

## FORAGING STRATEGY OF WANDERING ALBATROSSES THROUGH THE BREEDING SEASON: A STUDY USING SATELLITE TELEMETRY

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**ABSTRACT.**—Satellite telemetry of Wandering Albatrosses (*Diomedea exulans*) breeding on the Crozet Islands, southwestern Indian Ocean, revealed two distinct foraging strategies during successive stages of the breeding season: systematic foraging over extensive distances; and use of specific areas close to the colony. During early incubation, Wandering Albatrosses foraged over pelagic waters at an average range of 1,284 km. The length of the foraging trips decreased towards the end of the incubation period. During the first month of chick rearing when parents brood alternately for short periods, the foraging range, distance covered, and area prospected were further reduced. Males tended to return to an individual foraging area, located at the edge of the continental shelf, that had previously been visited during the long trips of the incubation period. Females mostly prospected pelagic waters just off the shelf. After the chick had been left alone on the nest, birds exhibited a two-fold strategy, combining long foraging trips over pelagic waters with short trips over the shelf. Generally, both sexes headed for and foraged over an extensive pelagic sector. Some males also foraged over the Kerguelen shelf. Females tended to forage over more northerly waters than males. The duration of the foraging trips was most closely related to the total distance covered, but also to the maximum range during the long trips of the chick-rearing period and to a lesser extent during the incubation period. There were no such significant relationships in the case of short trips. During long pelagic foraging trips, the birds had a looping course that was determined by the wind direction, suggesting random foraging with respect to prey distribution. We were able to show that Wandering Albatrosses use two foraging strategies to cope with the constraints imposed by the different stages of the breeding cycle, the availability of prey, and the distribution of the prey. Use by Wandering Albatrosses of two foraging strategies may be a compromise based on the simultaneous need to satisfy the different food requirements of chicks and parents. Received 20 February 1992, accepted 23 October 1992.

DURING THE breeding season, pelagic seabirds forage from a central place (often an island) and travel outward to feeding areas, where their foraging behavior is impossible to observe by island-based researchers. Heretofore, the only easily measurable feature of their foraging has been durations of foraging trips, determined from incubation bouts and chick feeding frequencies. Usually, it has been assumed that the duration of foraging trips depends on the distance an adult has to travel from its nest to find food (Lack 1968, Pearson 1968, Croxall and Prince 1980, Pennycuick et al. 1984). Ainley and Boekelheide (1990), however, showed that other factors can complicate this relationship. The virtual absence of time/energy budgets during foraging of pelagic seabirds has led to extensive speculation that requires confirmation with telemetric studies (e.g. Ricklefs 1983, Harrison and Seki 1987, Prince and Morgan 1987). The

utility of satellite telemetry for very large birds has been demonstrated in a study showing that four male Wandering Albatrosses (*Diomedea exulans*) moved during the early incubation period over thousands of kilometers, taking advantage of the prevailing winds (Jouventin and Weimerskirch 1990). This preliminary work supported the previous simplistic suggestions that albatrosses have an extensive foraging range during the breeding season (Tickell 1968, Croxall and Prince 1980, Pennycuick et al. 1984, Weimerskirch et al. 1986). Observations at the nest also have shown that foraging trips are reduced in duration as the hatching of the chick approaches and are very short when the chick is brooded (Tickell 1968, Weimerskirch et al. 1986). This pattern suggests that foraging parameters change during the breeding season.

Further information on the pelagic ecology of albatrosses has come from observations at sea

that give indications concerning the distribution of seabirds in relation to their environment (e.g. Ainley et al. 1983, Stahl et al. 1985). These studies have shown, for example, that Wandering Albatrosses forage from antarctic to subtropical waters and that males forage in more northerly waters than females (Weimerskirch and Jouventin 1987). However, because the birds observed were of unknown status and origin it was impossible to conclude whether the pattern observed concerned the breeding or nonbreeding parts of the population. Satellite telemetry can address such questions.

We report a study using satellite telemetry of the foraging strategy of Wandering Albatrosses throughout the different stages of the breeding cycle. We have addressed three main questions: (1) What are the foraging characteristics of the Wandering Albatross and do these characteristics vary according to the different stages of the breeding cycle? (2) Is foraging-trip duration related to the range or the distance covered? (3) Do the birds forage randomly or do they return to specific areas during each trip? Results are discussed in relation to the predictions and hypotheses concerning the foraging strategies of pelagic seabirds.

#### METHODS

The field study was carried out on Possession Island, Crozet Islands, in the southwestern Indian Ocean on a population of Wandering Albatrosses whose age and status has been studied since 1966 (Weimerskirch and Jouventin 1987). The birds fitted with transmitters for this study were individuals who had bred successfully in at least three previous seasons.

Wandering Albatross are among the largest pelagic seabirds. They have a mass between 8 and 10 kg, with males being 20% heavier than females (Tickell 1968). The breeding cycle lasts a complete year. At the Crozet Islands laying occurs from late December to early January (Fressanges du Bost and Segonzac 1976). The egg is incubated alternately by the male and the female for 80 days. While one bird incubates, usually for 4 to 33 days, the partner forages at sea to replace the body reserves used during the fast on the nest. After hatching, the chick is brooded alternately by each parent for one month and, thereafter, is left alone. The chick is fed regularly by both parents during the austral winter and spring, and fledging occurs in November-December. Parents successful in rearing the chick breed in alternate years (Tickell 1968).

The movements of wandering albatrosses were monitored using the Argos satellite tracking system (Fancy et al. 1988). The Argos system uses two NOAA

(National Oceanic and Atmospheric Administration, USA) satellites to receive a signal sent by transmitters. The data stored on the satellites are sent to ground telemetry stations at the end of each orbit cycle and relayed to CNES (Centre National des Etudes Spatiales) in Toulouse, France. At CNES the data are processed and the exact position of the transmitter is determined. The locations are made available within 2 h of the transmitter being located.

Study dates were from 10 January 1990 to 28 August 1990, and 10 January 1991 to 14 February 1991. Results obtained in 1989 for six males (Jouventin and Weimerskirch 1990) are included to increase sample size during the incubation period. In 1990-1991 nine different 185-g 2028C Toyocom transmitters (Toyo Communication Equipment Ltd, Minato-ku, Tokyo, Japan) were used. Only two were used in 1991-1992. The original transmitters were modified so that the total length was reduced from 180 to 110 mm, with the battery pack being relocated to the side of the electronics. Thus, the package was broader than the original, but its mass was reduced to 160 g. The lifetime of the batteries depends on the interval between two messages. In 1990-1991 the transmission interval was adjusted to 90 s, giving a battery lifetime of about 35 to 40 days. The transmitters were fitted on the birds using a 10-mm-wide harness made of fine goat leather with elastic sections (Weimerskirch et al. 1992). When fitted on the bird, the harness (24 g) was completely covered by feathers. Experiments with dummy transmitters were carried out in 1989 (Jouventin and Weimerskirch 1990); comparison of time spent at sea during incubation and brooding by birds fitted with transmitters and by other birds suggest that the presence of the transmitter probably did not alter the behavior of the birds (Weimerskirch et al. 1992).

Birds fitted with transmitters were breeding at two different colonies on Possession Island: Baie du Marin located at the eastern extremity of the island; and Pointe Basse on the northwestern coast (for description of colonies, see Weimerskirch and Jouventin 1987). Transmitters fitted on birds incubating eggs or brooding young chicks were recovered after one (incubation period) or several (brooding period) foraging trips at sea. After the chick was left alone on the nest (chick-rearing period), birds visiting the chick for feeding were captured and fitted with transmitters (until end of August). These transmitters were left in place for a period of one month and then recovered during a feeding visit.

Nine transmitters were used successively on a total of 30 individual birds, which included both sexes. Sixty-five foraging trips (17 by 9 individual females, 48 by 21 individual males) were built up from the 4,468 locations received. During some of the foraging trips, the unit stopped transmitting on the way back to Crozet. In this case, if the last location was less than 300 km from Crozet and if the bird fitted with the transmitter was recovered within one to two days

after the last location, the distance covered between the nest and the last location was assumed to be a direct line. Otherwise, only the maximum range was considered for these foraging trips. Transmission failure was caused by broken antennae, exhausted batteries, oxidation of contacts by sea water and unknown factors.

The data were analyzed using ELSA Software (Argos CLS, Toulouse, France). Four classes of location can be received with the Argos system, with accuracy of locational information (Anonymous 1989) as follows: (class 0) accuracy to be determined by investigator; (1) SD of 1 km; (2) SD of 350 m; (3) SD of 150 m. All classes of locations were used in the analysis, unless the location proved to be unreliable (i.e. implying a movement between the locations of more than 80 km/h, the maximum speed recorded and predicted for Wandering Albatrosses; from Pennycuik [1982] and Jouventin and Weimerskirch [1990]). In this case, the location was removed from the data set. Statistical tests were performed using STATITCF and LOHITHEQ software packages.

Information on wind direction and wind strength was obtained from the Bureau des Prévisions Marines, Météo France, Paris. The forecast maps of the southern Indian Ocean provided data twice daily on wind strength and direction at 10-m altitude for each 1.8° square.

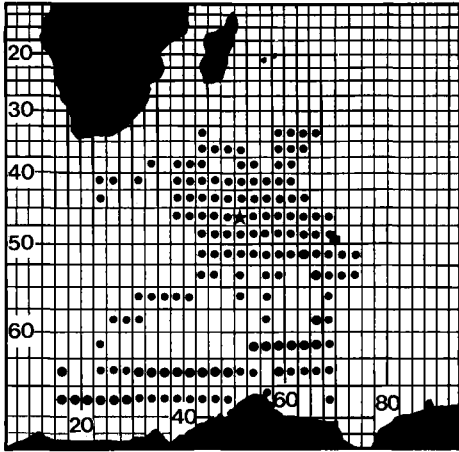
## RESULTS

*Changes in foraging pattern through breeding season.*—The maximum foraging range, distance covered and surface prospected varied greatly depending on the stage of the breeding cycle (Figs. 1 and 2, Table 1). During the first two months of the incubation period, when the two members of the pair alternate every 4 to 33 days on the egg (Table 1), Wandering Albatrosses foraged over pelagic waters from polar to subtropical latitudes (Fig. 1). However, one of the eight males foraged mostly over the inshore waters of the Crozet shelf and, otherwise, over the adjacent pelagic waters. Foraging trips during incubation followed a looping course from Crozet (Fig. 3A). During the trips of the entire incubation period, 5 of the 16 birds tracked interrupted their directional progress, spending a period of three to six days in a restricted area where they moved over short distances (Fig. 3A). For four birds, these areas were located north of the subtropical convergence in subtropical waters (see Fig. 3A); the fifth bird moved continuously over a shoal (Skiff Bank, 50°S, 64–66°E) west of the Kerguelen Archipelago. The other birds moved continuously over extensive

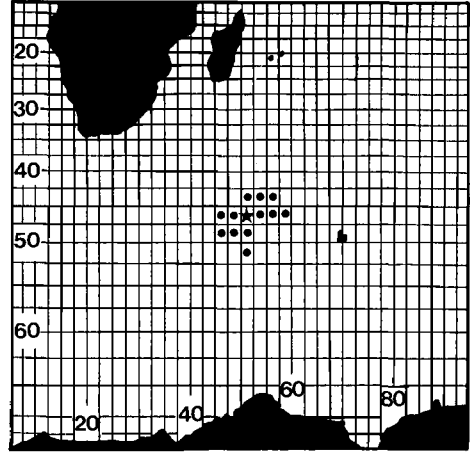
distances on a looping track. Birds covered an average of 5,991 km during each foraging trip, ranging as far as 2,602 km from their colony (Fig. 2, Table 1). During the last month of the incubation period (i.e. "late incubation"), maximum foraging ranges and distances covered were less than during the first two months ( $t = 3.2$  and  $2.8$ , respectively,  $P < 0.01$ ) so that the surface area prospected was reduced (Table 1, Figs. 1 and 2). At this time, before returning to the nest, all the birds spent one or two days foraging at the edge of the Crozet shelf. The locations of females had a significantly more northern distribution compared to those of males (Table 2, Fig. 4).

During the first month after hatching both parents alternated on the nest every one to five days to brood the chick (Table 1). The average maximum range was only 256 km, with the foraging area correspondingly reduced (Table 1, Figs. 1 and 2). Birds covered short distances (Table 1), and the foraging trips of males were interrupted by periods over restricted areas (Fig. 5A). These areas of "active foraging" were concentrated at the southern edge of the Crozet shelf (Fig. 6). However 1 of 11 males ranged over pelagic waters more than 1,000 kilometers from its nest (Fig. 2). It flew directly to the Ob Shoal (52°S, 41–42°E), where it spent two days before returning directly to Crozet. Unlike males, the four females did not forage intensively over specific areas of the shelf and appeared only to move rapidly over the shelf. They foraged over pelagic waters in the vicinity of the shelf (Fig. 5B).

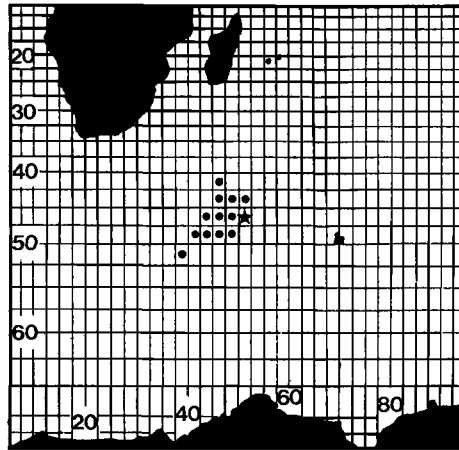
One month after hatching, the chick is left unattended on the nest, and both parents forage in order to feed it. At this time the adult birds mix short trips over inshore waters with long trips over pelagic subantarctic and subtropical waters (Fig. 7). There were no intermediate trips (Fig. 2) between long and short trips. Short trips had a similar pattern to those of the brooding period (Table 1). During long trips the average foraging range reached 1,534 km and the average distance covered 6,091 km (Table 1). During these long trips the birds foraged further north than they did during the incubation period, and no bird was observed in Antarctic waters (Figs. 1 and 4, Table 2). During the chick-rearing period, the long looping tracks rarely were interrupted by short-distance movements lasting only one to two days (Fig. 3B). During these long trips, three males foraged over or at



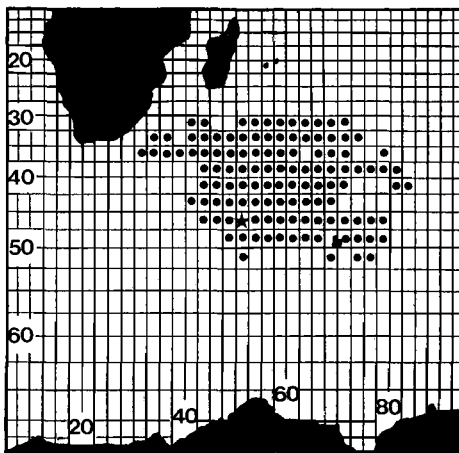
**INCUBATION**



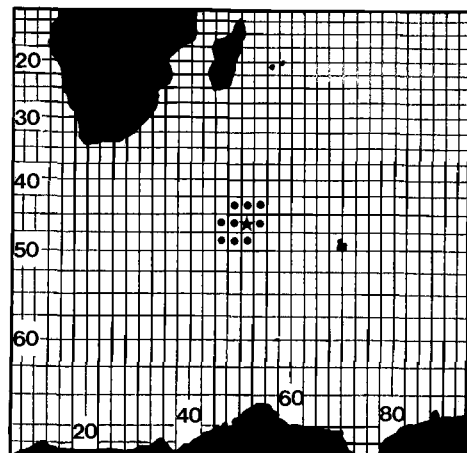
**LATE INCUBATION**



**BROODING**



**CHICK REARING - Long trips**



**CHICK REARING - Short trips**

Fig. 1. Areas prospected by Wandering Albatrosses during successive stages of breeding cycle. Each 2.5° square for which locations were obtained are marked with a point. Crozet Islands are indicated by a star (incubation 11 trips, 11 individuals; late incubation 5, 5; brooding 15, 8; fledging 34, 16).

the border of the Kerguelen shelf, whereas the other six males and three females foraged over pelagic subantarctic and subtropical waters (Fig. 8). Females tended again to forage over more northerly waters than males (Figs. 1 and 4, Table 2). During the short trips of the chick-rearing period, males breeding at the Baie du Marin colony had foraging zones mostly south of Possession Island and East Island, whereas those from the Pointe Basse colony were foraging mostly west of these zones (Fig. 6).

*Relationship between length of stay at sea and foraging range.*—During the long foraging trips of the incubation and chick-rearing periods, the time at sea was significantly related to the maximum range and distance covered (Fig. 9). The time spent at sea was more closely related to the distance covered than to the maximum range. In contrast, during the brooding period, there was no relationship between duration of foraging trips and either the maximum range or distance covered for tracks with a maximum range shorter than 500 km (Fig. 9). The relationship was significant if the longer tracks, spent mostly over pelagic waters, were included. When the chick was left alone at the nest, there was no relationship between the time spent at sea and the range or distance covered.

*Individual foraging tactics.*—During the long trips of the incubation period, we did not fit the same bird with a transmitter for successive foraging trips. During the late incubation period, just before its chick hatched, one male was tracked during two successive trips. The bird foraged twice over the shelf, spending most of its time over two adjacent but distinct areas (Fig. 10A). During the brooding period, it returned four times to the second area visited (see Fig.

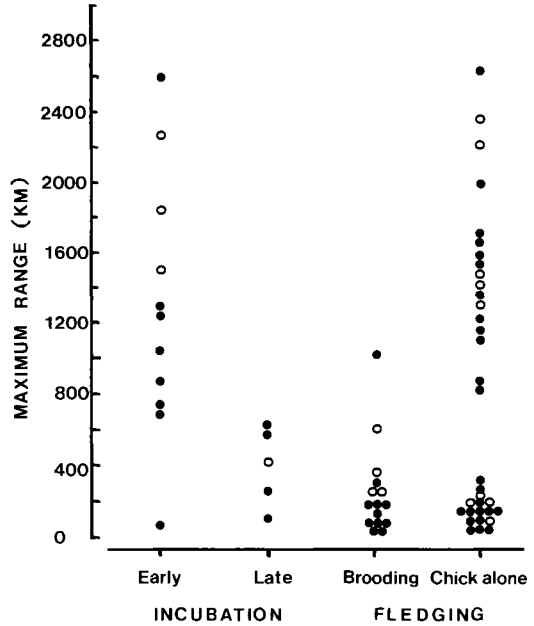


Fig. 2. Maximum ranges recorded for males (black points) and females (white points) during successive stages of breeding season.

5A). Similarly, two other individuals were tracked during the incubation period and thereafter during the brooding period. Both spent more than one day at specific zones on the edge of the shelf on the way back from their pelagic foraging trips of the incubation period. Later during the brooding period, they returned to the same restricted area of the shelf (Fig. 10B).

During short trips of the fledging period, nine males were tracked on successive foraging trips. Each individual tended to return to the same specific area, located at the edge of the shelf

TABLE 1. Maximum foraging range, distance covered and duration of foraging trips during successive stages of breeding cycle:  $\bar{x} \pm SD$ , range (*n*).

Period	Maximum range (km)	Distance covered (km)	Length (days)
Incubation (first two months)	1,284 ± 740	5,991 ± 4,264	14.0 ± 9.0
	75-2,602 (11)	1,282-15,200 (11)	4-33 (11)
Late incubation	395 ± 217	2,118 ± 1,068	9.6 ± 4.6
	110-612 (5)	908-3,664 (5)	4.2-14 (5)
Chick brooding	256 ± 257	923 ± 698	2.8 ± 0.9
	74-1,030 (15)	330-3,007 (15)	1.3-5 (15)
Chick rearing (long trips)	1,534 ± 509	6,091 ± 3,328	11.6 ± 6.2
	814-2,618 (17)	3,736-14,716 (14)	1.8-26.9 (14)
Chick rearing (short trips)	117 ± 77	532 ± 325	2.4 ± 1.0
	34-303 (17)	279-1,327 (10)	0.7-4 (14)

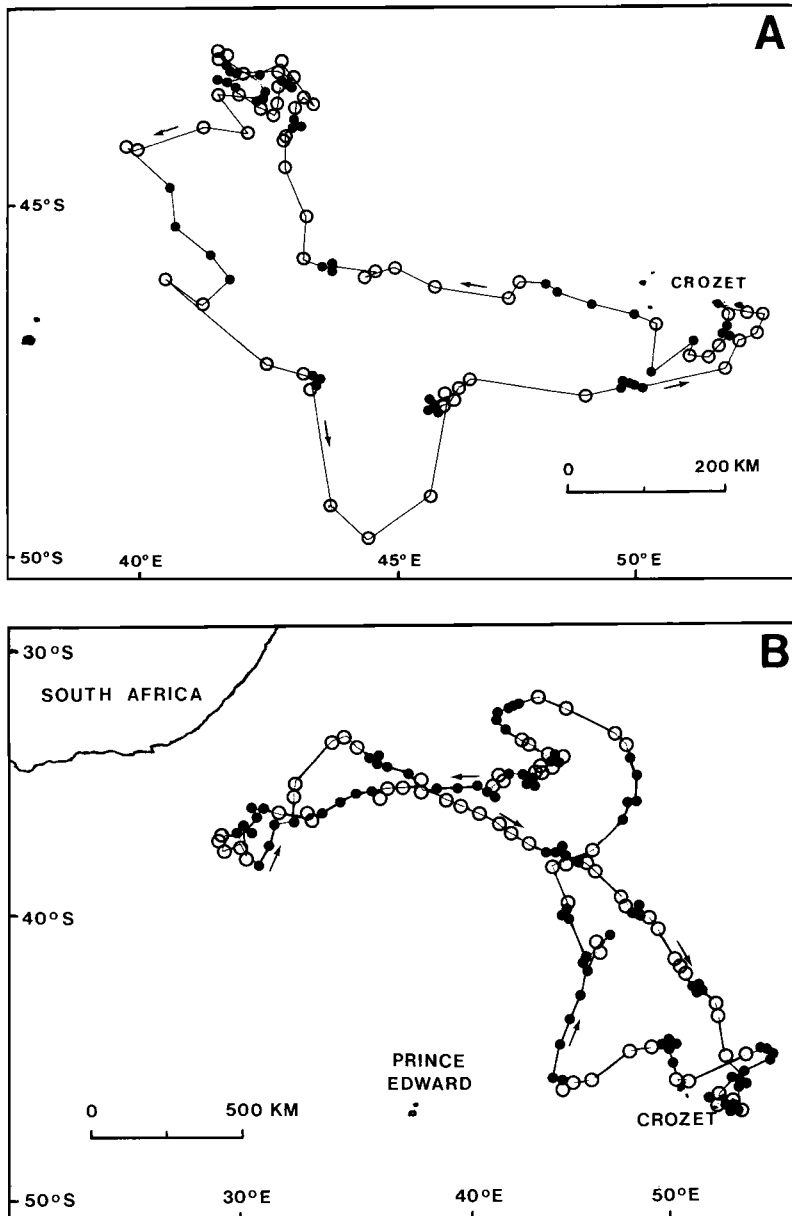


Fig. 3. Detailed tracks of long foraging trips of Wandering Albatrosses during: (A) incubation period with an interruption of several days of the loop (4,372 km covered by male BS 1989); and (B) fledging period (9,986 km covered by female CF 3742). White dots indicate daytime locations and black dots the nighttime locations.

(Fig. 6). For 15 pairs of successive short trips, the birds returned to the same area as visited previously in 73% of the cases. The birds used various routes to reach this area (sometimes flying over pelagic waters; Fig. 5A) and spent an average of 61.2% (SD = 19.8%,  $n = 15$ , range 32.0–90.7%) of the duration of the foraging trip

in the area. The three females tracked during successive short trips did not return to exactly the same pelagic area (see caption for Fig. 5B). After the brooding period, the same individual appeared to mix long trips with short trips. For example, male BS 6663 started with a long trip north of Crozet, then foraged on the shelf dur-

TABLE 2. Median latitudes (and ranges) of locations obtained for males and females during long foraging trips of incubation and fledging periods, with a test on equality of medians  $\times$  ranges.

	Males	Females	Chi square
Incubation	47.2 (36-68)	44.2 (32-56)	24.9***
Fledging	44.3 (30-60)	37.8 (30-48)	103.7***
Chi square	192.8***	46.1***	

\*\*\*,  $P < 0.001$ .

ing two successive short trips before finally returning to pelagic waters north of Crozet (Fig. 7A). Similarly, female CF 3043 started with a long trip over subtropical waters north of Crozet, foraged over pelagic waters close to the shelf, and returned thereafter to exactly the same pelagic area (Fig. 7B). Another male returned twice to the same extensive pelagic sector (Fig. 8A, tracks 4a and 4b). During long foraging trips, some birds headed for the Kerguelen shelf, and one bird tracked during two long trips returned twice to the Kerguelen shelf.

*Influence of wind.*—To evaluate the hypothesis that during long pelagic trips routes are primarily determined by wind direction, we had the opportunity to track two birds leaving Crozet at the same time for long foraging trips during the fledging period. The two birds were 60 km apart and flew so as to have the wind on the quarter (i.e. blowing from behind to one side). They followed similar courses during the first six days of their respective trips, then changed direction when the wind direction changed (Fig. 11), suggesting that wind was important in determining the route of the birds.

DISCUSSION

Our study has revealed several aspects of the foraging strategy of the Wandering Albatross. First, length of trip varied extensively according to the stage of the breeding season. Although we confirmed that Wandering Albatrosses are basically long-range pelagic feeders (Tickell 1968, Croxall and Prince 1980, Jouventin and Weimerskirch 1990), their foraging strategy can change substantially to cope with the constraints imposed by the breeding cycle. During the incubation period, pelagic trips are reduced in range and duration as the hatching of the chick approaches. This decrease in trip duration is known for several species of alba-

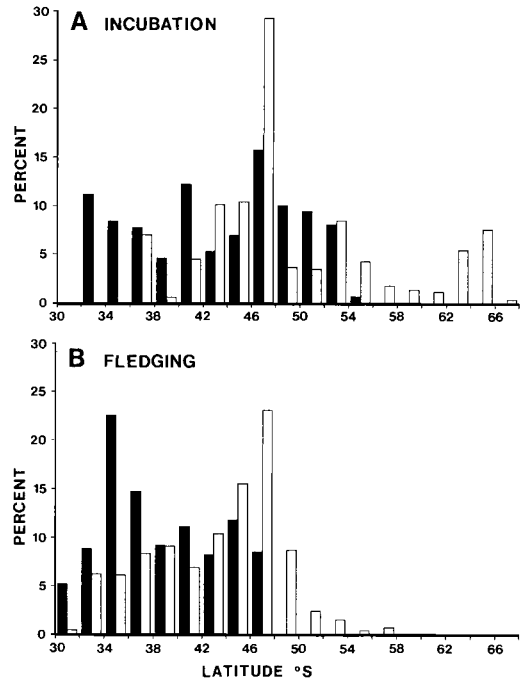


Fig. 4. Frequency distribution of locations of males (white columns) and females (black) between 30°S and 68°S during long foraging trips of: (A) incubation period ( $n = 285$  and  $1,308$  locations for females and males, respectively); and (B) fledging period ( $n = 306$  and  $978$  locations for females and males, respectively).

trosses (Tickell 1968, Tickell and Pinder 1975, Weimerskirch et al. 1986) and, generally, is assumed to ensure that on hatching the chick receives a meal quickly (Croxall 1984). During the brooding period, when the chick has to be fed every day or so, Wandering Albatrosses feed at the edge of the shelf close to the breeding colonies. After the brooding period parents resume foraging over distant waters. Although some changes in foraging behavior have been inferred from the change in duration of foraging trips, our data show clearly how substantial and clear cut are differences in foraging patterns during the different stages of the breeding season. However, pelagic feeding zones prospected in summer during incubation move north in winter. This shift to the north probably occurs because the high latitudes are ice covered during winter and there is a significant decrease in prey availability in antarctic waters compared to that in subantarctic or subtropical waters during the winter (Foxton 1956). Thus, the foraging behavior of the Wandering

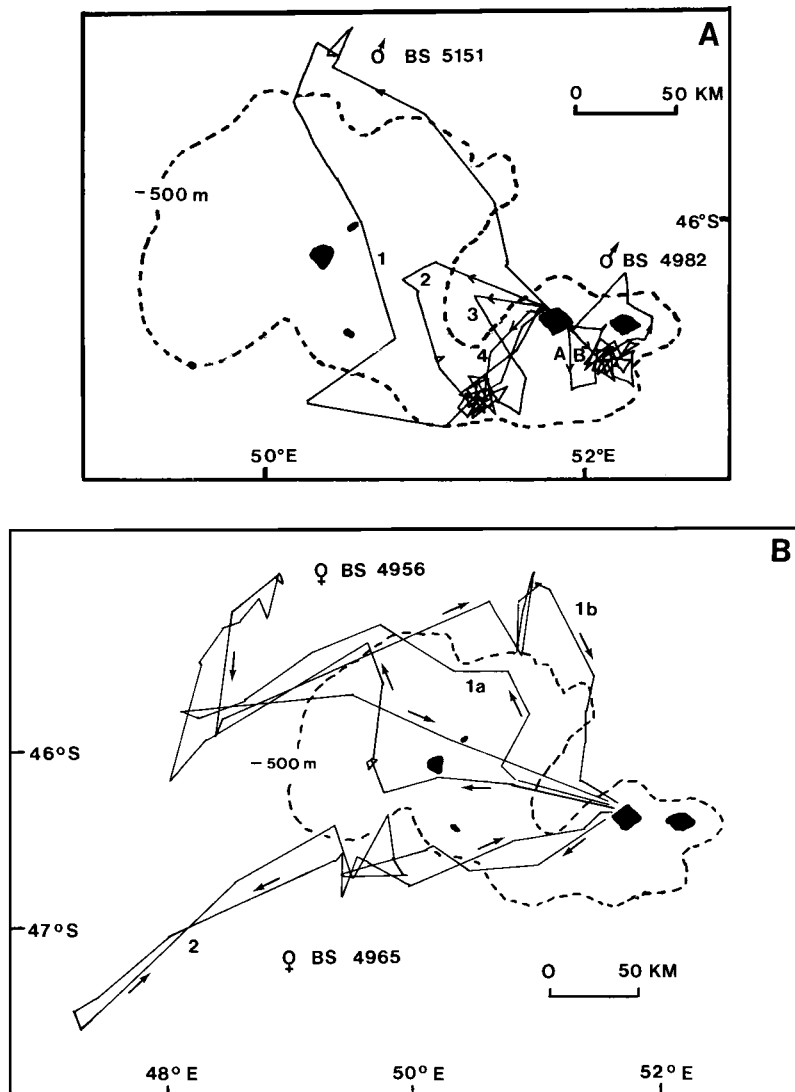


Fig. 5. Foraging trips of (A) two individual males and (B) two individual females during brooding period. Islands of Crozet group indicated in black and edge of shelf with dotted line. Four successive tracks (numbered 1-4) of male BS 5151, two successive tracks (A-B) of male BS 4982, two successive trips of female BS 4956 (1a and 1b), and one trip of female BS 4965 (2) represented. Arrows indicate flight direction.

Albatrosses appears to be influenced by constraints imposed by the breeding cycle and by changes in prey availability.

Second, in addition to being able to vary foraging tactics in relation to the different constraints of the breeding cycle, birds may mix (during the same stage of the season) long pelagic trips with short inshore trips during chick rearing. This suggests that previous deductions concerning foraging range during the chick-rearing period, based on the measurement of

feeding frequencies, are invalid in species that mix short and long distance trips.

Third, birds are able to return to specific areas in the ocean. During the short trips of the chick-rearing period, male Wandering Albatrosses returned to specific areas, at the edge of the shelf, on successive trips. These areas are restricted in size, and may be used by several birds or by only one. A particular restricted zone located at the edge of the shelf, south of Possession Island, appeared to be attractive to more than



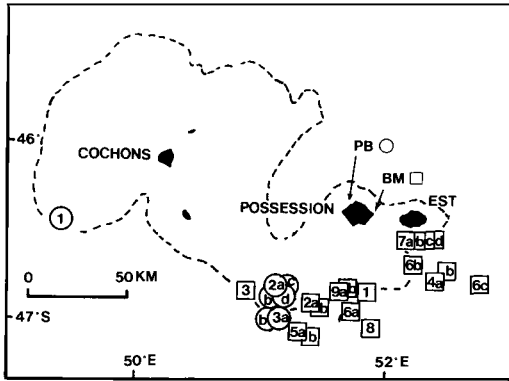


Fig. 6. Map of the Crozet shelf showing location of different oceanic sectors prospected during short trips during chick-rearing period by males originating from two colonies of Possession Island, Pointe Basse (PB, circles, three different birds) and Baie du Marin (BM, squares, nine different birds). When same bird tracked during successive trips, the area prospected is indicated with an "a" for first trip, "b" for second, etc.

two-thirds of the males tracked. These zones are likely to be areas of high food availability. The edges of shelves are often zones of turbulence with increased primary and secondary production (El Sayed et al. 1979). Complementary hypotheses could be that the birds from different colonies or from different islands forage preferentially over specific zones of the shelf. Birds from Possession Island could forage mostly over the southern edge of the shelf, south of Possession Island and East Island, whereas the birds from the large colony of Ile des Cochons could forage mostly over the extensive edge located south of that island. Our results suggest that the separation of feeding zones during the chick-rearing period could even occur between different colonies on Possession Island (Fig. 6). Such a separation of foraging zones has been detected in the Black-browed Albatross (*D. melanophris*; Weimerskirch et al. 1988) and fits with the hinterland model (Cairns 1989), which predicts that seabirds from neighboring colonies occupy nonoverlapping feeding zones and that colony size is a function of the size of these zones. If Wandering Albatrosses fit this model, it suggests that the size of the colony might be determined by the size of the feeding zone exploited during a short, but constraining, period (brooding) of the breeding cycle. During the long trips of the chick-rearing period, each bird returns to the same pelagic

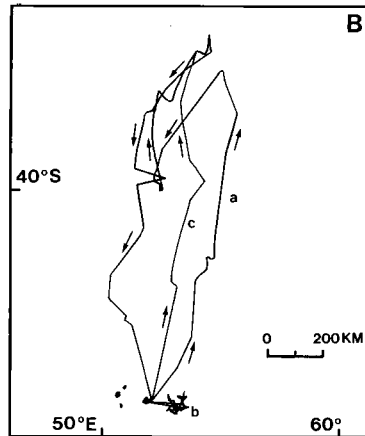
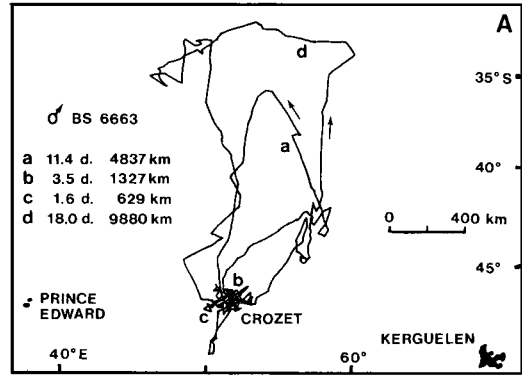


Fig. 7. Successive long and short foraging trips during chick-rearing period of one male and one female. (A) Four successive tracks (a-d) of same male (BS 6663) during chick-rearing period (27 May-30 June), with length (days) and distance covered during each trip. (B) Three successive trips (a-c) of female CF 3043, with two long trips in same pelagic sector. Track for second long trip is incomplete because batteries became exhausted.

sector, or to the inshore waters of the Kerguelen shelf. The sectors prospected are extensive, but the birds are able to return to a restricted area as shown by the successive tracks of some individuals (e.g. Fig. 6).

Fourth, different individuals seem to employ different foraging tactics. For example, during the incubation period one bird foraged close to or even over the Crozet shelf, while most other individuals foraged over pelagic waters. Conversely, during the brooding period, although most males return to specific areas at the edge of the shelf, one male made a short-duration trip across pelagic waters to reach a remote shelf. Although the individual area prospected dur-

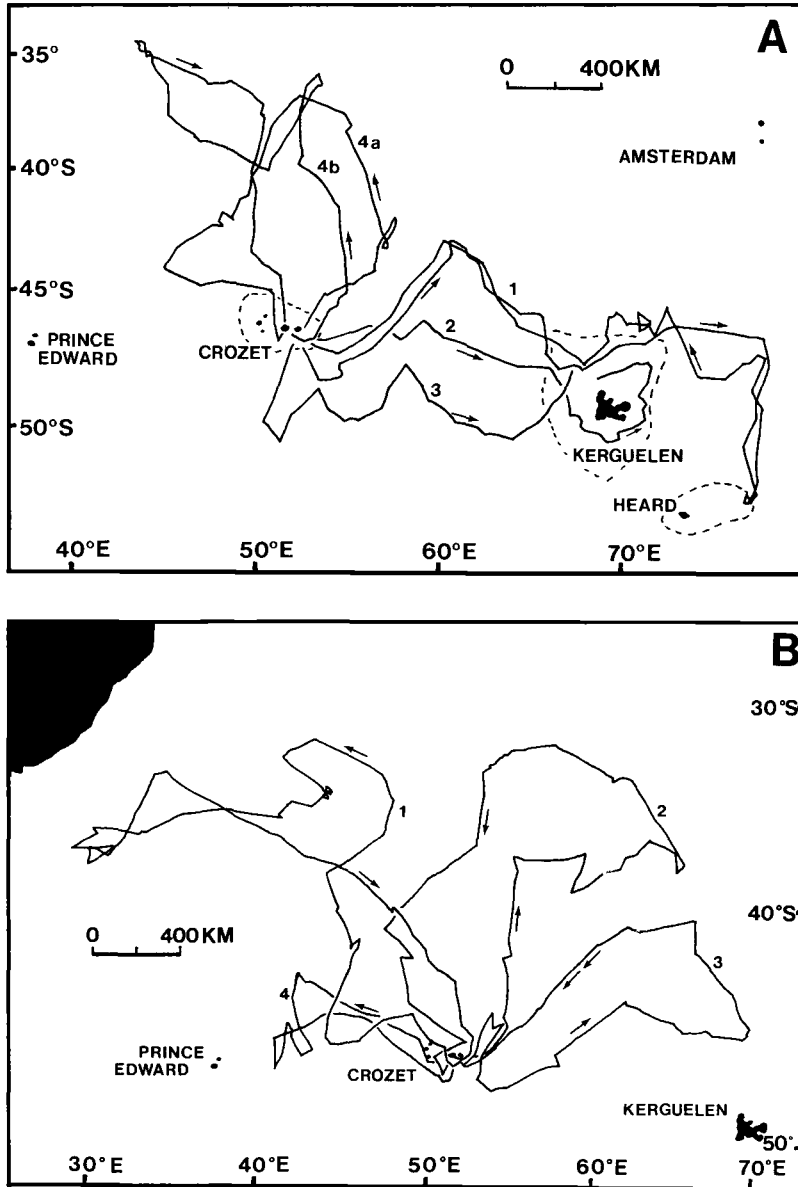


Fig. 8. Long foraging trips during chick-rearing period. (A) Two successive long trips of male BS 061 (4a, 4b) and three trips of three different males (BS 156 [1], BS 1308 [2] and BS 4138 [3] in Kerguelen area. (B) Long foraging trips in subtropical and subantarctic waters of one female (1) and three males (2, 3, 4).

ing the brooding period was the same for two-thirds of males, other males had distinct individual foraging zones. During the long trips of the chick-rearing period, most of the birds foraged over pelagic waters, but some visited the offshore waters of the Kerguelen shelf.

Fifth, the assumption that the duration of foraging trips is related to the distance the birds

have to travel from their nest to find food proved to be true for the long pelagic trips of the incubation and chick-rearing period. The close relationship observed during the latter period probably results from the fact that, during incubation, birds tended to interrupt their looping course with movements over specific oceanic sectors more frequently than they did

during the chick-rearing period. The closer relationship between the duration of foraging trips and the distance covered than with the maximum range suggests that the foraging strategy is not based on a simple return trip to a specific zone but rather on continuous foraging on a looping track. The longest distances covered were not distances travelled for commuting but distances spent foraging. For the short trips of the chick-rearing period, the relationship between time spent at sea and the range or distance covered was not significant when trips of more than 500 km were disregarded. The absence of a relationship for the inshore trips probably resulted from the fact that, during short inshore trips, birds foraged over a restricted area and probably limited their maximum range in order to return rapidly to the nest.

Sixth, although the sample size for females was small, some sex-specific differences in foraging behavior were apparent. The sex-specific differences in the foraging zones prospected during the brooding period might have resulted from competitive exclusion of the females by the larger males. Indeed, if almost all males (ca. 1,200 breeding males at this time of year, calculated from Weimerskirch and Jouventin 1987) foraged at the edge of the small Crozet shelf, intraspecific competition could be high and, consequently, access to a patchy resource could be difficult for females. By foraging farther away over neighboring pelagic waters, females may avoid competition with the larger males. During long trips of the incubation and chick-rearing periods, females tended to forage more to the north than did males. This tendency has already been detected by observations at sea of Wandering Albatrosses sexed using differences in plumage pattern (Weimerskirch et al. 1989). In the summer in the Indian Ocean, there is a larger proportion of female-plumaged birds than of males at the northern edge of the species range, whereas at the southern edge of the range, males are more abundant (Weimerskirch and Jouventin 1987).

Two distinct foraging strategies were distinguishable. They appear to be used, either alternately or mixed, to cope with the different constraints imposed by the breeding on land of a bird feeding at sea. The first strategy is that used during the long foraging trips. The route of the birds is strongly influenced by wind (see Jouventin and Weimerskirch [1990], but particularly Fig. 11). During long trips, Wandering Al-

batrosses cover great distances during daytime and remain stationary or move over short distances at night (Jouventin and Weimerskirch 1990). Prolonged absence of movements over several days, when birds drift on the sea surface, is caused by the absence of wind, which keeps albatrosses from flying (Jouventin and Weimerskirch 1990). Birds drifting with sea currents are clearly different from birds foraging actively (moving continuously) over a specific zone as observed during some incubation trips. The interruptions of long foraging loops when birds forage actively on a restricted oceanic area could relate to the presence of fishing boats. Wandering Albatrosses are well known to be ship followers and, particularly, are attracted to long-line fishing boats (Brothers 1990). Several Wandering Albatrosses from Crozet have been caught in long-line fishing gear in the subtropical waters of the Indian Ocean (Weimerskirch et al. 1985). These long-line fishing boats operate intensively in the subtropical waters north of Crozet (Brothers 1990), where three of the four birds paused in their foraging loops. The fourth bird foraged actively on a bank west of Kerguelen where trawlers operate at that time of year.

Apart from these interruptions of several days observed during incubation in some birds, they are likely to forage all along the long loops. Wandering Albatrosses feed mostly on squids (Imber and Russ 1975, Weimerskirch et al. 1986, Rodhouse et al. 1987). It was believed until recently that albatrosses catch live bioluminescent cephalopods at night (e.g. Imber and Russ 1975, Harper 1989). However some albatrosses may feed on dead squids located during the daytime (Weimerskirch et al. 1986). This suggestion has been supported by the observation that some procellariiforms feed more on squid species that float after death than on those that sink (Lipinski and Jackson 1989). Direct measurements of time of feeding in Wandering Albatrosses have now confirmed that feeding takes place mostly during the daytime, whereas at night birds mostly sleep (Weimerskirch and Wilson 1992). This fits well with our observation that birds never spent successive nights at the same location during the long foraging trips. Their routes are determined by the wind direction that is most favorable for flight, minimizing energy expenditure while maximizing the distance covered. Pennycuik (1982) estimated that with their dynamic soaring flight,

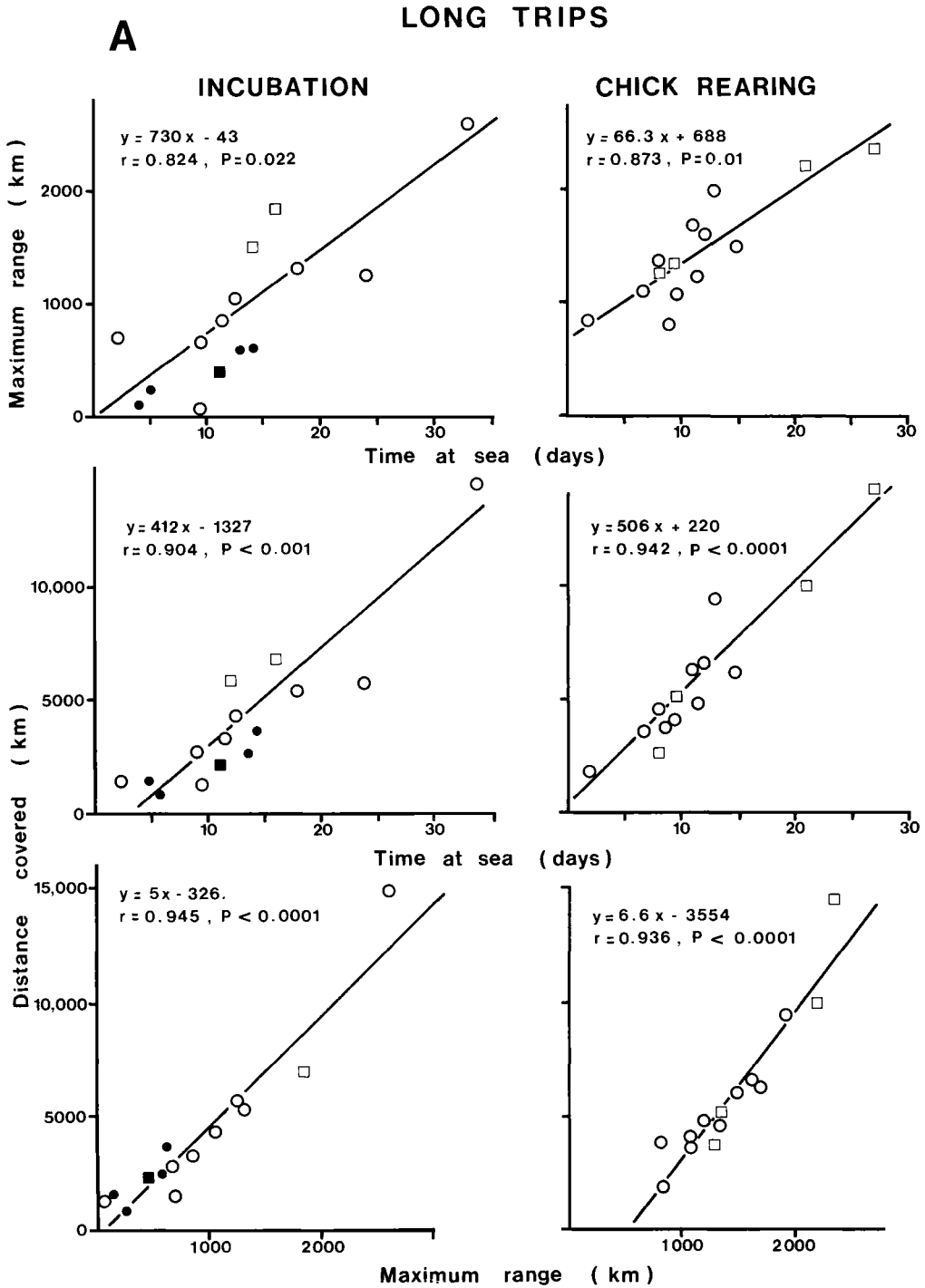


Fig. 9. Relationships of time spent at sea, maximum foraging range, and distance covered during successive stages of breeding season for (A) long trips and (B) short trips. Circles refer to males and squares to females. Black symbols refer to the late incubation period.

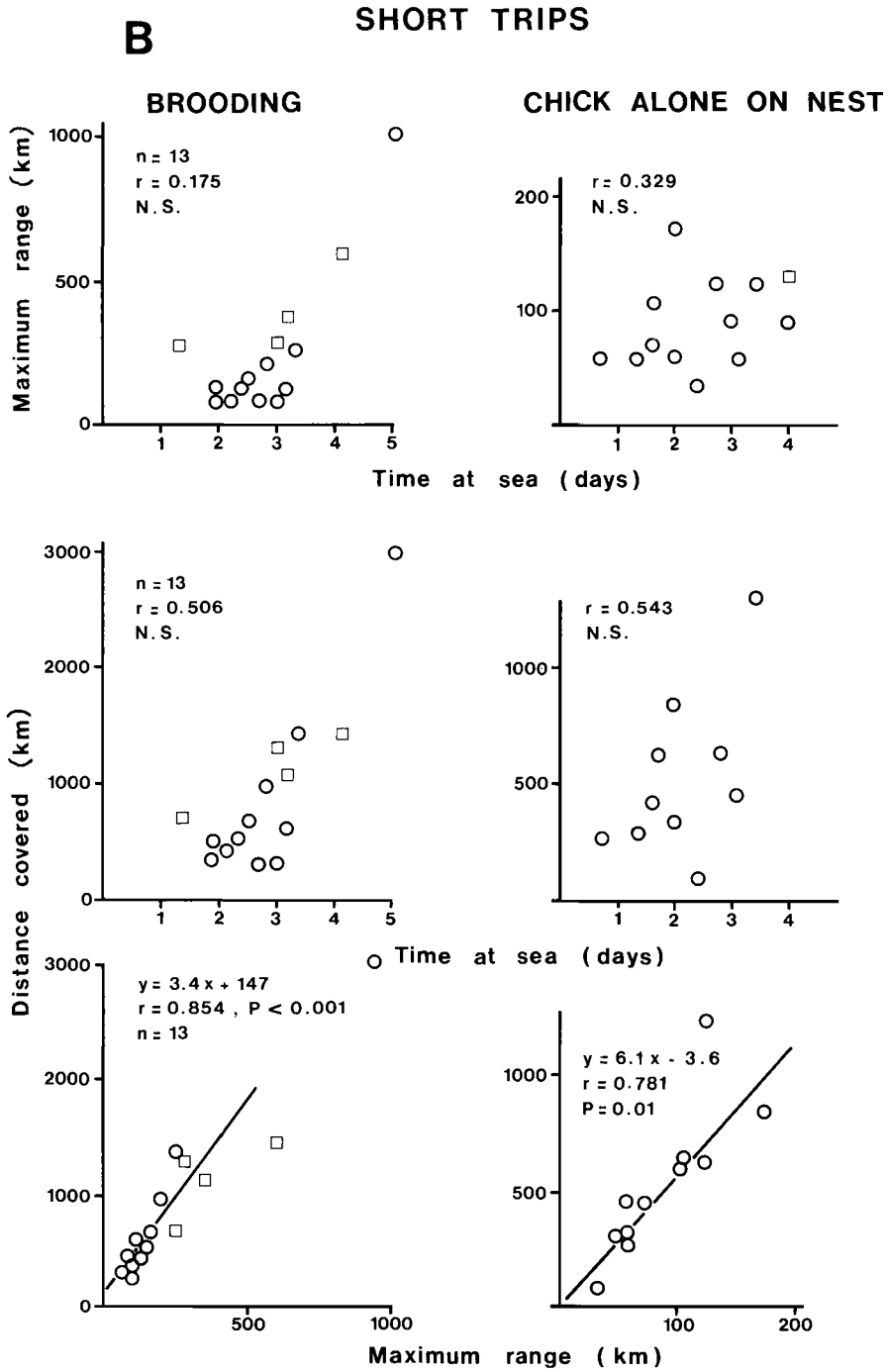


Fig. 9. Continued.

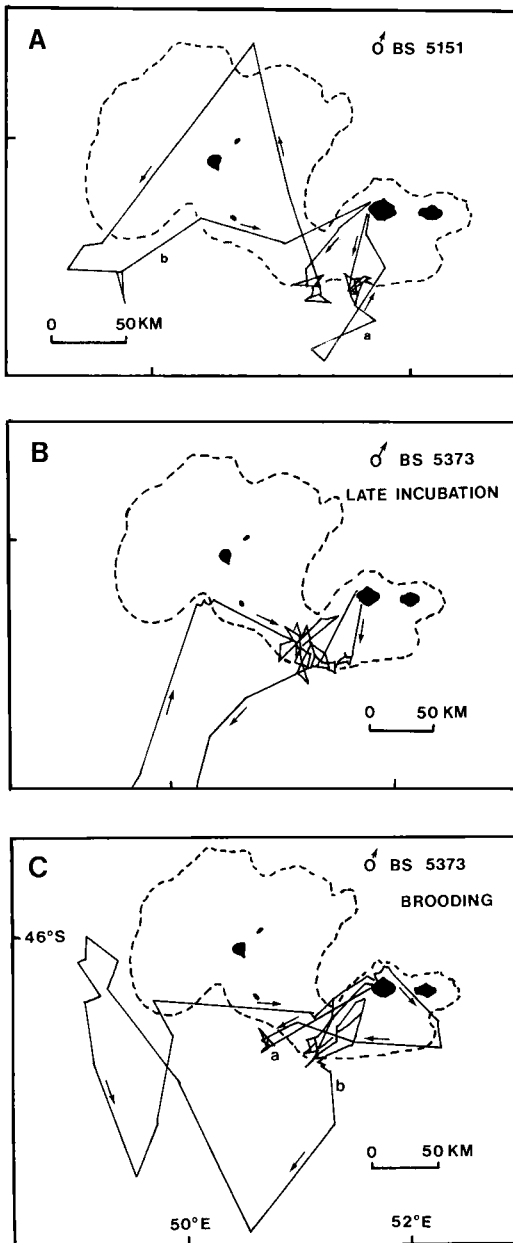


Fig. 10. Successive tracks of: (A) male BS 5151 just prior to hatching of chick (compare with Fig. 5A for successive trips of same bird after hatching); and of male BS 5373 for (B) one trip just before hatching and (C) two trips just after.

which extracts energy from the wind gradient, Wandering Albatrosses would need to consume only 1% of their body mass to cover 1,000 km: foraging over long distances, consequently,

could increase the probability of locating the sparse and scattered prey at the sea surface. Dead squid could be found in this way. Rodhouse et al. (1987) pointed out, for example, that mass mortality of squid after spawning could represent considerable but sporadic opportunities for surface-feeding seabirds. During the long foraging trips, most birds probably do not try to reach a specific area but forage continuously throughout their looping tracks. Continuous foraging during the long loops could allow the predator to scan a very large area. The surface area prospected by the Crozet population during the breeding season is very large (several millions of square kilometers). The low probability of finding sparse prey, thus, is offset by the surface area covered by each individual.

Models of optimal foraging suggest that central-place foragers should reduce the time for commuting to a minimum and stay in feeding zones until they have fulfilled their energy requirements (Charnov 1976, Orians and Pearson 1979). During long trips, Wandering Albatrosses move continuously and do not remain on specific areas except at night, suggesting that searching and exploiting resources are not mutually exclusive as assumed by the models of optimal foraging (Schoener 1971, Charnov 1976). Most theoretical work has concentrated on studies of animals facing distributions of food in distinct patches (Krebs et al. 1983), but often animals combine travelling and feeding when they move across their habitat (e.g. Krebs and McCleery 1984). Excluding the resting periods at night, the entire loop could be productive for the bird. As during the fledging period, Wandering Albatrosses catch several prey during a single trip, the transportation of prey to the central place is combined with foraging. This strategy is probably very efficient in petrels and albatrosses because for these species the food is transformed into a lipid-rich stomach oil (Clarke and Prince 1976, Warham et al. 1976). This adaptation reduces the mass of the food load while concentrating the dietary energy. Our results suggest that the food exploited by the Wandering Albatrosses during the long trips is probably not distributed in well-delimited distinct patches. Rather, these albatrosses forage for a resource with a spaced distribution. This is confirmed by direct measurements of time of feeding showing that Wandering Albatrosses swallow on average one prey every 100 km (Weimerskirch and Wilson 1992).

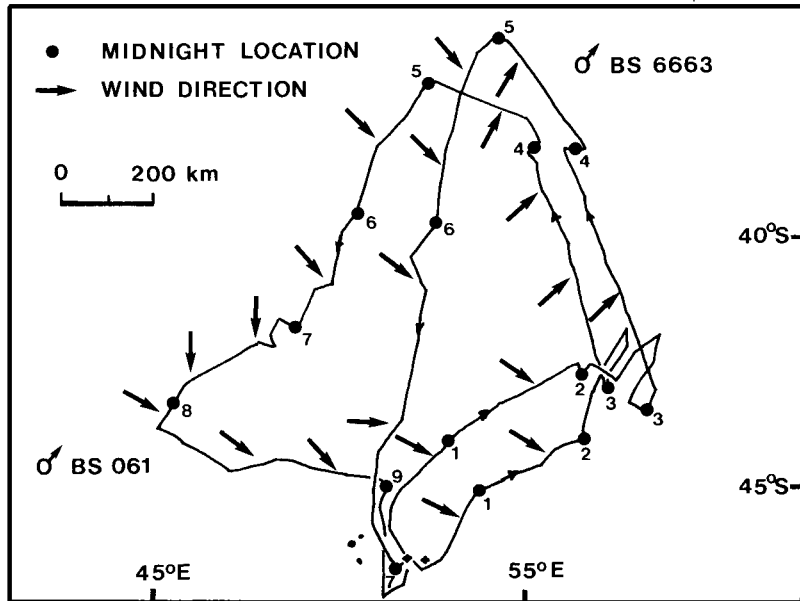


Fig. 11. Tracks of two males leaving Crozet Islands at same time on 28 May 1990, with successive-night locations indicated from 1 (night of 28–29 May) to 9 (night of 5–6 June). Arrows indicate wind direction.

Characteristics of short trips (with periods spent at specific areas), in contrast to those of long trips, are in closer accord with the central-place-foraging model. Commuting routes for short trips are likely not to be productive, and the birds remain in the same restricted area for a proportionately longer period. Either the birds locate their inshore feeding zones on the way back from their long foraging trips of the incubation period, or they return each breeding season to the same area. However, some birds changed feeding area from one short trip to the next. This suggests that either the choice of the feeding zones could be related to proximal food availability, which is evaluated during incubation for exploitation later on during the short trips, or that birds have traditional feeding zones. During the brooding period, one parent remains on the nest while the other has to find food for himself/herself and for the chick, whose needs increase rapidly. For this reason, models of energetics in breeding seabirds predict that the brooding period is probably the most constraining (Ricklefs 1983). In the Wandering Albatross, short inshore trips over the shelf area or to the neighboring pelagic waters enable parents to feed their chick frequently. However such trips could be particularly expensive energetically, because body condition

alters at this time (Weimerskirch unpubl. data). During the short trips, each bird has a preferential oceanic feeding zone to which it returns irrespective of the prevailing winds. These specific zones visited by the birds cannot be zones of trawling or long-lining because no commercial fishing activity takes place in the 370-km (200-nautical-mile) economic zone around Crozet. When birds are commuting they are likely to face adverse winds during the few days available to reach the feeding zones and return to the colony. Short travelling distances are likely to be more demanding energetically than the long foraging trips during which birds can use wind optimally to reduce foraging cost. Why then do birds not forage permanently over pelagic waters rather than alternate short inshore trips with long pelagic trips? Regular and frequent feedings increase the growth rate of chicks left alone on the nest (Schaffner 1990), increasing the chance of a chick fledging and surviving. The dual foraging strategy observed after the brooding period is probably a compromise resulting from the necessity for adult birds to feed their chick frequently without flying far from the colony and their need to forage with a minimum of energy expenditure, and thereby maintain body condition. This second requirement could only be achieved during long trips.

Based on a detailed study of feeding frequencies of males and females, a similar dual foraging strategy has been identified recently in another pelagic seabird, the Blue Petrel (*Halobaena caerulea*; Chaurand and Weimerskirch in press) and supports this hypothesis. It may be that this dual foraging strategy is a general feature of the ecology of pelagic procellariiforms (Weimerskirch et al. in press), but has not been identified previously because studies have not been able to determine which of the two parents are feeding the chick. The dual strategy probably also results in provisioning the chick with fresh food after the short trips and with a mixture of stomach oil and semidigested prey after the long trips. The prey caught during the two types of foraging trips are likely to be different, since one involves inshore foraging and the other occurs in pelagic waters. Thus, Croxall et al. (1988a) were surprised to find that the fish caught by a pelagic seabird like the Wandering Albatross were mostly species from the shelf. Conversely, Rodhouse et al. (1987) found that most of the squid were taken in pelagic waters. Given our results, we suggest that during short inshore trips Wandering Albatrosses feed on fish, whereas during long pelagic trips they forage for squid.

The existence of a dual strategy suggests that in pelagic seabirds the average rate of food intake is probably not maximized (Schoener 1971), but rather adjusted through a stereotyped foraging strategy so that the condition of the adult never deteriorates sufficiently for the bird's survival to be at risk. Models of life-history strategy predict that this risk is low in long-lived birds (Williams 1966, Weimerskirch et al. 1987), and the dual strategy could be one way of reducing this risk, while providing regular food loads to the chick. This strategy is therefore a compromise between the needs of the adult and those of the chick. It differs from the strategy predicted for long-lived vertebrates operating as long-distance, central-place foragers (Orians and Pearson 1979) that presumably forage until they have met their own requirements before collecting food for their chick (Charnov 1976, Croxall et al. 1988b). Mixing foraging in two distinct water masses for two different types of prey could permit individuals to compensate for any decrease in food availability in one area by increasing foraging effort in the other area or on another type of prey. This tactic could explain why, in Wandering Albatrosses, breed-

ing success varies so little from one season to the next (Weimerskirch and Jouventin 1987) and is not affected by local decreases in food availability (Croxall et al. 1988b).

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