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FORAGING ZONES OF SOUTHERN ROYAL ALBATROSSES

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Abstract. Southern Royal Albatrosses (*Diomedea epomophora*) were satellite-tracked from Campbell Island during the incubation period in 1997 and 1999. Their foraging activity was restricted to shelf and shelf-break areas within 1250 km of their breeding site. Foraging activity by 8 of the 14 individuals tracked was concentrated at a zone near the Snares Islands, on the Campbell Plateau. Southern and Northern Royal Albatrosses (*D. sanfordi*) foraged on average nearer their breeding site than two other species of greater albatrosses (Gibson's [*D. gibsoni*], and Wandering [*D. exulans*] Albatrosses) studied during the incubation period.

Key words: continental shelf, Diomedea epomophora, *foraging, resources, satellite tracking, Southern Royal Albatross.*

Zonas de Forrajeo de *Diomedea epomophora*

Resumen. Individuos de la especie de albatros *Diomedea epomophora* fueron seguidos por satélite desde la Isla Campbell durante su período de incubación en dos años diferentes. Sus actividades de forrajeo estuvieron restringidas a las áreas rocosas y los desfiladeros en un perímetro de 1250 km alrededor del lugar de anidación. La actividad de forrajeo de más de la mitad de los 14 individuos estudiados estuvo concentrada en la zona cercana a la Isla Snares, en la meseta de Campbell. *D. epomophora* y *D. sanfordi* forrajeron en promedio más cerca de sus lugares de anidación que otras especies de albatros más grandes (*D. gibsoni* y *D. exulans*) estudiadas durante el período de incubación.

The distribution of resources in the marine environment leads to particular problems for foraging higher predators. Physical and biological factors lead to high variability in prey abundance (Murphy et al. 1988, Hunt 1991, Rodhouse et al. 1996). Hydrographic features such as sea-ice, ocean fronts, eddies, and upwellings may lead to prey aggregations at mesoscales, while prey schooling behaviors, or predator-prey interactions, and wind-driven Langmuir cells are thought to concentrate prey into dense patches at finer scales (Hunt 1991). Albatrosses in the Southern Ocean epitomize foraging specialization in this difficult environment, using energy-efficient soaring flight to cover great distances in search of sparsely distributed prey (Arnould et al. 1996, Weimerskirch et al. 2000).

Recent technical developments in the study of behavior of large, wide-ranging procellariiform birds, such as satellite telemetry (Jouventin and Weimerskirch 1990) and the use of activity recorders, allow us to examine their behavior using spatial analyses (Wood et al. 2000). Indeed, the need to take into account spatial components of ecological data has been strongly emphasized recently (Tilman and Kareiva 1997, Selmi and Boulinier 2001, Yoccoz et al. 2001). Bird-activity density analyses enable us to take into account information about seabird behavior in relation to physical, biological, and anthropogenic factors in the marine environment, (Berrow et al. 2000, Gremillet et al. 2000, Wood et al. 2000).

In this paper we apply quantitative analytical tools to determine the characteristics of the feeding habitat of Southern Royal Albatrosses (*Diomedea epomophora*) foraging during two breeding seasons in New Zealand. We compare foraging characteristics of this species with published reports of three other greater albatross species: Northern Royal Albatross (*D. sanfordi*) and Gibson's Albatross (*D. gibsoni*), which were studied using satellite telemetry in New Zealand, and Wandering Albatross (*D. exulans*), which was studied at the Crozet Islands. Formerly these four species were considered to be only two distinct taxa, Wandering and Royal Albatrosses, but we follow the taxonomy proposed by Robertson and Nunn (1997).

METHODS

Southern Royal Albatrosses were satellite-tracked at Campbell Island (52°33′S, 169°09′E) during incubation. Four birds were tracked during 6–15 February 1997 and 10 birds during 12 January–11 February 1999. Transmitters were attached to the back feathers of incubating birds using surgical-grade (Tesa) tape and removed after one foraging trip. Locations were received through the ARGOS system (Argos CSL, Toulouse, France). Data were classified into 6 classes of decreasing accuracy and quality: Class 3 (error radius of 150 m), 2 (350 m), 1 (1 km), 0, A, and B

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TABLE 1. Characteristics of 14 Southern Royal Albatross foraging trips followed by satellite telemetry, indicating the time spent at sea (trip duration), the maximum distance from the colony attained by each bird (maximum range), and the distance traveled by each bird along its trip (cumulative distance traveled). The first two digits of each bird number indicate the year of study. For bird 97-3, the transmitter stopped functioning after 3.5 days at sea; thus minimum distances only are given.

Bird no.	Trip duration (days)	Maximum range (km)	Cumulative distance traveled (km)
97-1	8.8	223	4289
97-2	9.9	213	2959
97-3	3.5+	107+	1394+
97-4	2.1	125	875
99-1	16.0	1259	6589
99-2	15.2	773	5497
99-3	9.6	493	3487
99-4	6.8	343	2835
99-5	15.9	1214	6051
99-6	9.0	506	3302
99-7	16.3	517	3250
99-8	12.8	638	3338
99-9	8.8	768	4263
99-10	9.9	512	5323

(accuracy to be determined by the user). The threshold for rejection of low-quality satellite locations was a flight speed of >90 km hr^{-1} between successive uplinks. Trip durations were calculated from a combination of satellite locations and observations of birds leaving or returning to their nests.

Data were treated using a custom software package (''Diomedea,'' D. Filippi, unpubl. program; see Weimerskirch et al. 2000 for details and other examples of its use). The system estimates the mean speed of travel between successive satellite locations at 1 min or greater intervals, allowing environmental databases to be linked to locational estimates. The pattern of activity of individuals can then be analyzed in relation to the environment they are exploiting. In this study we chose to examine bathymetric data (Integrated Global Ocean Services System, unpubl. data) in relation to bird foraging movements. Further, we generated a matrix of density of bird activity (time spent per unit area) and integrated this with the bathymetric data using Matlab 5 (Mathworks Inc. 1996).

Data for comparison of trip parameters between albatrosses of different species were obtained from publications, and maximum ranges were estimated for Northern Royal Albatross to the nearest 10 min of longitude and latitude from published maps (Nicholls et al. 1994). As there are considerable differences in foraging ranges and strategies between periods of the breeding season for this group of birds (Weimerskirch et al. 1993, Stahl and Sagar 2000a, 2000b), we restricted our comparison to trips followed during the incubation period.

STATISTICAL ANALYSES

Due to high variances in the foraging parameters measured, nonparametric statistics were used to test between-group differences in foraging parameters (Mann-Whitney *U*-tests for two-sample tests, Kruskall-Wallis tests for four-way comparisons of means; Sokal and Rohlf 1995, SAS Institute 2001). There were no differences between results from these and parametric tests (two-sample *t*-test, ANOVA). Statistical tests were carried out using SAS v.8 (SAS Institute 2001), with $P < 0.05$. Values reported are means $\pm$ SD.

RESULTS

SOUTHERN ROYAL ALBATROSS FORAGING ZONES

The characteristics of the flights of 14 Southern Royal Albatrosses satellite tracked from Campbell Island are shown in Table 1. There were no significant differences in foraging parameters between years, except for maximum range (trip duration 1997 = 6.9 $\pm$ 4.2 days, 1999 = 11.7 $\pm$ 3.6 days, $U = 6.0$, $P = 0.1$; maximum range 1997 = 187 $\pm$ 54 km, 1999 = 703 $\pm$ 351 km, $U < 0.01$, $P < 0.01$; distance traveled 1997 = 2707 $\pm$ 1721 km, 1999 = 4004 $\pm$ 1554 km, $U = 7.0$, $P = 0.02$). Differences in maximum range could be explained by the slightly later period of study during the first season. We chose to pool all results between years (Table 2).

All 14 Southern Royal Albatrosses tracked used the Campbell Plateau during their foraging trips, either as a thoroughfare or as a foraging site in itself. A single zone was very intensively prospected, south of the Snares Islands, in a wide band from the west to the

TABLE 2. Comparison of mean $\pm$ SD foraging parameters for four species of greater albatrosses.

Site	Albatross species	Year(s)	*n*	Trip duration (days)	Maximum range from colony (km)	Cumulative distance traveled (km)
Campbell Island[a]	Southern Royal Albatross	1997, 1999	13	10.8 ± 4.1	584 ± 351	4004 ± 1554
Otago Peninsula[b]	Northern Royal Albatross	1993	3	3.9 ± 1.9	145 ± 69	—
Crozet Island[c]	Wandering Albatross	1992, 1994	10	10.2 ± 8.4	1456 ± 1059	5739 ± 4781
Auckland Islands[d]	Gibson's Albatross	1994	3	12.1 ± 1.1	1275 ± 211	4538 ± 922

[a] This study.
[b] Nicholls et al. 1994.
[c] Weimerskirch et al. 1994, Weimerskirch, Wilson, and Lys 1997.
[d] Walker et al. 1995.

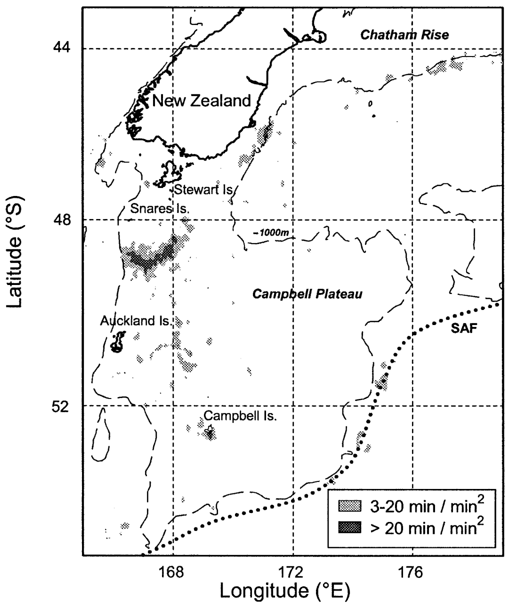

FIGURE 1. Density plot of 14 Southern Royal Albatross tracks, showing use of waters over the Campbell Plateau and other bathymetric features. The lower shelf break (1000 m deep; dashed), coast (solid), and approximate position of the Sub-Antarctic Front (SAF; as indicated by the 8°C sea-surface temperature isotherm, dotted) are shown. Density is indicated in minutes of bird time per unit area (minute latitude × minute longitude)². One degree of latitude represents 109 km.

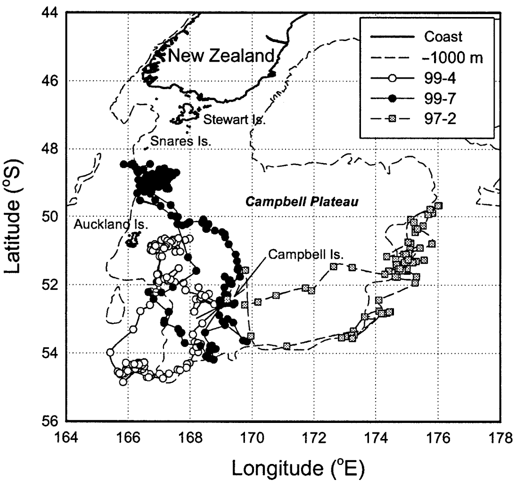

FIGURE 2. Three individual tracks from foraging trips using the southern (individual 99–4, unfilled circles) and southeastern shelf breaks of the Campbell Plateau (individual 97–2, gray squares) and Snares Islands hotspot (individual 99–7, filled circles). Symbols represent satellite fixes, which occurred at irregular intervals. The coastline (solid) and 1000-m isobath (dashed) are shown. One degree of latitude represents 109 km.

center of the plateau (Fig. 1). This zone (hereafter referred to as the Snares Islands hotspot) lies along the inner shelf-break at a depth of 200 m. A second feature of the foraging strategy of the tracked birds was the intensive activity in the vicinity of steep bathymetric gradients (1000–3000 m depth). For example, peaks of bird activity were concentrated on the continental shelf slope to the southeast of Campbell Plateau (used by two birds), along the Chatham Rise (two birds), off the Otago Peninsula (three birds), and at the Puysegur Trough off the southwest corner of New Zealand (one bird). While one or a few individuals used these diverse zones, eight birds, including birds from both years of study, frequented the Snares Islands hotspot. The tracks of three individuals are shown in Figure 2.

We divided the area used by the birds into four zones depending on the bathymetry, and calculated the time spent by birds in each. These zones correspond to (1) the inner continental shelf (<200 m depth), a zone dominated by swimming predators (e.g., seals and sea-lions, penguins, shags); (2) the continental shelf (200–800 m depth), a zone that is more productive than open ocean waters; (3) lower shelf-slope waters (800–1500 m depth), where the bathymetric gradient descends rapidly, a zone which may be associated with mixing and nutrient upwelling; (4) deep oceanic waters (1500–6000 m depth) in which foraging resources are generally scarce (Schneider 1997). For the 14 birds tracked, inner shelf waters received little attention (14 ± 12% of bird time), while foraging activity was centered over continental shelf waters (59 ± 21%) or lower shelf-slope waters (21 ± 22%). Deeper waters were rarely used (5 ± 6%).

COMPARISON AMONG GREATER ALBATROSSES

We compared foraging trip parameters for greater albatrosses followed by satellite telemetry at four sites (Table 2). Data were available for Wandering Albatrosses (Crozet Islands 1992, $n = 5$, Weimerskirch et al. 1994; and 1994, $n = 5$, Weimerskirch, Wilson, and Lys 1997) Gibson's Albatross, (Auckland Islands, 1994, $n = 4$, Walker et al. 1995) and for Northern Royal Albatross (Otago Peninsula, $n = 4$, 1993, Nicholls et al. 1994).

There were no significant between-year differences in the foraging parameters for Wandering Albatrosses tracked from the Crozet Islands; thus these samples were pooled (trip duration 1992 = 5.4 ± 3.2 days, 1994 = 15.0 ± 9.6 days, $U = 4.0$, $P = 0.09$; maximum range 1992 = 1196 ± 763 km, 1994 = 1717 ± 1331 km, $U = 12.0$, $P = 1.0$; distance traveled 1992 = 2868 ± 2364 km, 1994 = 6695 ± 4696 km, $U = 5.0$, $P = 1.0$).

There were significant differences between species in all foraging parameters (duration $H_3 = 7.6$, $P = 0.05$; maximum range $H_3 = 15.1$, $P < 0.01$; distance traveled $H_3 = 10.5$, $P = 0.01$; Table 2). In particular, Northern Royal Albatross carried out short foraging trips of limited range, while Wandering and Gibson's Albatrosses performed trips with greater maximum range than did the Southern or Northern Royal Albatrosses.

DISCUSSION

SOUTHERN ROYAL ALBATROSS FORAGING ZONES

The study revealed a characteristic foraging pattern for Southern Royal Albatross, that of a shelf- and shelf-break-feeding species which, despite foraging trips of moderate duration, does not venture far from its breeding site. Southern Royal Albatrosses used the continental plateau extensively, with one hotspot south of the Snares Islands. Further, they seemed to concentrate their foraging effort over shelf-breaks. They may use sites with upwelling and eddies associated with the concurrence of oceanic fronts and the submarine relief, a feature common in the foraging strategies of many marine top predators (Rodhouse et al. 1996, Veit et al. 1993). In the two study periods, the 8°C isotherm passed along the southwestern edge of the Campbell Plateau (Integrated Global Ocean Services System, unpubl. data), indicating that the Sub-Antarctic Front was located in this zone (Heath 1981, Belkin and Gordon 1996). A concurrent study of Black-browed and Grey-headed Albatrosses (*Thalassarche melanophrys* and *T. chrysostoma*) also nesting at Campbell Island showed some overlap between these species and Southern Royal Albatross in their usage of the Campbell Plateau, but both *Thalassarche* species also made extensive use of the oceanic waters to the east and south of the plateau (Waugh et al. 1999). Segregation of foraging habitat relative to water depth has been well documented in marine birds, and is thought to be related to differences in primary productivity over shelf or deep-water environments (Schneider 1997).

Several of the areas prospected by Southern Royal Albatrosses were also used extensively by Buller's Albatrosses (*T. bulleri*) satellite-tracked from the Snares and Solander Islands (Stahl and Sagar 2000a, 2000b). The main area of overlap with Southern Royal Albatross was along the continental shelf edge off the Otago Peninsula and Chatham Rise. Buller's Albatrosses nest in winter; thus the periods of study do not allow us to examine between-species interactions over the same foraging zones using the current data set.

The use of the shelf-break as a principal feeding area for Southern Royal Albatrosses has previously been inferred from dietary analysis, where oceanic squid species were conspicuously absent (Imber 1999). Southern Royal Albatrosses rely on a relatively narrow range of prey, taking squid from only five families compared to 27 families for Wandering Albatross (Cherel and Klages 1997).

In addition to noting which zones are most frequented by a population or some smaller sample of birds, it is of interest to examine *how* they use their environment. In particular, operating in an energy-efficient manner is important for birds that travel over large distances in search of sparsely or patchily distributed prey. One strategy used by procellariiform seabirds to maximize prey-capture rates and minimize energy spent in locomotion is to make long looping flights, covering vast distances to maximize encounter rates with sparse prey, and thus attain predictable prey yields (Weimerskirch, Wilson, and Lys 1997). Fauchald et al. (2000) showed that Common Murres (*Uria aalge*) use the hierarchical patch structure of their principal prey, capelin (*Mallotus villosus*), to guide them to areas of high prey density, as prey patches are predictable in neither time nor location. In contrast to these two patterns, optimal energy acquisition in the foraging environment of the Campbell Plateau may favor the visitation of known locations, regardless of the energetic costs of commuting between these areas and the breeding site. This pattern of activity has already been shown for Black-browed Albatrosses feeding at the Kerguelen Islands (Weimerskirch, Mougey, and Hindermeyer 1997). The foraging patterns of Southern Royal Albatross show a strong link to physical attributes in the marine environment, suggesting that location, and not prey density, orients their mesoscale foraging search toward particular zones. The cues that albatrosses use to identify these areas and locate profitable prey patches within them are unknown. It may be that at finer scales prey-patch tracking also occurs, as for murres exploiting bands of capelin (Fauchald et al. 2000).

COMPARISON AMONG GREATER ALBATROSSES

In comparison with the other greater albatrosses, both Southern Royal Albatrosses satellite tracked from Campbell Island (this study) and Northern Royal Albatrosses from Otago Peninsula (Nicholls et al. 1994) restricted their foraging to shelf areas or shelf-breaks, at relative proximity to their breeding sites. This is in spite of similar trip durations for Southern Royal Albatross, Wandering Albatross and Gibson's Albatross. The two Royal Albatross species appear to have foraging characteristics most similar to those described for Wandering Albatrosses from South Georgia, which clustered near the 1000-m isobath and made extensive use of the coastal shelf-slope and Patagonian Shelf (Prince et al. 1997). This pattern of behavior contrasts with that of Wandering Albatrosses from the Crozet Islands (Weimerskirch et al. 1994, Weimerskirch 1997, Weimerskirch, Wilson, and Lys 1997), and Gibson's Albatross (Walker et al. 1995) which feed more frequently over oceanic waters and forage significantly farther from their nests than do Royal Albatrosses during the incubation phase. The contrasting strategies of Gibson's Albatross and Southern Royal Albatross from Campbell Island suggest that the former species may be excluded from feeding over shelf waters, as they do not frequent the Snares Islands hotspot, despite its proximity to their Auckland Islands breeding site.

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