birds, model III shows their depth and depth slope preferences

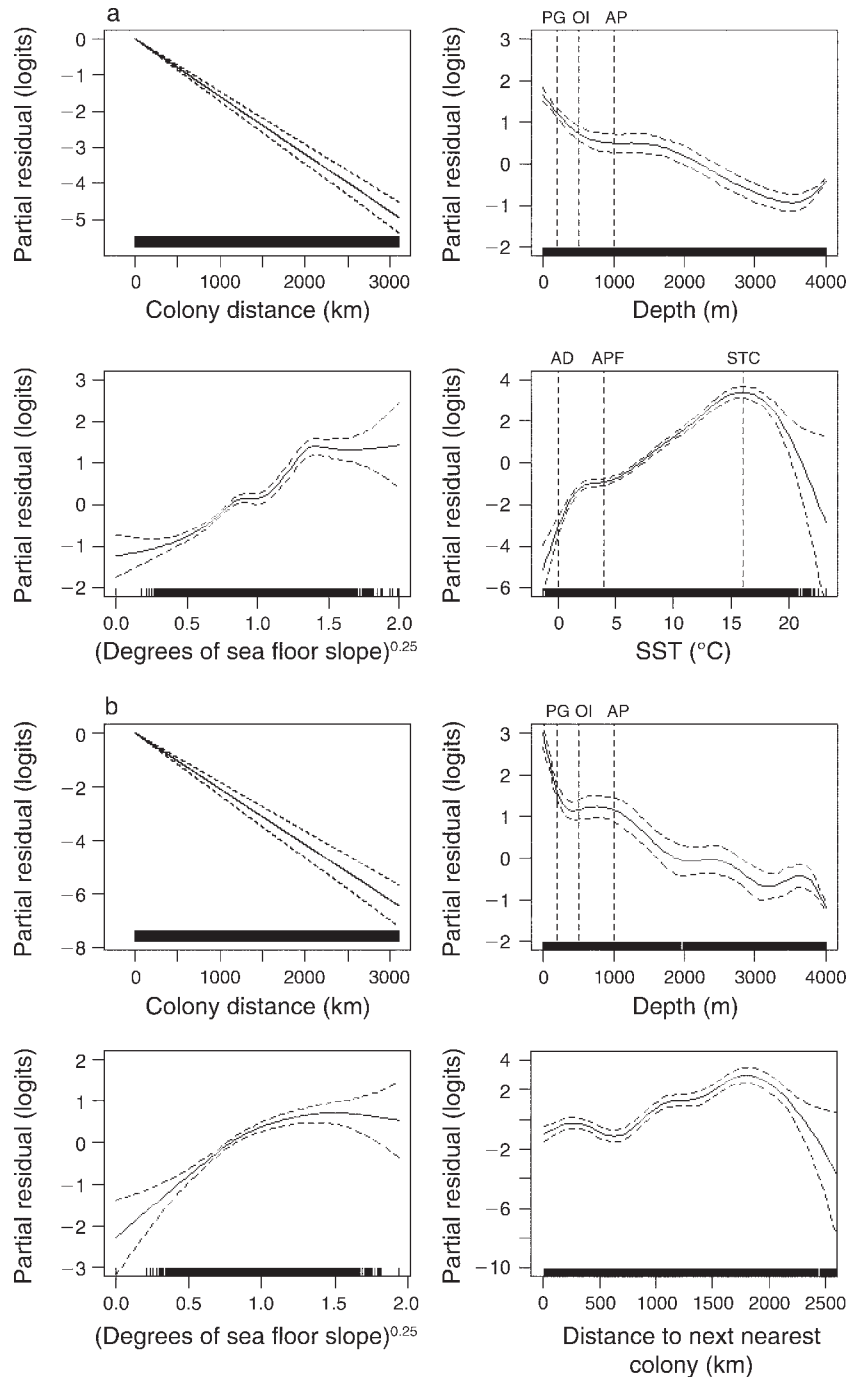


FIG. 9. Fixed-effects covariates retained in models fitted to all spatial usage data collected during (a) incubation (model I) and (b) post-brood chick-rearing (model III). The y-axes show the partial residuals once the effects of all other covariates have been removed (i.e., the contribution to η in logits; Eq. 3). Hence, the plots can be interpreted as showing relative population-level habitat preferences (Aarts et al. 2008). Dashed lines indicate estimated 95% CIs. The approximate depth of the shelf-break bounding Patagonia (PG), oceanic island colonies (OI), and the Antarctic Peninsula (AP), as well as the approximate summertime sea surface temperature (SST) of the Antarctic Divergence (AD), Antarctic Polar Front (APF), and Subtropical Convergence (STC) are shown.

were very similar to those of incubation stage birds (Fig. 9b). Model IV indicated that habitat preference with respect to depth also peaks in shallow habitats for chick-rearing CBA, but depth was most parsimoniously

structured as a linear covariate in this model (Appendix C: Fig. C1b). CBA habitat preference also exhibited a weak increase with positive SLAs, peaking at ~ 9 cm (Fig. 10b, Appendix C: Fig. C1b).

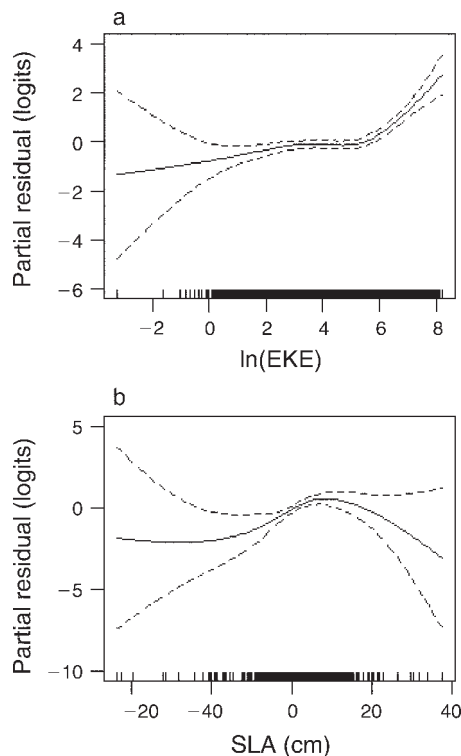


FIG. 10. Selected fixed-effects covariates retained in models of spatial usage fitted to data from (a) Black-browed Albatrosses tracked from northwest South Georgia during incubation (model II) and (b) Campbell albatrosses tracked during post-brood chick-rearing (model IV). The y -axes show the partial residuals once the effects of all other covariates have been removed (i.e., the contribution to η in logits; Eq. 3). Hence, the plots can be interpreted as showing relative population-level habitat preferences (Aarts et al. 2008). Dashed lines indicate estimated 95% CIs; EKE is eddy kinetic energy; and SLA is sea level anomaly. For remaining covariates see Appendix C.

Parapatric intraspecific density (ρ_c) was not retained in any model. However, the minimum biological distance to the next nearest super-colony (d_n), was retained in model III, indicating that during chick-rearing, BBA habitat preference increases with d_n up to ~ 250 km from the nearest colony, decreases again to a minima at ~ 700 km, before increasing again to a maximum at ~ 1800 km (Fig. 6b).

Estimated usage

Monthly plots of predicted mean spatial usage show that the majority of the world's breeding BBA are confined to the southwest Atlantic, southern Chilean coastal waters, and the Humboldt Current (Fig. 11). During incubation, they are predicted to range from $\sim 31^\circ$ S to 60° S, whereas during chick-rearing their range extends southward, to 75° S on the Antarctic Peninsula. During incubation, estimated densities are highest (maximum 15 birds/km²) in waters deeper than 1500 m on the Patagonian Shelf, south of the Rio de la

Plata (36° S), and around Cape Horn, the Chilean coast, and Humboldt Current Upwelling south of Chiloe Island (42° S). Smaller areas of high density are predicted in the Brazil-Malvinas Confluence ($\sim 42^\circ$ S, 053° W), the APFZ to the north of South Georgia, and on the South Georgia peri-insular shelf. Birds are predicted to occur at lower densities in oceanic waters bounding these areas, especially in the APFZ and STCZ in the southwest Atlantic. During chick-rearing, the maximum predicted density is higher (73 birds/km²), with birds concentrated in the same neritic areas as

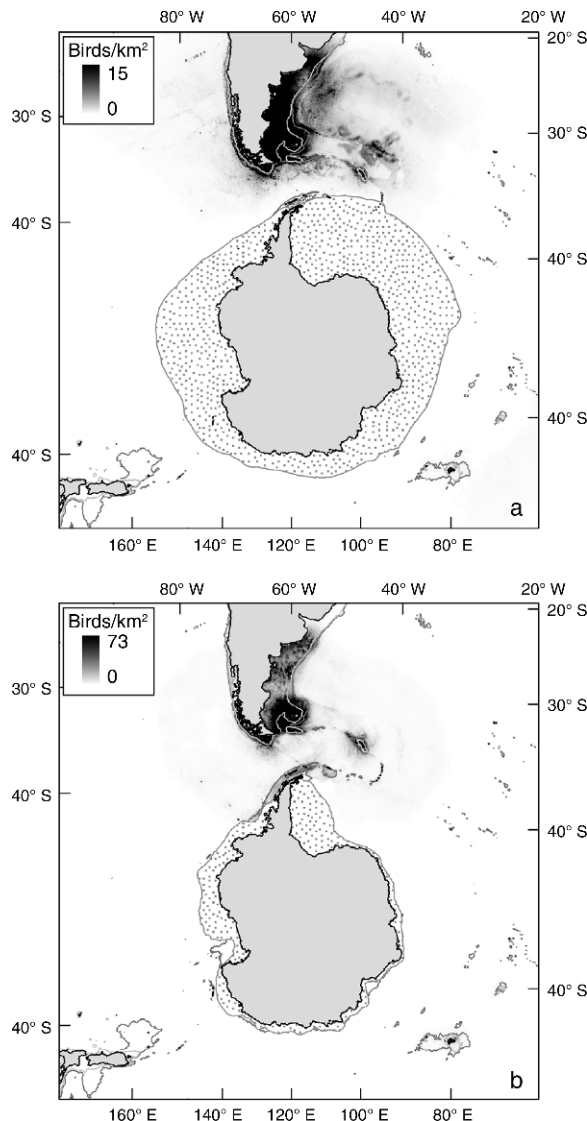


FIG. 11. Estimated worldwide distribution (birds/km²) of breeding Black-browed Albatrosses during (a) incubation (November 2000) and (b) post-brood chick-rearing (February 2001). Predictions were made using model II for incubation-stage South Georgia birds, model I for all other incubation-stage populations, and model III for all post-brood chick-rearing populations. The 200-m and 1000-m depth contours are from the GEBCO digital atlas (IOC 2003).

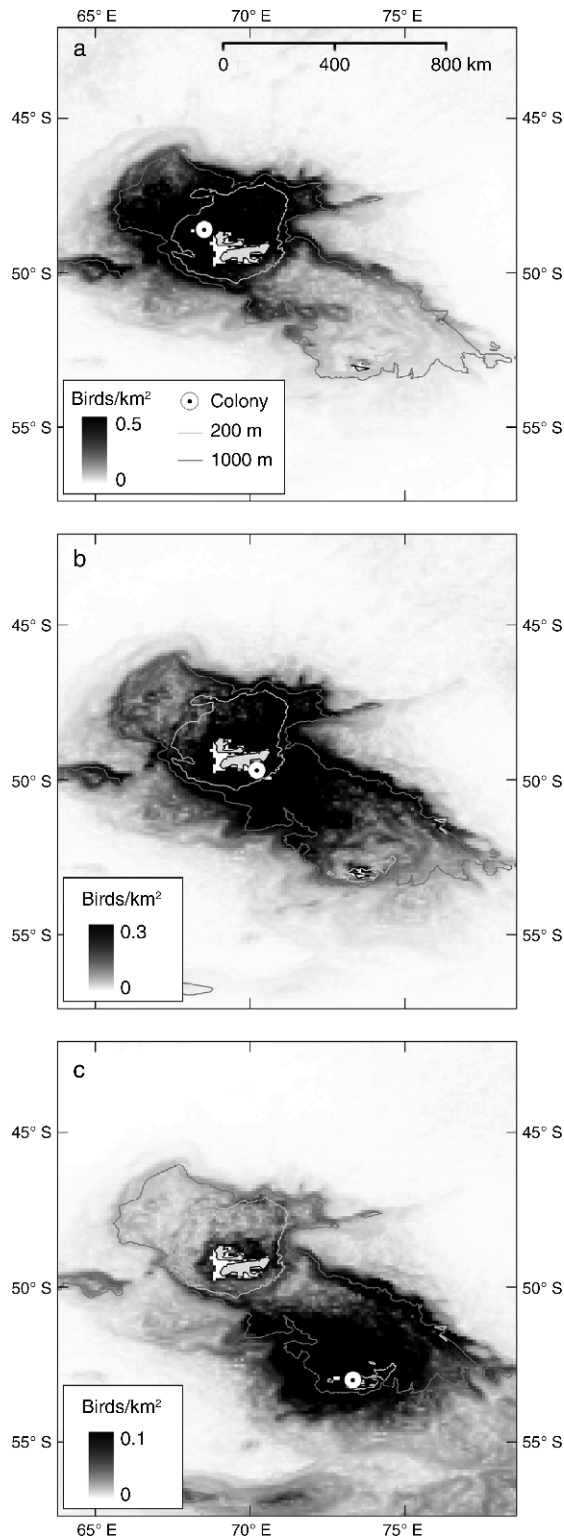


FIG. 12. Estimated distribution (birds/km²) of post-brood chick-rearing Black-browed Albatrosses from the Kerguelen Archipelago showing the partially overlapping areas used by birds from adjacent super-colonies. Predicted distributions are shown for birds from (a) northwest Kerguelen, (b) southeast Kerguelen, and (c) Heard and MacDonal Islands. Densities

during incubation, but at lower densities in oceanic areas. The ice-free, neritic waters of the western Antarctic Peninsula and the South Orkney islands are also expected to hold large numbers of BBA during chick-rearing. During both stages, BBA are also predicted to occur at relatively low densities in neritic waters close to breeding colonies in the southern Indian and Pacific Oceans. Plots of the estimated spatial usage for the post-brood chick-rearing period show the predicted effects of intraspecific competition: namely, that the degree of overlap between the foraging areas predicted for populations from adjacent colonies is smaller than would be expected if such competition were not influential (Fig. 12).

DISCUSSION

Model performance and limitations

We used a combination of satellite-tracking, bathymetric, and remotely-sensed oceanographic data to model the spatial usage of breeding Black-browed Albatrosses as a function of habitat preference and parapatric intraspecific competition, controlling for the effects of unequal habitat accessibility caused by the central-place constraint. In so doing, we were able to quantitatively estimate, with unprecedented accuracy, the worldwide distribution at sea of an abundant, wide-ranging, pelagic seabird. Our models performed satisfactorily, as shown by the high congruity between predicted spatial usage by BBA from Heard Island during chick-rearing, and recently published satellite-tracking data that were not available for our analysis (cf. Fig. 2 in Lawton et al. [2008] with Fig. 12c in this paper). The ability to use individual movement and environmental data to estimate the population-level distribution of wide-ranging marine predators represents a considerable advance (Aarts et al. 2008). In the past, distribution has been inferred directly from plots of tracks, tracking locations, or the kernel density of these locations (e.g., Prince et al. 1998, Wood et al. 2000, BirdLife International 2004). Such methods result in representations of distribution heavily biased by the spatial usage of the individuals tracked, and may be poorly representative of population as a whole (cf. Fig. 3.2 in BirdLife International [2004] with Fig. 10 in this paper). Nonetheless, there were some apparent limitations to the predictive capacity of our models. For example, spatial usage on the northern Patagonian Shelf was over-predicted, and that on the coast of central Chile was under-predicted. This result, and a small amount of residual spatial autocorrelation evident in model I, suggests that an important covariate may not have been considered in our analysis (Aarts et al. 2008).

← were predicted using model III, which includes the effects of parapatric intraspecific competition. Depth contours (200 m and 1000 m) are from the GEBCO digital atlas (IOC 2003).

We accounted for the effects of unequal habitat accessibility and intraspecific competition in our models, and then assumed that within tolerable limits the remaining variability in spatial usage was the result of habitat selection. In reality, a number of other factors may also have affected spatial usage. For example, contrary to the assumptions of the ideal free distribution (Fretwell and Lukas 1970), albatrosses may have an incomplete knowledge of the distribution of habitat patches accessible to them (Kennedy and Gray 1993). Hence, poor-quality habitat patches may have been used while birds were searching for more suitable foraging areas (Fauchald 1999, Pinaud and Weimerskirch 2005). At small scales this can lead to a mismatch between the distributions of high-quality habitat and foraging albatrosses (Kennedy and Gray 1993). Furthermore, commuting birds may use poor-quality habitats incidentally or they may remain faithful to foraging areas, despite the fact that habitat quality varies over time in those areas (Gremillet et al. 2008). Such factors would reduce the accuracy of our estimates of habitat preference and our models' predictive performance at small spatial scales, but would be less likely to compromise our large-scale predictions, because at these scales pelagic seabirds are thought to rely on predictably distributed resources (reviewed by Weimerskirch 2007). Future studies should aim to quantify such behavioral effects and so produce more accurate estimates of albatross habitat preferences and distributions (Wakefield et al. 2009a). In addition, the results of spatial models could usefully be complimented by demographic approaches to quantifying habitat quality (Pulliam 2000, Johnson 2007).

The spatiotemporal resolution of our models was also limited by that of the environmental data used (minimum of 33 km, 1 month), but was sufficient to detect responses to mesoscale phenomena such as eddies and meanders. However, because the SST data set we used (NOAA_OI_SST_V2) had a relatively low spatial resolution (1°), we were only able to detect responses to water masses at large scales (>100 km). More recent studies would be able to exploit SST data with higher spatial (25 km) and temporal (daily) resolution to examine interactions with oceanic frontal systems, such as the Antarctic Polar Front (Boehme et al. 2008). In addition, GPS loggers (which can be accurate to <10 m) are now readily available, and enable more detailed investigations of factors limiting spatial usage at the submesoscale level (Awkerman et al. 2005). Such data might have improved our capacity to model the hot spots of spatial usage in central Chilean coastal waters, which we suspect occur in response to high levels of primary production associated with the Humboldt Current Upwelling (Longhurst 1998). A higher resolution spatial model, fitted at regional or colony level, could also resolve the response of BBA to topographically constrained fronts on the Patagonian Shelf (Acha et al. 2004), and spatial usage in the complex channels of

the Chilean fjords. In addition, our models could be extended to consider time-lagged biological responses to physical processes, such as phytoplankton blooms induced by mixing or ice recession (Ainley et al. 1993, Hunt et al. 1999, Gremillet et al. 2008). Furthermore, the inclusion of individual characteristics (sex, age, experience, quality, and so forth) would have been an appropriate refinement (Aarts et al. 2008), particularly as male and female BBA from at least one population exhibit different spatial usage patterns (Phillips et al. 2004). However, such characteristics were not known for the majority of birds tracked. Finally, anthropogenic activities (i.e., fishing) may affect spatial usage of BBA in relation to the physical environment (Thompson 1992, Waugh et al. 2005).

Accessibility

Our data support hypothesis 1 that the spatial usage of breeding BBA and CBA decreases with distance from the colony d_c . Hence, this aspect of their behavior is as predicted by central-place foraging theory (Orians and Pearson 1979) and is similar to that of some but not all central-place foragers examined so far (e.g., Adler and Gordon 2003, Olsson et al. 2008, Osborne et al. 2008). Although other studies of pelagic seabird habitat use have acknowledged the importance of central-place constraints, few have explicitly considered accessibility in their analyses, which is clearly an important omission (Pinaud and Weimerskirch 2005, Louzao et al. 2006). In our approach, we assumed a null model in which spatial usage in the absence of other factors was proportional to accessibility α (i.e., the central-place constraint was built into the model by generating pseudo-absence [control] locations at a rate proportional to $1/d_c$). However, in addition colony distance (d_c) was also retained in our most parsimonious models as an explanatory covariate, indicating that in reality α declines at a greater rate than $1/d_c$. This tendency has also been observed in some other colonial breeders (Matthiopoulos 2003, Nemeth et al. 2005, Aarts et al. 2008) and suggests that further refinement could be made in the null usage model. This could be achieved by firstly determining whether energetic (intrinsic) or time (extrinsic) costs ultimately limit α (Ydenberg et al. 1994, Hedenström and Ålerstam 1995). During incubation, the time available for foraging trips is determined by the partner's ability to fast on the nest, whereas during chick-rearing, it is the endurance of the chick that is limiting (Shaffer et al. 2003, Humphreys et al. 2006). In order to fledge successfully, a chick requires a high rate of energy delivery; hence, its parent returns much more frequently than during incubation. The rate of decline in α with d_c is greater during chick-rearing than incubation, suggesting that extrinsic factors limit α ; a conclusion further supported by the low energetic cost of flight in albatrosses (Bevan et al. 1995, Arnould et al. 1996). Secondly, both the temporal and energetic costs of albatross flight also vary with relative wind speed

(Weimerskirch et al. 2000, Wakefield et al. 2009b). As wind field is a highly dynamic variable, its relationship to α is potentially complex. However, could this relationship be modeled, it would further refine models of spatial usage (Felicísimo et al. 2008, Wakefield et al. 2009b). Finally, α alters dramatically in polar regions due to seasonal changes in the extent of sea ice. Although we allowed this to restrict accessibility on a monthly time scale, sea ice cover may change more rapidly (Heil and Allison 1999), and therefore a higher temporal resolution might improve model fit.

Black-browed Albatross habitat preferences

Previous studies have described habitat use of breeding BBA (Weimerskirch et al. 1997, Gremillet et al. 2000, Wood et al. 2000, Huin 2002, Pinaud and Weimerskirch 2002, 2007, Phillips et al. 2004, Terauds et al. 2006b) and CBA (Waugh et al. 1999), but this is the first study to quantify and compare their habitat preferences. By accounting for the effects of unequal habitat accessibility comparing habitat use with availability (Manly et al. 2002), our study confirms that, in all populations, habitat preference decreases with depth; birds use neritic habitats (0–500 m) more frequently than would be expected by chance alone, followed by shelf-break and shelf-slope (500–1000 m), and then oceanic habitats (>1000 m). Habitat preference also increases with sea floor slope, to a maximum of $\sim 3^\circ$. Although such slopes are typical of the shelf-break, the interaction between depth and depth slope was not retained in our models, indicating that areas with steeper relief are used more frequently, regardless of depth. Comparison of spatial usage collected over multiple breeding seasons suggests that this preference varies little between years (Prince et al. 1998, Wood et al. 2000, Pinaud and Weimerskirch 2002, Phillips et al. 2004).

Primary production in neritic and shelf-break waters is often strongly seasonal, peaking in spring, summer, and autumn, when albatrosses are breeding. Hence, aggregations of prey occur predictably at large temporal and spatial scales (months, hundreds of kilometers) in the neritic waters accessible to BBA (e.g., Murphy et al. 1997, Waluda et al. 2001, Murphy et al. 2007, Duhamel and Hauteceur 2009). Furthermore, prey aggregate predictably at smaller scales (days, tens of kilometers) due to the presence of tidal and shelf-break fronts. As these and other shallow water processes are topographically constrained, they occur at similar depths in different regions (Lefevre 1986, Acha et al. 2004). Consequently, physical forcing may explain why bathymetric habitat preferences are similar for birds from widely separated colonies, despite considerable variation in the depths of different continental and peri-insular shelves (e.g., Patagonian Shelf ~ 200 m; Antarctic Peninsula Shelf ~ 500 m; Kerguelen Shelf ~ 1000 m). Given that BBA prefer neritic waters and that, in biological terms, the transition between neritic and oceanic regimes, which

occurs in the vicinity of the shelf-break, is often abrupt, one might expect a step in the preference function (Fig. 9) at the shelf-break depth. That this does not occur may be because at some spatial scales, depth increases with d_c (i.e., shallow habitats are more accessible), although the form of this relationship is highly variable with location (cf. the bathymetry around Macquarie with that of the Falklands). Hence, it could be hypothesized that BBA utilize neritic waters more frequently simply because their breeding islands lie on continental or peri-insular shelves. Although it is difficult to separate the ultimate and proximate causes of specialization, this seems unlikely: Firstly, because BBA also forage in distant neritic waters (e.g., during chick-rearing, birds from northwest South Georgia and Islas Diego Ramirez travel >1600 km to forage on the shelf of the west Antarctic Peninsula), and secondly because sympatric congeners, such as the Grey-headed Albatross *T. chrysostoma*, which is morphologically very similar to the BBA, forages more frequently in oceanic waters (Nel et al. 2001, Phillips et al. 2004).

In common with the majority of seabirds, BBA are long-lived, have low fecundity, locate patchily dispersed prey by searching, and have a catholic diet, which includes carrion (Croxall and Prince 1994, Cherel and Klages 1998). Although these are all traits typical of generalists (Begon et al. 2006), we have shown that the same habitats were most frequently used by all but one population, suggesting a degree of habitat specialization. This exception was exhibited by BBA from northwest South Georgia during incubation, which foraged not only in neritic, shelf-break, and shelf-slope habitats, but also in the distant oceanic waters of the Brazil-Malvinas Confluence. This was reflected by an increase in habitat preference with EKE above $\sim 250 \text{ cm}^2/\text{s}^2$ for that population. Because we did not track all populations in the same year (Table 1), it is conceivable that this difference arose because of anomalous environmental conditions in 2002, the year in which BBA from northwest South Georgia were tracked. For example, in any one breeding season, either Antarctic krill *Euphausia superba*, fish, or squid may predominate in the diet of BBA from this population (Xavier et al. 2003). Although this may simply reflect changes in the relative abundance of prey, which varies between years in the vicinity of South Georgia (Murphy et al. 2007, Xavier et al. 2007), it is also possible that BBA make large-scale switches in foraging areas in response to changes in prey distribution and environmental conditions. However, the broad-scale spatial usage of the populations which we tracked during the same breeding stage in multiple years (southeast Kerguelen and Isla Diego Ramirez) showed little interannual variability. Therefore, it is unlikely that the South Georgia BBA's use of the Brazil-Malvinas Confluence is anomalous.

Eddy kinetic energy in the Brazil-Malvinas Confluence exceeded $3600 \text{ cm}^2/\text{s}^2$, indicating intense mesoscale activity. In the subtropical Southern Hemisphere such activity occurs only in this region, the Agulhas Current

Extension off the Cape of Good Hope, and on the east coast of Australia (Ducet et al. 2000). Notably, the latter two areas are exploited by nonbreeding BBA (Tickell 2000, Phillips et al. 2005, Petersen et al. 2008). Mixing and advection at the edges of mesoscale meanders and eddies, where EKE values are highest, may lead to enhanced primary and secondary production, as well as the aggregation of prey (Mann and Lazier 2006). Numerous studies have demonstrated associations with mesoscale eddies by wide-ranging higher predators, including southern elephant seals *Mirounga leonine* in the Brazil–Malvinas Confluence (Campagna et al. 2006) and Grey-headed Albatrosses in the APFZ (Nel et al. 2001).

Stage-specific habitat preference

Although the variation in habitat preference with depth was similar across breeding stages, the spatial usage of birds during incubation also varied with SST, supporting hypothesis 2, that BBA express stage-specific habitat preferences. During incubation, birds from some populations also made occasional, or in the case of birds from northwest South Georgia, frequent, trips into distant oceanic waters. This can be interpreted in a number of ways. For example, during incubation, BBA have sufficient time to make longer trips, allowing them to access oceanic subantarctic waters between the APF and the STCZ. This may be profitable because complex fronts, meanders and eddies give rise to comparatively high levels of primary and secondary production in these areas (Lutjeharms et al. 1985). Alternatively, the peak in habitat preference at warmer SSTs may be spurious, arising because BBA have a more northerly distribution during incubation for other reasons, e.g., if BBA were broadly tracking resources, because primary production peaks during November in the mid-southern latitudes, and two months later in high latitudes (Yoder et al. 1993). If this is the explanation, any causal link between SST and spatial usage would be indirect. However, Pinaud and Weimerskirch (2002) have shown that, over an 18-year period, breeding success of BBA at Kerguelen is positively correlated with the mean monthly SST anomaly in core foraging areas, implying a more direct link between SST and foraging success. During chick-rearing, there was no significant variation in BBA habitat preference with SST. However, 21 of the 54 BBA we tracked in this stage visited areas covered by sea ice earlier in the season, whereas during incubation, only one of 109 birds visited the marginal ice zone. This shift to foraging in marginal sea ice was synchronized with recession of pack ice, which is followed a period of high productivity (El Sayed and Taguchi 1981). Alternatively, BBA may simply be exploiting previously inaccessible neritic, shelf-break, and shelf-slope areas, which are preferred per se (Ainley et al. 1993). Indeed, the extent of open water <1000 m deep within 3200 km of the Islas Diego Ramirez increases on average by 230 000 km² as the sea ice retreats between December and February, and such areas are often replete with Antarctic krill

(Murphy et al. 2007). Finally, changes in dietary requirement with breeding stage may play a role in habitat selection. Although there is a wealth of data on the diets of seabirds during chick-rearing, very little is known about the diet of incubating, or indeed nonbreeding, birds (e.g., Croxall and Prince 1980, Cherel and Klages 1998). However, fatty acid analysis has shown recently that diet may differ between breeding stages (Williams et al. 2008). Such a shift is likely to occur in some populations of BBA, because they forage south of the APF (which marks the biogeographical limit of the Southern Ocean) only during chick-rearing (Fig. 4). Hence, the differences in BBA habitat preference we observed could be interpreted in terms of stage-dependent foraging niches, mediated by intrinsic factors such as the dietary or energetic requirements of adults and chicks (Charrassin et al. 1998, Humphreys et al. 2006), or by extrinsic factors.

Campbell Albatross habitat preference

Closely related species often occupy different niches. As such, it may be unsurprising that the chick-rearing stage habitat preferences of CBA and BBA differ. However, differences in habitat preference can also arise due to differences between the relative availability of habitats to different (allopatric) populations (Mysterud and Ims 1998, Boyce et al. 2002). The oceanographic regime in waters surrounding the Campbell Island differs in a number of respects from that in waters bounding BBA colonies. Firstly, although the Campbell Plateau is extensive, it is also deep (600–1000 m) in comparison to typical continental or peri-insular shelves (usually <200 m deep). Hence, although CBA have access to comparatively small areas of neritic waters close to their colony, there are large areas of waters of intermediate depth (Table 1). Secondly, topographic steering of the Antarctic Circumpolar Current around the plateau gives rise to intense mesoscale eddy activity in the subantarctic and subtropical frontal zones, in very predictable areas close to the island (Morris et al. 2001). Hence, because of the paucity of truly neritic waters around Campbell Island, CBA may select shallower waters in a similar way to BBA, but also exploit predictable oceanic frontal zones (Vaughn et al. 1999), as indicated by an increase in habitat preference with positive SLA values. As such, the habitat preference of CBA during incubation may be similar to that of BBA from South Georgia. The questions of whether observed differences in chick-rearing stage habitat preference of CBA and BBA arise due to specialization or are simply differences in the relative availability of habitats could be addressed by tracking and modeling the habitat preferences of the small population of BBA that breed sympatrically with CBA on Campbell Island.

Parapatric intraspecific competition

Our null model assumes that spatial usage decreases with d_c (Matthiopoulos 2003). A corollary of this is that



PLATE 1. Agonistic interactions between Black-browed Albatrosses foraging in association with Northern Giant Petrels in the vicinity of South Georgia. Photo credit: E. D. Wakefield.

the capacity of individuals to compete for resources declines with d_c , because energetic reserves and/or the time available to locate and capture prey also diminish with d_c . Direct competition between BBA can be intense, with frequent agonistic encounters between birds over prey (Cherel et al. 2002) (see Plate 1). Hence, in order to minimize intraspecific competition, locations should be preferred if they are both close to the nest and distant from other colonies. If prey is uniformly distributed, this would give rise to a partial spatial segregation along colony lines, perhaps enhanced by cultural effects and wind patterns (Gremillet et al. 2004). Such segregation has been noted between some adjacent populations of BBA (Weimerskirch et al. 1988, Huin 2002), and in other colonial central-place foragers, including seabirds (e.g., Giraldeau et al. 1994, Brown and Gordon 2000, Ainley et al. 2003, Gremillet et al. 2004). However, if colonies are far enough apart, the decrease in usage with d_c alone may be sufficient to give rise to an apparent exclusivity in foraging areas (Lea et al. 2008). The hinterland model (Cairns 1989) proposes a similar mechanism to explain spatial segregation in seabirds. However, our tracking data show that this model is inappropriate for BBA: Firstly, because it predicts that

the foraging zones of birds from adjacent colonies are always mutually exclusive, whereas foraging BBA from the three main Chilean colonies, which are located 100–700 km from one another, overlap extensively (Figs. 1a and 4a), and secondly, because the predicted positive correlation between foraging area and colony size does not hold true for BBA. Similarly, contrary to Lewis et al. (2001), BBA from larger colonies do not necessarily travel further to forage (Fig. 5), a mechanism by which it was proposed birds could avoid indirect competition with sympatric intraspecifics. Indeed, birds from Beauchêne Island, which is the second largest BBA colony in the world, forage relatively close to their colony (Figs. 3 and 4). This is perhaps unsurprising, as it seems reasonable to assume that on average the fitness of two birds from the same colony diminishes at the same rate with d_c (see also Forero et al. 2002).

During model selection, we rejected parapatric intraspecific density (ρ_c) as an explanatory variable. Distance to the next nearest colony (d_n) was, however, retained in our post-guard model (III). BBA apparently responded to d_n at two scales. At the mesoscale, they showed a preference for areas ~200 km from the next nearest colony, while at the macroscale (thousands of

kilometers), they preferred areas ~1800 km away. We interpret this as a behavioral response to an increased need to avoid direct competition with parapatric conspecifics during chick-rearing (Fig. 12). During this stage, encounters with parapatric conspecifics in the vicinity of neighboring colonies would be more likely, both because foraging ranges contract and twice as many adults are at sea (during incubation, half of the breeding population must remain on the nest). Hence, BBA either make short trips in the vicinity of the home colony but far from neighboring colonies (such as in the Falklands populations), and/or longer trips to areas remote from both the home and neighboring colonies. The latter strategy is exhibited by BBA from South Georgia and Islas Diego Ramirez, which also travel to the South Orkneys Islands and the west Antarctic Peninsula during chick-rearing (Fig. 4b). Hence, while hypothesis 4 is supported, it should be emphasized that spatial usage is a function not just of intraspecific competition but also of accessibility and habitat preference. Therefore, in some circumstances, gains associated with reducing competition may be outweighed by gains associated with reduced travel costs (if two colonies are very close together, foraging zones may still overlap) or access to richer resources.

CONCLUSIONS

We have shown that BBA breeding at colonies throughout the species' range prefer to forage in neritic habitats. Furthermore, tracking and ringing recoveries indicate that nonbreeding BBA generally overwinter in neritic areas (Tickell 1975, Gremillet et al. 2000, Phillips et al. 2005), leading to the conclusion that this species is primarily a neritic specialist. However, important differences in habitat preference were found between BBA from South Georgia and other populations and between BBA and closely related CBA. In the latter case, this may reflect divergent niche specialization. In contrast, differences in habitat preference were not noted between BBA from the Falkland Islands and intraspecifics from other populations, despite the fact that it has been argued that the Falkland Island population is genetically distinct enough to warrant subspecies status (Burg and Croxall 2001). Differences or similarities in habitat preference may arise because of the relative composition of habitats available to different populations and so should be interpreted with caution. Indeed, our results indicate that differences in habitat preferences estimated using use-availability data can be as great within species as between species. Because we tracked populations in different years we were unable to quantify the uncertainty in our estimates of spatial usage associated with interannual variability. As multiyear tracking data sets become available it should be a priority for marine ecologists to investigate how foraging site choice varies from year to year at both the individual and population level (Pinaud et al. 2005).

Our estimates of spatial usage show that the vast majority of the world's BBA are concentrated during the breeding season on the Patagonian Shelf, Southern Chilean continental shelf, and in the Humboldt Current Upwelling (Fig. 11). These highly productive areas support large trawl and longline fisheries, which are responsible for unsustainable levels of BBA bycatch (Croxall and Gales 1998, Sullivan et al. 2006). To date, although considerable efforts have been made to put bycatch mitigation measures in place on the Patagonian Shelf, less attention has been paid to Chilean waters, which hold large numbers of BBA throughout the year (Moreno et al. 2006). Efforts to reduce the bycatch of this endangered species should therefore focus on both areas as a priority.

ACKNOWLEDGMENTS

This study was carried out while the first author was in receipt of a UK Natural Environment Research Council CASE studentship (NER/S/A/2005/13648) in partnership with the British Antarctic Survey. We are indebted to Geert Aarts, who initially developed the modeling techniques used in this study. We thank Simon Wood for advice on the implementation of GAMMs, and Andrew Fleming and Peter Fretwell for the provision of environmental data. We also thank Larkin Powell and an anonymous reviewer for constructive comments on an earlier version of this paper.

LITERATURE CITED

- Aarts, G., M. MacKenzie, B. McConnell, M. Fedak, and J. Matthiopoulos. 2008. Estimating space-use and habitat preference from wildlife telemetry data. *Ecography* 31:140–160.
- Acha, E. M., H. W. Mianzan, R. A. Guerrero, M. Favero, and J. Bava. 2004. Marine fronts at the continental shelves of austral South America physical and ecological processes. *Journal of Marine Systems* 44:83–105.
- Adler, F. R., and D. M. Gordon. 2003. Optimization, conflict, and nonoverlapping foraging ranges in ants. *American Naturalist* 162:529–543.
- Ainley, D. G., R. G. Ford, E. D. Brown, R. M. Suryan, and D. B. Irons. 2003. Prey resources, competition, and geographic structure of kittiwake colonies in Prince William Sound. *Ecology* 84:709–723.
- Ainley, D. G., C. A. Ribic, G. Ballard, S. Heath, I. Gaffney, B. J. Karl, K. J. Barton, P. R. Wilson, and S. Webb. 2004. Geographic structure of Adelie Penguin populations: overlap in colony-specific foraging areas. *Ecological Monographs* 74: 159–178.
- Ainley, D. G., C. A. Ribic, and L. B. Spear. 1993. Species-habitat relationships among Antarctic seabirds: a function of physical or biological factors. *Condor* 95:806–816.
- Alderman, R., M. C. Double, J. Valencia, and R. P. Gales. 2005. Genetic affinities of newly sampled populations of Wandering and Black-browed Albatross. *Emu* 105:169–179.
- Arata, J., G. Robertson, J. Valencia, and K. Lawton. 2003. The Evangelistas Islets, Chile: a new breeding site for black-browed albatrosses. *Polar Biology* 26:687–690.
- Arnould, J. P. Y., D. R. Briggs, J. P. Croxall, P. A. Prince, and A. G. Wood. 1996. The foraging behaviour and energetics of wandering albatrosses brooding chicks. *Antarctic Science* 8: 229–236.
- Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103:458–473.
- Austin, M. 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecological Modelling* 200:1–19.

- Awkerman, J. A., A. Fukuda, H. Higuchi, and D. J. Anderson. 2005. Foraging activity and submesoscale habitat use of waved albatrosses *Phoebastria irrorata* during chick-brooding period. *Marine Ecology Progress Series* 291:289–300.
- Ballance, L. T., R. L. Pitman, and P. C. Fiedler. 2006. Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: a review. *Progress in Oceanography* 69:360–390.
- Begon, M., C. R. Townsend, and J. L. Harper. 2006. *Ecology: from individuals to ecosystems*. Blackwell, Malden, Massachusetts, USA.
- Bevan, R. M., P. J. Butler, A. J. Woakes, and P. A. Prince. 1995. The energy expenditure of free-ranging black-browed albatrosses. *Philosophical Transactions of the Royal Society B* 350:119–131.
- 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.
- Bock, C. E., and Z. F. Jones. 2004. Avian habitat evaluation: Should counting birds count? *Frontiers in Ecology and the Environment* 2:403–410.
- Boehme, L., M. P. Meredith, S. E. Thorpe, M. Biuw, and M. Fedak. 2008. Antarctic Circumpolar Current frontal system in the South Atlantic: monitoring using merged Argo and animal-borne sensor data. *Journal of Geophysical Research-Oceans* 113. [doi: 10.1029/2007JC004647]
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281–300.
- Breed, G. A., I. D. Jonsen, R. A. Myers, W. D. Bowen, and M. L. Leonard. 2009. Sex-specific, seasonal foraging tactics of adult grey seals (*Halichoerus grypus*) revealed by state-space analysis. *Ecology* 90:3209–3221.
- Brown, M. J. F., and D. M. Gordon. 2000. How resources and encounters affect the distribution of foraging activity in a seed-harvesting ant. *Behavioral Ecology and Sociobiology* 47:195–203.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2004. *Advanced distance sampling*. Oxford University Press, Oxford, UK.
- 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.
- Burger, A. E., and S. A. Shaffer. 2008. Application of tracking and data-logging technology in research and conservation of seabirds. *Auk* 125:253–264.
- Burnham, K. P., and D. R. Anderson. 1998. *Model selection and multimodel inference*. Second edition. Springer, New York, New York, USA.
- Cairns, D. K. 1989. The regulation of seabird colony size: a hinterland model. *American Naturalist* 134:141–146.
- Campagna, C., A. R. Piola, M. R. Marin, M. Lewis, and T. Fernandez. 2006. Southern elephant seal trajectories, fronts and eddies in the Brazil/Malvinas Confluence. *Deep-Sea Research Part I-Oceanographic Research Papers* 53:1907–1924.
- Charrassin, J. B., C. A. Bost, K. Putz, L. Lage, T. Dahier, T. Zorn, and Y. Le Maho. 1998. Foraging strategies of incubating and brooding king penguins *Aptenodytes patagonicus*. *Oecologia* 114:194–201.
- Cherel, Y., and N. T. W. Klages. 1998. A review of the food of albatrosses. Pages 113–136 in G. Robertson and R. Gales, editors. *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.
- Cherel, Y., H. Weimerskirch, and C. Trouve. 2002. Dietary evidence for spatial foraging segregation in sympatric albatrosses (*Diomedea* spp.) rearing chicks at Iles Nuageuses, Kerguelen. *Marine Biology* 141:1117–1129.
- Croxall, J. P., and R. Gales. 1998. An assessment of the conservation status of albatrosses. Pages 46–65 in G. Robertson and R. Gales, editors. *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.
- Croxall, J. P., and E. D. Prince. 1980. Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biological Journal of the Linnean Society* 14:103–131.
- Croxall, J. P., and P. A. Prince. 1994. Dead or alive, night or day: How do albatrosses catch squid? *Antarctic Science* 6: 155–162.
- Ducet, N., P. Y. Le Traon, and G. Reverdin. 2000. Global high-resolution mapping of ocean circulation from TOPEX/Poseidon and ERS-1 and -2. *Journal of Geophysical Research-Oceans* 105:19477–19498.
- Duhamel, G., and M. Hauteceour. 2009. Biomass, abundance and distribution of fish in the Kerguelen Islands Eez (Ccamlr Statistical Division 58.5.1). *CCAMLR Science* 16:1–32.
- El Sayed, S. Z., and S. Taguchi. 1981. Primary production and standing crop of phytoplankton along the ice-edge in the Weddell Sea. *Deep-Sea Research Part a-Oceanographic Research Papers* 28:1017–1032.
- ESRI. 2006. ArcGIS spatial analyst package. Version 9.2. ESRI, Redlands, California, USA.
- Fauchald, P. 1999. Foraging in a hierarchical patch system. *American Naturalist* 153:603–613.
- Felicesimo, A. M., J. Munoz, and J. Gonzalez-Solis. 2008. Ocean surface winds drive dynamics of transoceanic aerial movements. *PLoS ONE* 3:e2928.
- Fetterer, F., K. Knowles, W. Meier, and M. Savoie. 2002, updated 2008. Sea ice index. National Snow and Ice Data Center, Boulder, Colorado, USA. Digital media.
- Forero, M. G., J. L. Tella, K. A. Hobson, M. Bertellotti, and G. Blanco. 2002. Conspecific food competition explains variability in colony size: a test in Magellanic Penguins. *Ecology* 83:3466–3475.
- Fretwell, S. D., and H. L. Lukas. 1970. On terrestrial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16–36.
- Furness, R. W., and T. R. Birkhead. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature* 311:655–656.
- Gales, R. 1998. Albatross populations: status and threats. Pages 20–45 in G. Robertson and R. Gales, editors. *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.
- Giraldeau, L. A., D. L. Kramer, I. Deslandes, and H. Lair. 1994. The effect of competitors and distance on central place foraging eastern chipmunks, *Tamias striatus*. *Animal Behaviour* 47:621–632.
- Gremillet, 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.
- Gremillet, D., S. Lewis, L. Drapeau, C. D. van der Lingen, J. A. Huggett, J. C. Coetzee, H. M. Verheye, F. Daunt, S. Wanless, and P. G. Ryan. 2008. Spatial match-mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *Journal of Applied Ecology* 45:610–621.
- Gremillet, D., R. P. Wilson, S. Wanless, and T. Chater. 2000. Black-browed albatrosses, international fisheries and the Patagonian Shelf. *Marine Ecology Progress Series* 195:269–280.
- Griffin, L. R., and C. J. Thomas. 2000. The spatial distribution and size of rook (*Corvus frugilegus*) breeding colonies is affected by both the distribution of foraging habitat and by intercolony competition. *Proceedings of the Royal Society B* 267:1463–1467.

- Guinet, C., L. Dubroca, M. A. Lea, S. Goldsworthy, Y. Cherel, G. Duhamel, F. Bonadonna, and J. P. Donnay. 2001. Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographic information systems. *Marine Ecology Progress Series* 219:251–264.
- Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147–186.
- Hall, L. S., P. R. Krausman, and M. L. Morrison. 1997. The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin* 25:173–182.
- Hays, G. C., M. Dray, T. Quaipe, T. J. Smyth, N. C. Mironnet, P. Luschi, F. Papi, and M. J. Barnsley. 2001. Movements of migrating green turtles in relation to AVHRR derived sea surface temperature. *International Journal of Remote Sensing* 22:1403–1411.
- Hedenström, A., and T. Alerstam. 1995. Optimal flight speed of birds. *Philosophical Transactions of the Royal Society B* 348: 471–487.
- Heil, P., and I. Allison. 1999. The pattern and variability of Antarctic sea-ice drift in the Indian Ocean and western Pacific sectors. *Journal of Geophysical Research-Oceans* 104: 15789–15802.
- Huin, N. 2002. Foraging distribution of the black-browed albatross, *Thalassarche melanophrys*, breeding in the Falkland Islands. *Aquatic Conservation: Marine and Freshwater Ecosystems* 12:89–99.
- Huin, N., and T. Reid. 2006. Census of the Black-browed Albatross population of the Falkland Islands 2000 and 2005. Falklands Conservation. (<http://www.falklandsconservation.com/wildlife/birds/AlbatrossCensusReport05-06.pdf>)
- Humphreys, E. M., S. Wanless, and D. M. Bryant. 2006. Stage-dependent foraging in breeding black-legged kittiwakes *Rissa tridactyla*: distinguishing behavioural responses to intrinsic and extrinsic factors. *Journal of Avian Biology* 37: 436–446.
- Hunt, G. L., K. O. Coyle, S. Hoffman, M. B. Decker, and E. N. Flint. 1996. Foraging ecology of short-tailed shearwaters near the Pribilof Islands, Bering Sea. *Marine Ecology Progress Series* 141:1–11.
- Hunt, G. L., F. Mehlum, R. W. Russell, D. Irons, M. B. Decker, and P. H. Becker. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. Pages 2040–2056 in 22nd International Ornithological Congress. BirdLife South Africa, Durban, South Africa.
- Hyrenbach, K. D. 2001. Albatross response to survey vessels: implications for studies of the distribution, abundance, and prey consumption of seabird populations. *Marine Ecology Progress Series* 212:283–295.
- Hyrenbach, K. D., P. Fernandez, and D. J. Anderson. 2002. Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. *Marine Ecology Progress Series* 233:283–301.
- Intergovernmental Oceanographic Commission [IOC]. 2003. Centenary edition of the GEBCO Digital Atlas. Intergovernmental Oceanographic Commission and the International Hydrographic Organization as part of the General Bathymetric Chart of the Oceans, British Oceanographic Data Centre, Liverpool, UK. [CD-ROM.]
- IUCN. 2008. *Thalassarche melanophrys*. 2008 IUCN red list of threatened species. IUCN, Gland, Switzerland. (www.iucnredlist.org)
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Johnson, M. D. 2007. Measuring habitat quality: a review. *Condor* 109:489–504.
- Kennedy, M., and R. D. Gray. 1993. Can ecological theory predict the distribution of foraging animals: a critical analysis of experiments on the ideal free distribution. *Oikos* 68:158–166.
- Lawton, K., R. Kirkwood, G. Robertson, and B. Raymond. 2008. Preferred foraging areas of Heard Island albatrosses during chick raising and implications for the management of incidental mortality in fisheries. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18:309–320.
- Lea, M. A., C. Guinet, Y. Cherel, M. Hindell, L. Dubroca, and S. Thalmann. 2008. Colony-based foraging segregation by Antarctic fur seals at the Kerguelen Archipelago. *Marine Ecology Progress Series* 358:273–287.
- Lefevre, J. 1986. Aspects of the biology of frontal systems. *Advances in Marine Biology* 23:163–299.
- Lewis, S., T. N. Sherratt, K. C. Hamer, and S. Wanless. 2001. Evidence of intra-specific competition for food in a pelagic seabird. *Nature* 412:816–819.
- Lidicker, W. Z. 1975. The role of dispersal in the demography of small mammals. Pages 103–128 in F. B. Golley, K. Petruszewicz, and L. Ryszkowski, editors. *Small mammals: their productivity and population dynamics*. Cambridge University Press, Cambridge, UK.
- Longhurst, A. L. 1998. *Ecological geography of the sea*. Academic Press, San Diego, California, USA.
- Louzao, M., K. D. Hyrenbach, J. M. Arcos, P. Abello, L. G. De Sola, and D. Oro. 2006. Oceanographic habitat of an endangered Mediterranean procellariiform: implications for marine protected areas. *Ecological Applications* 16:1683–1695.
- Lutjeharms, J. R. E., N. M. Walters, and B. R. Allanson. 1985. Oceanic frontal systems and biological enhancement. Pages 11–21 in W. R. Siegfried, P. R. Condy, and R. M. Laws, editors. *Antarctic nutrient cycles and food webs*. Springer-Verlag, Berlin, Germany.
- Manly, B. F., L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. *Resource selection by animals. Statistical design and analysis for field studies*. Second edition. Springer-Verlag, Berlin, Germany.
- Mann, K. H., and J. R. N. Lazier. 2006. *Dynamics of marine ecosystems*. Third edition. Blackwell Publishing, Malden, Massachusetts, USA.
- Martin, S. 2004. *An introduction to ocean remote sensing*. Cambridge University Press, Cambridge, UK.
- Matthiopoulos, J. 2003. The use of space by animals as a function of accessibility and preference. *Ecological Modelling* 159:239–268.
- McConnell, B., M. Fedak, H. R. Burton, G. H. Engelhard, and P. J. H. Reijnders. 2002. Movements and foraging areas of naive, recently weaned southern elephant seal pups. *Journal of Animal Ecology* 71:65–78.
- Moore, J. K., M. R. Abbott, and J. G. Richman. 1999. Location and dynamics of the Antarctic Polar Front from satellite sea surface temperature data. *Journal of Geophysical Research-Oceans* 104:3059–3073.
- Moore, P. J. 2004. Abundance and population trends of mollymawks on Campbell Island. *Science for Conservation* 242. Department of Conservation, Wellington, New Zealand.
- Moreno, C. A., J. A. Arata, P. Rubilar, R. Huckle-Gaete, and G. Robertson. 2006. Artisanal longline fisheries in Southern Chile: lessons to be learned to avoid incidental seabird mortality. *Biological Conservation* 127:27–36.
- Morris, M., B. Stanton, and H. Neil. 2001. Subantarctic oceanography around New Zealand: preliminary results from an ongoing survey. *New Zealand Journal of Marine and Freshwater Research* 35:499–519.
- Murphy, E., P. Trathan, I. Everson, G. Parkes, and F. Daunt. 1997. Krill fishing in the Scotia Sea in relation to bathymetry, including the detailed distribution around South Georgia. *CCAMLR Science* 4:1–17.
- Murphy, E. J., et al. 2007. Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a

- krill centred food web. *Philosophical Transactions of the Royal Society B* 362:113–148.
- Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology* 79:1435–1441.
- Nel, D. C., J. R. E. Lutjeharms, E. A. Pakhomov, I. J. Ansorge, P. G. Ryan, and N. T. W. Klages. 2001. Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche chrysostoma* in the southern Indian Ocean. *Marine Ecology Progress Series* 217:15–26.
- Nemeth, E., P. Bossew, and C. Plutzar. 2005. A distance-dependent estimation of foraging ranges of neighbouring bird colonies. *Ecological Modelling* 182:67–73.
- Olsson, O., J. S. Brown, and K. L. Helf. 2008. A guide to central place effects in foraging. *Theoretical Population Biology* 74:22–33.
- Orians, G. H., and N. E. Pearson. 1979. On the theory of central place foraging. Pages 155–177 in D. J. Horn, G. R. Stairs, and R. G. Mitchell, editors. *Analysis of ecological systems*. Ohio State University Press, Columbus, Ohio, USA.
- Osborne, J. L., A. P. Martin, N. L. Carreck, J. L. Swain, M. E. Knight, D. Goulson, R. J. Hale, and R. A. Sanderson. 2008. Bumblebee flight distances in relation to the forage landscape. *Journal of Animal Ecology* 77:406–415.
- Patterson, T. A., L. Thomas, C. Wilcox, O. Ovaskainen, and J. Matthiopoulos. 2008. State-space models of individual animal movement. *Trends in Ecology and Evolution* 23:87–94.
- Petersen, S. L., R. A. Phillips, P. G. Ryan, and L. G. Underhill. 2008. Albatross overlap with fisheries in the Benguela Upwelling System: implications for conservation and management. *Endangered Species Research* 5:117–127.
- Phillips, R. A., J. R. D. Silk, J. P. Croxall, V. Afanasyev, and V. J. Bennett. 2005. Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. *Ecology* 86:2386–2396.
- Phillips, R. A., J. R. D. Silk, B. Phalan, P. Catry, and J. P. Croxall. 2004. Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proceedings of the Royal Society 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.
- Pinaud, D., Y. Cherel, and H. Weimerskirch. 2005. Effect of environmental variability on habitat selection, diet, provisioning behaviour and chick growth in yellow-nosed albatrosses. *Marine Ecology Progress Series* 298:295–304.
- Pinaud, D., and H. Weimerskirch. 2002. Ultimate and proximate factors affecting the breeding performance of a marine top-predator. *Oikos* 99:141–150.
- Pinaud, D., and H. Weimerskirch. 2005. Scale-dependent habitat use in a long-ranging central place predator. *Journal of Animal Ecology* 74:852–863.
- Pinaud, D., and H. Weimerskirch. 2007. At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: a comparative study. *Journal of Animal Ecology* 76:9–19.
- Poncet, S., G. Robertson, R. A. Phillips, K. Lawton, B. Phalan, P. N. Trathan, and J. P. Croxall. 2006. Status and distribution of wandering, black-browed and grey-headed albatrosses breeding at South Georgia. *Polar Biology* 29:772–781.
- Prince, E. D., J. P. Croxall, P. N. Trathan, and A. G. Wood. 1998. The pelagic distribution of South Georgia albatrosses and their relationship with fisheries. Pages 137–167 in G. Robertson and R. Gales, editors. *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- Pulliam, H. R. 2000. On the relationship between niche and distribution. *Ecology Letters* 3:349–361.
- R Development Core Team. 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (<http://www.R-project.org>)
- Reynolds, R. W., N. A. Rayner, T. M. Smith, D. C. Stokes, and W. Q. Wang. 2002. An improved in situ and satellite SST analysis for climate. *Journal of Climate* 15:1609–1625.
- Robertson, C. J. R., and G. B. Nunn. 1998. Towards a new taxonomy for albatrosses. Pages 13–19 in G. Robertson and R. Gales, editors. *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.
- Robertson, G., C. A. Moreno, K. Lawton, J. Arata, J. Valencia, and R. Kirkwood. 2007. An estimate of the population sizes of black-browed (*Thalassarche melanophrys*) and grey-headed (*T. chrysostoma*) albatrosses breeding in the Diego Ramirez archipelago, Chile. *Emu* 107:239–244.
- Robertson, G., C. Moreno, K. Lawton, R. Kirkwood, and J. Valencia. 2008. Comparing census methods for black-browed albatrosses breeding at the Ildefonso Archipelago, Chile. *Polar Biology* 31:153–162.
- Shaffer, S. A., D. P. Costa, and H. Weimerskirch. 2003. Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. *Functional Ecology* 17:66–74.
- Simberloff, D., and T. Dayan. 1991. The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics* 22:115–143.
- Spear, L. B., L. T. Ballance, and D. G. Ainley. 2001. Response of seabirds to thermal boundaries in the tropical Pacific: the thermocline versus the Equatorial Front. *Marine Ecology Progress Series* 219:275–289.
- Sullivan, B. J., T. A. Reid, and L. Bugoni. 2006. Seabird mortality on factory trawlers in the Falkland Islands and beyond. *Biological Conservation* 131:495–504.
- Terauds, A., R. Gales, G. B. Baker, and R. Alderman. 2006a. Foraging areas of black-browed and grey-headed albatrosses breeding on Macquarie Island in relation to marine protected areas. *Aquatic Conservation: Marine and Freshwater Ecosystems* 16:133–146.
- Terauds, A., M. D. Sumner, R. Gales, and R. Alderman. 2006b. Foraging areas of Macquarie Island black-browed and grey-headed albatrosses and their relationship with mesoscale oceanographic features. *Aquatic Conservation: Marine and Freshwater Ecosystems* 16:133–146.
- Thompson, K. R. 1992. Quantitative analysis of the use of discards from squid trawlers by black-browed albatrosses *Diomedea melanophrys* in the vicinity of the Falkland Islands. *Ibis* 134:11–21.
- Tickell, W. L. N. 1975. The distribution of black-browed and grey-headed albatrosses. *Emu* 76:64–68.
- Tickell, W. L. N. 2000. *Albatrosses*. Pica Press, Sussex, UK.
- Tremblay, Y., S. Bertrand, R. W. Henry, M. A. Kappes, D. P. Costa, and S. A. Shaffer. 2009. A review of analytical approaches to investigate seabird-environment interactions. *Marine Ecology Progress Series* 391:153–163.
- Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Victoria, Australia.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893–901.
- Venables, W. N., and B. D. Ripley. 2002. *Modern applied statistics with S*. Fourth edition. Springer-Verlag, New York, New York, USA.
- Vincent, C., B. J. McConnell, V. Ridoux, and M. A. Fedak. 2002. Assessment of Argos location accuracy from satellite tags deployed on captive gray seals. *Marine Mammal Science* 18:156–166.
- Wakefield, E. D., R. A. Phillips, and J. Matthiopoulos. 2009a. Quantifying the habitat use and preference of pelagic seabirds

- using individual movement data: a review. *Marine Ecology Progress Series* 391:165–182.
- Wakefield, E. D., R. A. Phillips, J. Matthiopoulos, A. Fukuda, H. Higuchi, G. J. Marshall, and P. Trathan. 2009b. Wind field and sex constrain the flight speeds of central place foraging albatrosses. *Ecological Monographs* 79:663–679.
- Waluda, C. M., P. G. Rodhouse, P. N. Trathan, and G. J. Pierce. 2001. Remotely sensed mesoscale oceanography and the distribution of *Illex argentinus* in the South Atlantic. *Fisheries Oceanography* 10:207–216.
- Waugh, S., D. Filippi, A. Fukuda, M. Suzuki, H. Higuchi, A. Setiawan, and L. Davis. 2005. Foraging of royal albatrosses, *Diomedea epomophora*, from the Otago Peninsula and its relationships to fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* 62:1410–1421.
- 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. 2007. Are seabirds foraging for unpredictable resources? *Deep-Sea Research Part II-Topical Studies in Oceanography* 54:211–223.
- 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., T. Guionnet, J. Martin, S. A. Shaffer, and D. P. Costa. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society B* 267:1869–1874.
- Weimerskirch, H., T. Mougey, and X. Hindermeier. 1997. Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behavioral Ecology* 8:635–643.
- 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.
- Williams, C. T., S. J. Iverson, and C. L. Buck. 2008. Stable isotopes and fatty acid signatures reveal age- and stage-dependent foraging niches in tufted puffins. *Marine Ecology Progress Series* 363:287–298.
- 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.
- Wood, S. N. 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. *Journal of the American Statistical Association* 99:673–686.
- Wood, S. N. 2006. Generalized additive models: an introduction with R. Chapman and Hall/CRC, Boca Raton, Florida, USA.
- Woodward, R. H., and W. W. Gregg. 1998. An assessment of SeaWiFS and MODIS ocean coverage. NASA/TM-1998-208607. NASA, Goddard Space Flight Center, Greenbelt, Maryland, USA.
- 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.
- Xavier, J. C., A. G. Wood, P. G. Rodhouse, and J. P. Croxall. 2007. Interannual variations in cephalopod consumption by albatrosses at South Georgia: implications for future commercial exploitation of cephalopods. *Marine and Freshwater Research* 58:1136–1143.
- Ydenberg, R. C., C. V. J. Welham, R. Schmidhempel, P. Schmidhempel, and G. Beauchamp. 1994. Time and energy constraints and the relationships between currencies in foraging theory. *Behavioral Ecology* 5:28–34.
- Yoder, J. A., C. R. McClain, G. C. Feldman, and W. E. Esaias. 1993. Annual cycles of phytoplankton chlorophyll concentrations in the global ocean: a satellite view. *Global Biogeochemical Cycles* 7:181–193.

APPENDIX A

Estimated breeding population and locations of all known *Thalassarche melanophrys* and *T. impavida* super-colonies (*Ecological Archives* M081-007-A1).

APPENDIX B

Probability of the presence of Black-browed Albatrosses satellite-tracked from northwest South Georgia during incubation, predicted using the fixed effects part of model I, fitted to data from all populations and model III, fitted to data from northwest South Georgia alone (*Ecological Archives* M081-007-A2).

APPENDIX C

Remaining fixed-effects covariates retained in model II, fitted to spatial usage data from incubation-stage Black-browed Albatrosses from northwest South Georgia, and model IV, fitted to data from post-brood-stage Campbell Albatrosses (*Ecological Archives* M081-007-A3).