FORAGING RANGES AND PARTITIONING OF FEEDING ZONES IN THREE SPECIES OF SOUTHERN ALBATROSSES[1]

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Abstract. Foraging ranges and zones of breeding Black-browed (*Diomedea melanophris*), Gray-headed (*D. chrysostoma*), and Wandering (*D. exulans*) albatrosses were studied in the southwest Indian Ocean, using individuals color-marked at the Kerguelen Islands. Black-browed Albatrosses forage mainly over the surrounding continental shelf and had a maximum foraging range of 470 km; Gray-headed and Wandering albatrosses foraged over pelagic waters up to 1,850 km and 1,420 km respectively from their nest. Black-browed Albatrosses breeding at two Kerguelen colonies appeared to have essentially separate foraging zones but overlap occurred in an area where trawlers provided an additional food source. Our findings support the hypothesis that separation of feeding zones is an extensive means of resource partitioning in albatross communities and populations.

Key words: Foraging range; feeding zones; partitioning of resources; albatrosses.

INTRODUCTION

Albatrosses (Procellariiformes: Diomedeidae) are medium to large pelagic seabirds. They forage over thousands of kilometers of ocean, making use of prevailing winds in order to reduce flight energy consumption (Pennycuick 1982). Recapture of banded birds suggests long-range dispersal among immatures and nonbreeding adults (Tickell 1967, Tickell and Gibson 1968, Robertson and Kinsky 1972, Robbins and Rice 1973, Weimerskirch et al. 1985). During the nesting season only scarce direct observations suggest that breeding albatrosses cover long distances when foraging for food during incubation and chick rearing. Two recaptures of banded birds known to be rearing a chick occurred 840 km (Gray-headed Albatross, *Diomedea chrysostoma*; in Prince and Francis 1984) and 1,200 km (Wandering Albatross, *D. exulans*; in Weimerskirch and Jouventin 1987) from their breeding grounds and Light-mantled Sooty Albatrosses,

Phoebetria palpebrata, fed their chick with prey species occurring no closer than 1,000 km from the nest site (Weimerskirch et al. 1986). Intervals between successive feedings of chicks by their parents have been used as an index of distance travelled to find food (Croxall and Prince 1980), but a recent study has shown that at least some species forage for food close to their nesting grounds but feed their chicks less frequently than do other species which forage farther offshore (Weimerskirch et al. 1986). Characterization of the foraging ranges of breeding albatrosses by recording birds at sea is difficult because the provenance and breeding status of observed birds is unknown. The problem is complicated by biennial breeding and delayed sexual maturity of most albatross species, resulting in only a part of the whole population breeding each season (as little as 30% in Sooty Albatrosses, *P. fusca*; Jouventin and Weimerskirch 1984). Finally, because of the ability of albatrosses to cover long distances, overlap could occur in the foraging zones of birds originating from different islands.

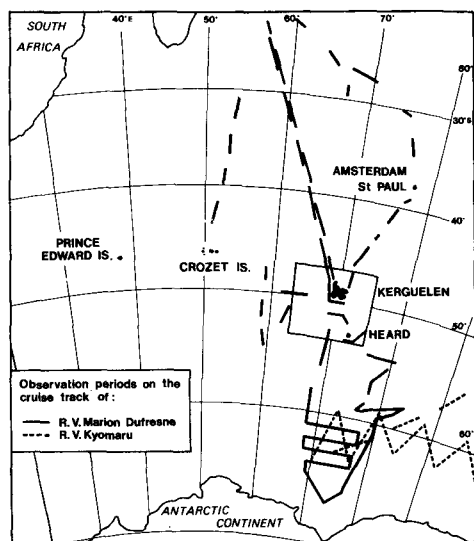It is possible, however, to study the foraging range of breeding albatrosses by marking them

FIGURE 1. Map of the southwest Indian Ocean showing the transects during which observations were made from two research vessels.

at the time they are incubating the egg or rearing the chick, and subsequently recording the distribution at sea of marked individuals (Tickell 1968). Moreover, by marking breeding individuals of different species foraging patterns can be compared. Finally, by marking breeding individuals of the same species in different colonies, it is possible to find whether or not birds from different colonies have separate foraging zones.

This study was carried out on the Kerguelen Islands. Large numbers of breeding albatrosses of different species and from different colonies of a single species were marked with plumage dyes to record their distribution at sea over coastal and pelagic waters of the southwest Indian Ocean. This paper reports: (1) the extent of long-range foraging in breeding albatrosses, (2) differences in the foraging pattern of three albatross species, and (3) the degree of overlap between foraging zones of Black-browed Albatrosses

(*D. melanophris*) originating from two different colonies.

METHODS

Incubating birds of three albatross species were dyed at three localities on the Kerguelen Islands (49°S, 70°E) southwest Indian Ocean in 1984 to 1985 (Table 1, Figs. 1, 2). Two different dyes were used to mark a total of 3,989 birds (Table 1), powdered Rhodamine B and picric acid, both dissolved in an ethanol-water mixture. Patches, 15- to 20-cm diameter, were sprayed on breasts of the birds with a portable agricultural sprayer. It was not necessary to handle the birds during spraying. Rhodamine B is red when first applied, becomes pink after the bird has been at sea several days, and disappears progressively after 3 to 4 months. Picric acid is yellow when first applied, turns orange-brown after 2 to 3 days, and remains visible for at least 4 to 5 months, probably disappearing when the bird molts.

Observers aboard the R. V. Marion Dufresne, R. V. Kyo Maru (cruise tracks shown in Fig. 1), and aboard two trawlers operating on the Kerguelen shelf were requested to report sightings of marked albatrosses according to species and color of the dye (red-pink or yellow-orange-brown). Aboard the two research vessels observations were conducted continuously along the cruise tracks between 2 January and 30 March. Aboard trawlers, sightings for marked albatrosses were conducted every day during two observations lasting 1 hr each between 28 December and 10 March. Thus, resightings were conducted during the incubation period of the Wandering Albatross and chick-feeding period of Black-browed and Gray-headed albatrosses. All squares of 15' latitude by 20' longitude in which at least one observation exists (from R. V. Marion Dufresne and trawler) are outlined in Figure 2 by a circle (dyed birds) or a star (no dyed bird seen).

At the breeding grounds, 36 to 77 nests with dyed birds were visited daily in order to (1) monitor the periods spend on the nest by incubating

TABLE 1. Locality, number of birds dyed, dye used, and date of dyeing for three albatross species.

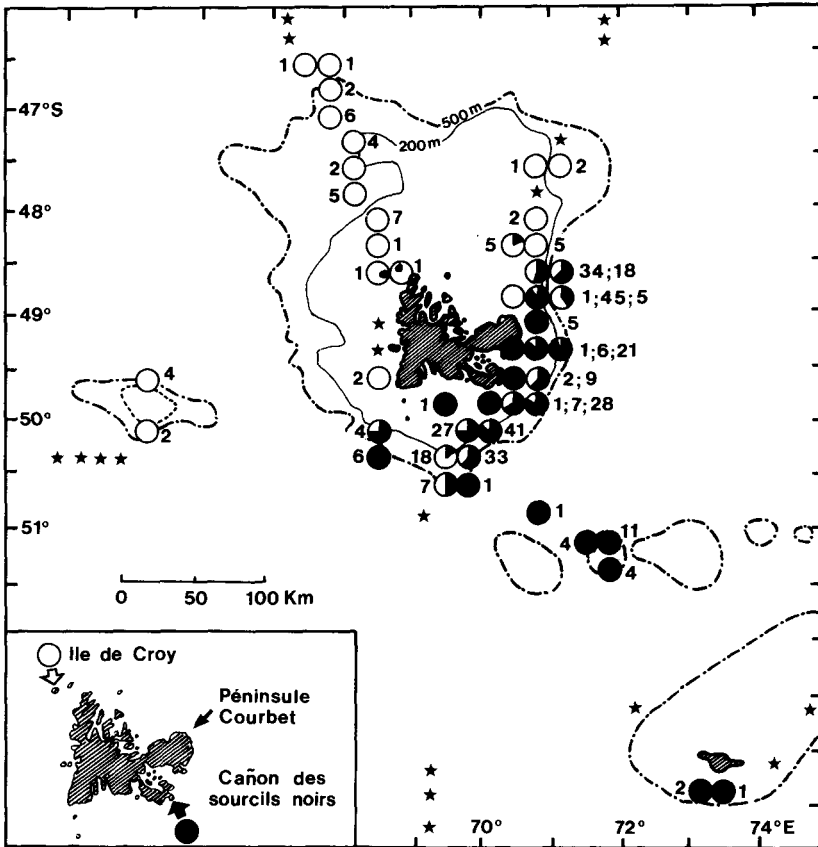| Species	Locality	Dye used	Number	Date
Wandering Albatross	Peninsule Courbet	Rhodamine B	178	2–5/01/85
Gray-headed Albatross	Ile de Croy	Picric acid	2,437	4–12/12/84
Black-browed Albatross	Ile de Croy	Picric acid	749	4–12/12/84
Black-browed Albatross	Canon des Sourcil Noirs	Rhodamine B	625	27–28/12/84

FIGURE 2. Sightings of dyed breeding Black-browed Albatrosses in the area of the Kerguelen-Heard shelves. The proportion of black and white in a circle indicate the proportion of birds originating from Ile de Croy (white) and from Canon des Sourcils Noirs (black) in 15' latitude and 20' longitude squares. The figure adjacent to each circle indicates the total number of dyed birds sighted in each square and the stars indicate the absence of dyed birds.

and brooding birds, and (2) estimate the frequency of feeding of chicks. Although the periods of nest checking were too short to follow the lengths of individual stints, the number of checks and the frequencies of changeovers or feedings allowed the calculation of average durations. Estimates of feeding frequency were based on daily mass determination with spring balances accurate to 0.5% of capacity: an increase between successive daily weights representing a feed. The diet was studied by noting the predominant prey in each regurgitate obtained from chicks (see Weimerskirch et al. 1986 for details).

RESULTS

In all, 411 observations of dyed albatrosses (one of Wandering Albatross, 12 of Gray-headed Albatrosses, and 390 of Black-browed Albatrosses)

were made in the southern Indian Ocean during this study (Figs. 2, 3). An additional sighting of a dyed Gray-headed Albatross was reported from the R. V. Africana in March north of the Antarctic continent (J. Enticott, pers. comm.). Finally, seven observations of Black-browed Albatrosses dyed on Ile de Croy were recorded in June, i.e., out of the breeding season, off South Australia: six off Kangaroo Island, 35°54′S, 137°53′E (A. Lishmar, pers. comm.) and one off Port MacDonnell, 37°45′S, 140°E (A. Milbride, pers. comm.).

Dyed Gray-headed Albatrosses were reported from the western part of the Kerguelen shelf and shelf break, the western satellite bank, and oceanic waters of the antarctic zones at distances of 30 to 1,850 km. Six were resighted over oceanic waters, four in close proximity to shelves, and

three over shelves (Fig. 3). The ratio of the number marked to the number subsequently sighted is 174:1. At Kerguelen, the mean duration of foraging trips during incubation for 36 nests between 18 and 30 November and between 1 and 11 December were 10.2 and 10.7 days, respectively.

The 390 observations of marked Black-browed Albatrosses were at distances of 10 to 470 km from the breeding grounds and all but one were on, or at the edge, of the Kerguelen-Heard shelves or adjacent banks (depths to 500 m, Fig. 3). The ratio of the number of birds marked to the number which were subsequently sighted is 3.5:1. Breeding Black-browed Albatrosses nesting on Ile de Croy appeared to forage mostly on the northern half of the Kerguelen shelf, and on the western satellite bank (Fig. 2). In contrast, those nesting on Canon des Sourcils Noirs were sighted on the south half of the Kerguelen shelf, on the southern satellite banks and on the Heard shelf (Fig. 2). However, foraging ranges of the two populations overlapped broadly at the southeastern part of the Kerguelen plateau (Fig. 2). The mean duration of foraging trips during incubation was 4.5 days during 5 to 11 December ($n = 77$ nests). During the brooding period (26 to 28 December) foraging trips lasted on average only 1.7 days ($n = 45$ nests) and during the fledging period (28 to 30 January) on average 3.9 days ($n = 47$ nests). From 43 chick regurgitations containing identifiable material, fish remains predominated in 87% of samples, squids in 7%, crustaceans and carrion in 3% each. Penguin feathers were present in four of the samples. The single observation of a dyed Wandering Albatross was recorded 1,420 km south from the bird's nesting place (Fig. 3).

DISCUSSION

Most observations of dyed albatrosses in the breeding season were from the Kerguelen shelf, particularly along the southeastern and eastern edges. The concentration of observations here partly reflects the distribution of the trawlers from which observations were made. Trawling for fish (mostly Nototheniidae) is concentrated in summer on this part of the shelf (Duhamel and Hureau 1981). However, considering the greater length of transects and observer effort from research vessels over oceanic waters compared to that over shelves, few records were made of dyed birds over oceanic waters. Another bias could
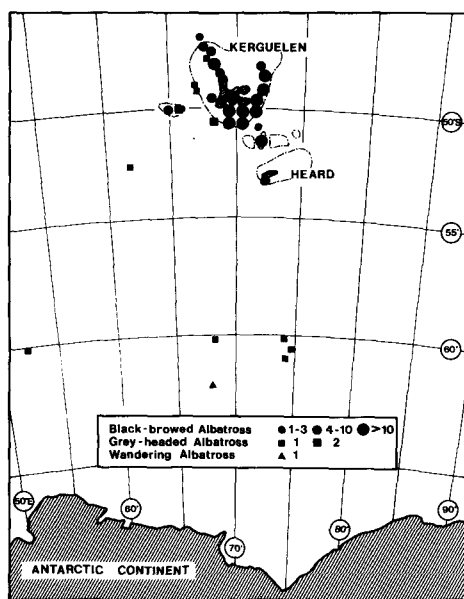

FIGURE 3.   Sightings of breeding albatrosses in the southwest Indian Ocean after dye-marking at Kerguelen.

come from the fact that some of the sightings of dyed birds might include individuals that failed to hatch their egg or lost their chick. These birds might behave differently at sea from those still feeding chicks. However, chick mortality in Gray-headed and Black-browed albatrosses after hatching and particularly after the brooding period (i.e., during the study period) is usually low, from 2 to 10% according to the year (unpubl. data).

INTERSPECIFIC DIFFERENCES IN FORAGING RANGE AND FORAGING ZONES

The distribution of sightings of dyed individuals shows substantial differences in foraging ranges and habitat preferences between the similar-sized Black-browed and Gray-headed albatrosses. The first species concentrate over the Kerguelen-Heard shelves while the second forage over oceanic waters. These results confirm the conclusion of an earlier study of the Crozet albatross community based on observations of unmarked birds at sea (Weimerskirch et al. 1986). Thus, as on the Crozet Islands, breeding Black-browed Albatrosses (and nonbreeding also) specialized in foraging for food over neritic waters. At Kerguelen they also take advantage of the offal from

ships trawling for fish. This extra source of food could explain why the interval between two consecutive feedings of the chick was 1.3 days shorter ($P < 0.05$) on the Kerguelen Islands than on the Crozet Islands where no trawling has been permitted in the 200-mile economic zone since 1978 (Duhamel and Hureau 1981). Furthermore, while birds from Kerguelen fed almost entirely on fish, fish predominated in only 58% of samples from birds from the Crozet Islands (Weimerskirch et al. 1986).

Although nearly twice as many Gray-headed Albatrosses as Black-browed Albatrosses were marked, only three observations of Gray-headed Albatrosses were recorded on the shelf. We therefore assume that breeding Gray-headed Albatrosses mainly forage over antarctic and subantarctic waters, as far as 1,850 km from their nest. In consequence, the foraging breeding population is diluted over a much larger area so that the probability of recording marked birds is relatively small, explaining the high ratio of number marked to number subsequently sighted. Further, Gray-headed Albatrosses remain at sea for a similar length of time to the Crozet birds, twice the time taken by Black-browed Albatrosses. This result confirms the more oceanic habits of the former species compared to the similar-sized but neritic Black-browed Albatross.

The single record of a dyed Wandering Albatross, in pelagic waters at a high latitude, led us to suppose that, like Gray-headed Albatrosses, Wandering Albatrosses do not forage on the Kerguelen shelves. This situation is supported by other observations at sea (Weimerskirch et al. 1986, Stahl 1987) and differs completely from that occurring over the Crozet shelf where Wandering Albatrosses feed in large numbers (Weimerskirch et al. 1986).

INTRASPECIFIC DIFFERENCES IN FORAGING ZONES OF BREEDING KERGUELEN BLACK-BROWED ALBATROSSES

Black-browed Albatrosses rearing their chicks forage over neritic waters relatively close to their colonies. The farthest resighting indicates a foraging range of up to 470 km during chick rearing, which corresponds to the remotest shelf area available around Kerguelen. However, sightings of marked birds from the only two Kerguelen colonies suggest different at-sea distributions. For example, although the northern part of the Kerguelen shelf is only 200 km from the Canon des

Sourcils Noirs colony it is not frequented by birds nesting there. Breeding birds from each colony seem to have mostly separate feeding zones, each zone being an area not easily reached by birds nesting at the other colony. Some overlap does occur, however, in the southeastern part of the Kerguelen shelf. This part of the shelf corresponds to the zone of regular intensive trawling, and it is possible that the additional food source here is sufficiently rich to allow an overlap in foraging zones.

RESOURCE PARTITIONING IN ALBATROSSES

The results of this study suggest that the separation of foraging zones is an extensive means of resource partitioning in albatrosses. This has also been described for other seabird communities; in the Atlantic seabird community (Pearson 1968), among tropical terns (Ashmole and Ashmole 1967, Diamond and Prŷs-Jones 1986), and possibly among six alcid species (Cody 1973, but see Bédard 1976). In albatrosses, the separation of foraging habitats during the breeding season has now been established not only between different species of the same community (Weimerskirch et al. 1986, this study), but also between colonies (this study), between immatures and adults (Jouventin et al. 1982, Stahl 1987), and between the two sexes (Weimerskirch and Jouventin 1987). An intra- and interspecific separation of foraging zones also has been observed in albatrosses outside the breeding season (Tickell 1967, Weimerskirch et al. 1985). In ecological communities, the habitat dimension is generally more important than food type or temporal dimensions in resource partitioning (Schoener 1974). But of all seabird groups, only for albatrosses has it been possible to describe such an extent of resource partitioning through separation of feeding habitats. The reasons for such a marked degree of separation, at least in part, could be caused by vastness of the two-dimensional habitat (sea-surface) and the long travelling capabilities of albatrosses. The extent of the spatial dimension might result in the partitioning of habitats being less subtle than, for example, amongst inshore feeders. Moreover, albatrosses are convenient birds to study because they are large, conspicuous, and readily identifiable seabirds, easily handled without risk of adversely affecting their behavior or breeding success. It is therefore possible that among other seabird

groups separation of feeding zones could be a more widely established mode of resource partitioning than has yet been supposed. Preliminary studies on petrels tend to confirm this supposition (Jouventin et al. 1985).

ACKNOWLEDGMENTS

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