

FORAGING FLIGHTS OF BREEDING THICK-BILLED MURRES (*URIA LOMVIA*) AS REVEALED BY BIRD-BORNE DIRECTION RECORDERS

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ABSTRACT.—A bird-borne data logger, which stores flight directions at regular intervals, was used to reveal the foraging patterns of Thick-billed Murres (*Uria lomvia*) breeding at Latrabjarg in northwestern Iceland. Tracked birds traveled 10 to 168 km one-way to foraging sites in a narrow sector to the northwest of the breeding colony. The pattern of foraging activity was rather constant. Outbound birds stopped briefly several times, possibly testing prey availability. The longest stops occurred at sites close by the turning point of the outbound journey. During the inbound flight, stops were less frequent and shorter than on the outbound flight, suggesting that the sequence of stops was not the expression of a disturbance caused by the instruments. Received 29 July 1996, accepted 29 May 1997.

THE THICK-BILLED MURRE (*Uria lomvia*) is a highly specialized arctic seabird with a circumpolar breeding distribution. The biology of the Thick-billed Murre has been studied in detail in the eastern Canadian Arctic, where it is an abundant breeder (see Birkhead and Nettleship 1981, Gaston and Nettleship 1981, Birkhead 1993, Gaston et al. 1994). Much information has been gathered on its foraging ecology, including diet composition, foraging pattern, and diving behavior (Gaston and Nettleship 1981, Gaston 1985, Prince and Harris 1988, Croll et al. 1992, Gaston and Bradstreet 1993). Pelagic foraging ecology and behavior of alcids heretofore have been inferred mainly from ship-based observations and aerial surveys, which have allowed the acquisition of data on spatial distribution of foraging birds around colonies and the orientation of foraging routes (see Schneider et al. 1990). However, a lack of adequate technology has prevented researchers from recording actual patterns of the feeding routes of murres, except for general features of foraging range and behavior (Gaston and Nettleship 1981, Cairns et al. 1990, Hatch et al. 1995).

Although the Thick-billed Murre is a common breeding bird in Iceland (Einarsson 1979, Gardarsson 1995), very little is known about many aspects of its biology. The breeding distribution

and population size (Einarsson 1979, Gardarsson 1995), attendance at breeding colonies (Sigfusson 1985), as well as food selection during the non-breeding season (Lilliendahl 1990) and the breeding season (Lilliendahl and Solmundsson 1997) have been studied. Owing to reports of drastic population declines of Thick-billed Murres in Canada, Greenland, and northern Norway (Barrett 1994), work on Thick-billed Murres and related species has been intensified in Iceland in order to determine the role of these seabirds in the marine ecosystem (Petersen et al. 1994).

In order to investigate foraging routes of Thick-billed Murres, we ran a series of tests on birds equipped with data-loggers that recorded and stored information related to flight directions. The direction recorder, devised by Bramanti et al. (1988) to investigate the homing behavior of pigeons (Papi et al. 1991, Ioalè et al. 1994), subsequently was used to study homing strategies of a wild species, Cory's Shearwater (*Calonectris diomedea*), subjected to passive displacement by humans (Dall'Antonia et al. 1995). Our report, therefore, represents the first successful attempt to use this instrument in a study of the spontaneous foraging activities of birds.

MATERIALS AND METHODS

Experimental birds.—The nine Thick-billed Murres used in our experiments were captured at Latrabjarg, northwestern Iceland (65°30'N, 24°32'W). Latrabjarg is a huge sea cliff (11.5 km long; mean height

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284 m) that supports an estimated 118,000 pairs of Thick-billed Murres, 298,000 pairs of Common Murres (*U. aalge*), and 230,000 pairs of Razorbills (*Alca torda*) (Gardarsson 1995).

We captured breeding murres on nesting ledges where they attended their chicks. Birds were snared from the cliff edge using a 7-m-long noose-pole and immediately weighed, measured, banded, and equipped with a direction recorder. A patch of fine-meshed, plastic-covered nylon netting was glued by cyanoacrylate on the back feathers, which had been clipped to about half of their original length. The instrument was fastened to the net by soft brass wire, enabling temporary removal when the birds were recaptured for data recovery. Murres were released at the capture site, with the exception of three that were transported by car to release sites 21, 29, and 47 km from the colony (home direction 239°, 259°, and 244°, respectively).

Of the 12 birds equipped with route recorders (nine Thick-billed and three Common Murres), three Common Murres and one Thick-billed Murre were never recaptured. We conducted no systematic observations to compare breeding success of experimental birds with that of unmanipulated birds. In attempting to maximize the recovery of recorders, we limited visits to the colony to the time necessary for recapturing the experimental birds one or two days after they had been equipped with the recorders. For the same reason, we refrained from making detailed observations to determine the prey types that experimental birds brought to their chicks.

The direction recorder.—The instrument used in our tests, devised by our research group, records the direction of the main axis of the bird's body with respect to geomagnetic north at a set time interval (see Bramanti et al. 1988, Dall'Antonia et al. 1993). In the present experiments, periods between successive data recordings were 4 or 8 s. The basic component of the device is a traditional compass equipped with a transducer to convert the angular values into electrical resistance values. Flight-path reconstruction is possible because the birds have a sufficiently constant flight speed (murres are ideal for these kinds of experiments owing to their high wing loading). The sum of the vectors between the bird's velocity with respect to the air and that of the wind (recorded in the test area) is considered the bird's actual velocity with respect to the ground. The instrument can store 32,000 bytes of data, which is sufficient for continuous recording for 35.5 or 71 h, depending on the sampling interval. The direction recorder, including the waterproof container and other components, weighed 29 g. The external measurements of the streamlined container were: width, 22 mm; height, 14 to 19 mm (with the exception of the plug, which measured 24 × 21 mm); and total length, 97 mm. The maximum cross-sectional area was 4.3 cm², corresponding to less than 5% of the estimated frontal area of a Thick-billed Murre. None of the recovered containers, which had been tested in the lab

under a pressure of 7 to 8 atmospheres, had been damaged by excessive pressure.

The compass of each device compensated for the effects of deviation from a horizontal position and thus was sufficiently accurate even if the birds' back was not horizontal during flight. Laboratory tests showed that tilting the device 30° from the horizontal plane resulted in deviations from correct directions by a maximum of 3°. Only data collected during flights were used to reconstruct travel routes. Flight data were easily distinguishable from the stable and stereotypic data acquired while birds were on the cliff. In order to distinguish data recorded during flight from data recorded during swimming or diving, we used a saltwater switch consisting of two electric wires connected to the instrument. The distal ends of the wires were glued to feathers on the bird's abdomen and thus were short-circuited by seawater whenever the bird was swimming or diving. When the electrodes were short-circuited, the direction recorder produced only two types of data. These data indicated only whether the axis of a bird's body was pointed toward the northern or southern sector of the horizon. As soon as the recorders were recovered, data were downloaded in the field to a portable computer.

Data analysis.—Data were analyzed according to standard procedures (see Papi et al. 1991; Dall'Antonia et al. 1993, 1995; loalè et al. 1994), which included corrections for local magnetic declination and the influence of winds (procedures for wind drift described in Bramanti et al. 1988). Corrections for wind drift were calculated automatically by a specially designed software package that incorporated wind data recorded at the release site.

We conducted displacement experiments to verify whether the instrument could collect meaningful data in the adverse geomagnetic conditions of our study area; these conditions included a steep inclination angle of the magnetic field vector (−76°) due to high geographic latitude, and possible magnetic anomalies caused by central volcanic complexes offshore in the vicinity of the colony (Kristjánsson 1976). Moreover, displacement experiments provided us with scale values used in analyzing data from spontaneous foraging routes. Accurate estimates of flight speed are essential for interpretation of data because the direction recorder does not record the geographic location of the birds. Instead, it generates a series of vectors whose length depends on the bird's flight speed. Displacement experiments produced homing routes between two known locations (the nest colony and the release site), thus allowing us to estimate the bird's flight speed. Our estimate of 65 km/h was very similar to that reported by Gaston and Nettleship (1981) for Thick-billed Murres (70 km/h) and by Pennycook (1987) for Common Murres (68.8 km/h). We used our estimated airspeed from the homing routes to calculate the length of the foraging routes.

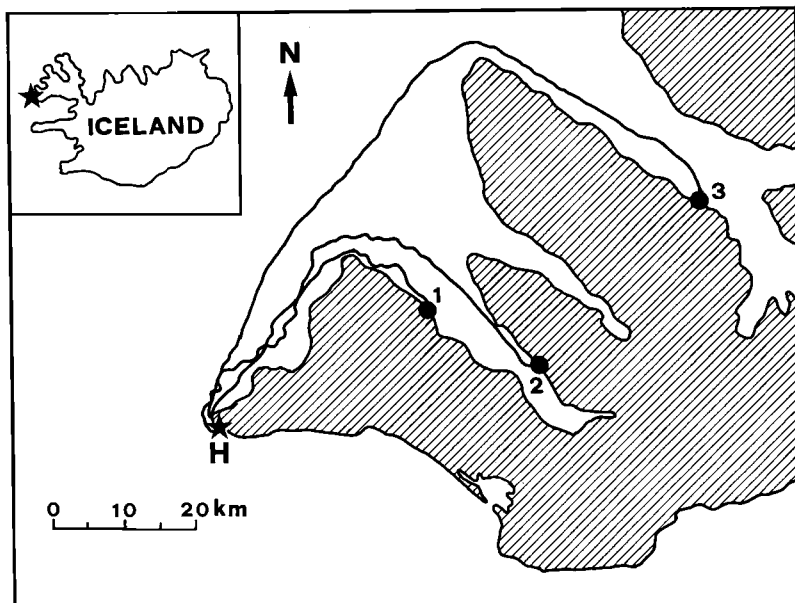


FIG. 1. Homing routes of three Thick-billed Murres that were passively displaced from their breeding colony (indicated by H and star). Numbers mark the location of the release sites.

In contrast to homing routes, these procedures did not produce a satisfactory agreement between the end of foraging tracks and the home colony. This probably was due to both passive (induced by sea currents or winds) and active (swimming) displacement during stops along the foraging path, as well as to errors in calculations caused by discrepancies between wind measurements and winds actually experienced by the birds. In order to achieve an agreement on the map between the end of the recorded route and the actual goal, we moved the starting point of the homeward leg so that the repositioned route, parallel to the recorded one, actually ended at the colony. Because of this procedure, the accumulated displacement of the entire route appears to occur only during the last stop of the outward journey (see Figs. 2 and 3), whereas it may occur at any stopping site (probably in proportion to the duration of the stop), as well as during flights. However, because the duration of the last stop in the outbound flight (or the first in the inbound flight), where sustained feeding activity occurs, is much longer than the duration of the other stops along the outbound and inbound routes, our procedure cannot have altered the shape of the routes drastically.

RESULTS

Displacement experiments—The homing routes of three displaced birds are shown in Figure 1. Shortly after release, the murres rested on the

sea surface for one to three hours; this behavior may have been induced by capture and subsequent experimental manipulations. After this period, the birds flew nonstop to the breeding colony. Homing flights of displaced birds were influenced by the local topography in that the birds never crossed land masses that occurred between release sites and the home colony. Consequently, the actual paths taken by the birds were much longer than the beelines between the release sites and the colony (36 vs. 21 km, 51 vs. 29 km, and 70 vs. 47 km in routes 1, 2, and 3, respectively; see Fig. 1).

When data collection is subjected to bias, a homing route does not end at the proper location (i.e. the bird's goal), but at a certain distance from it depending on the magnitude of the bias. The angular deviations of the track ends that we measured, with respect to the birds' goals, did not exceed 3° .

Foraging flights.—Six complete and three incomplete foraging routes of five different individuals are shown in Figures 2, 3, and 4, and the relevant data related to the birds' foraging flights are reported in Table 1. The incompleteness of three routes was caused by failure of the saltwater electrodes. It is striking that the foraging flights, all of which were disrupted by

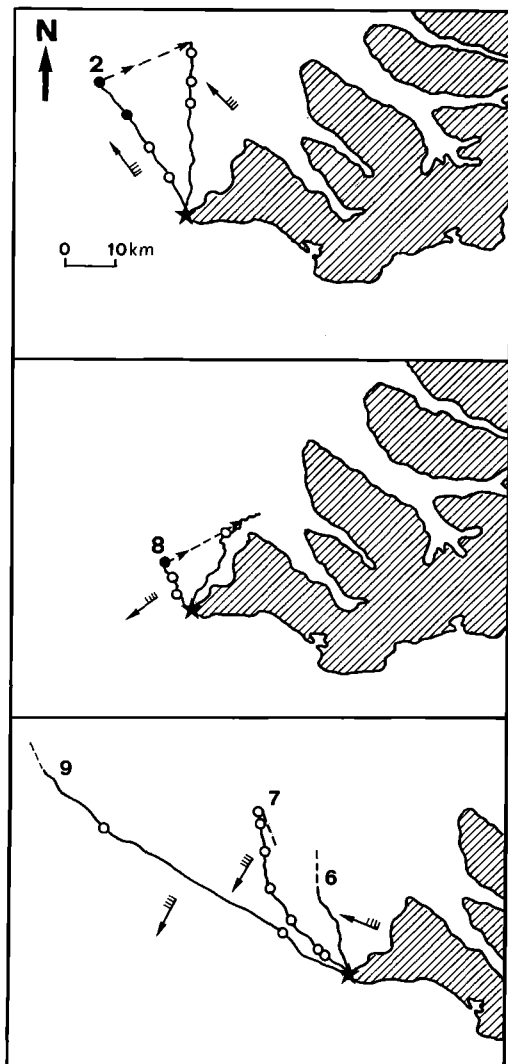


FIG. 2. Five short-distance foraging flights of breeding Thick-billed Murres. Three birds were involved: one on routes 2 and 6, one on 7 and 8, and one on route 9 (numbers as in Table 1). Foraging routes are shown by lines extending into the open sea. Open symbols indicate short stops, and filled symbols indicate long stops where sustained feeding may have occurred (significantly above the mean stop time). Dashed lines and sequence of arrows between the outbound and inbound journeys indicate the cumulative, active, or passive displacement during stops. Prevailing wind directions are indicated by arrows and mean wind speed by perpendicular flags (m/s). Due to a malfunctioning saltwater switch, we could not record the inbound path of route 7 and obtained only a part of the outbound path of routes 6 and 9.

several landings on the sea surface (Table 1), were almost rectilinear. Furthermore, the angular variation among the nine different tracks was very limited (average direction was $324^\circ \pm 11.2^\circ$ angular deviation, range 37°). This preference agrees with results of radar observations of seabird tracks near the colony carried out in the same period as the recorder tests (average reverse direction of incoming tracks = $315.5^\circ \pm 46^\circ$, $n = 186$; Gudmundsson unpubl. data). With regard to the length of the routes, foraging flights were divided into two rather homogeneous categories: some of the birds fed relatively close to the colony (10 to 37 km), whereas others performed much longer flights (128 to 168 km). In the latter case, all of the birds' goals were close to the edge of the pack ice in an area where the sea depth was at least 400 m. We recorded two successive flights of three murres (see Table 1). Bird 323889 fed twice at a short distance from the home colony (10 and 37 km; duration of trips 18 h and unknown, respectively), whereas bird 323984 fed twice at a long distance (139 and 168 km; 12.8 and 16.0 h, respectively). On the other hand, B2802 did one short (31 km; 1.9 h) and one long (128 km; 12.3 h) foraging trip; a third flight of the same bird produced only an incomplete outbound leg.

Foraging flights often were interrupted by swimming and/or diving. These stops usually were rather short, with the exception of the last one on the outward journey and sometimes the previous stop or the first of the homeward journey (see Fig. 5). In all six cases in which data from complete routes were available, the number and duration of the stops during the outbound flights were greater than those on the inbound (homeward) journeys. Birds undergoing long flights appeared to stop near the end points of birds undergoing short flights. The mean stop times on the outbound and inbound journeys were $103.1 \pm \text{SD of } 205.4 \text{ min}$ ($n = 34$) and $48.8 \pm 71.2 \text{ min}$, respectively ($n = 13$).

As mentioned above, the saltwater switch did not provide accurate recordings of flight directions when murres were swimming or diving. These data indicated only whether the direction of the bird's body axis was pointed toward the northern or southern sectors of the horizon. On the whole, these data agreed with the direction of the shift that the inbound track was subjected to, with respect to the outbound

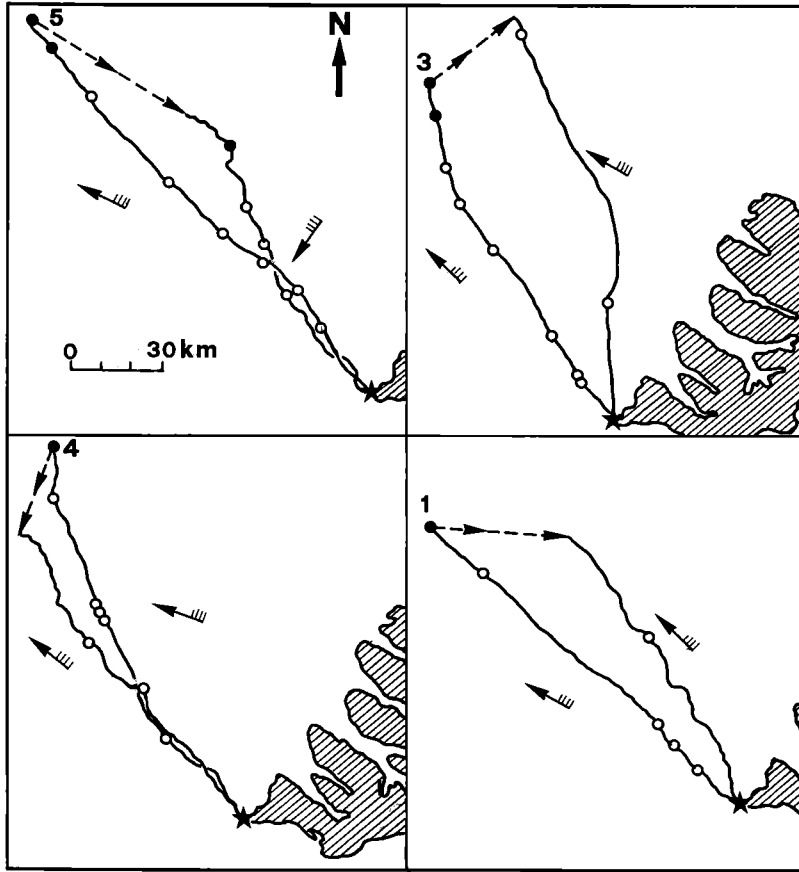


FIG. 3. Four long-distance foraging flights of breeding Thick-billed Murres. Three birds were involved: one on routes 1 and 5, one on route 4, and one on route 3. The latter bird was the same as that for routes 2 and 6 in Figure 2. Other explanations as in Figure 2.

flight, in order to achieve a geographic agreement between the end of the inbound track and the home goal. The amplitude of total displacement was globally related to the duration of the stops.

We recorded body mass of instrumented birds at the first capture and at most subsequent recaptures. Body mass among birds carrying the recorders did not change drastically (in one case mass did not change, and in another mass increased during the test period; Table 1).

DISCUSSION

The main problem with the kind of experiments we carried out is the possible disagreement between the recorded track and the bird's actual path (which is unknown). The displacement experiments demonstrated that our in-

struments can provide reliable data under the geomagnetic conditions found in our study area. We have assumed that the reason for discrepancies in the spontaneous foraging routes between the end of the calculated tracks and the birds' actual goals (the colony) was not due to a malfunctioning of the instruments, but to passive and/or active displacement of the birds during the stops. This assumption is based on: (1) close agreement between topographic features and homing routes of passively displaced birds, (2) similarity of the accumulated displacement calculated for most tracks, (3) agreement between the direction recorded by the "short-circuited" electrodes of the saltwater switches and the calculated accumulated displacement, and (4) agreement between total displacement and cumulative duration of the stops.

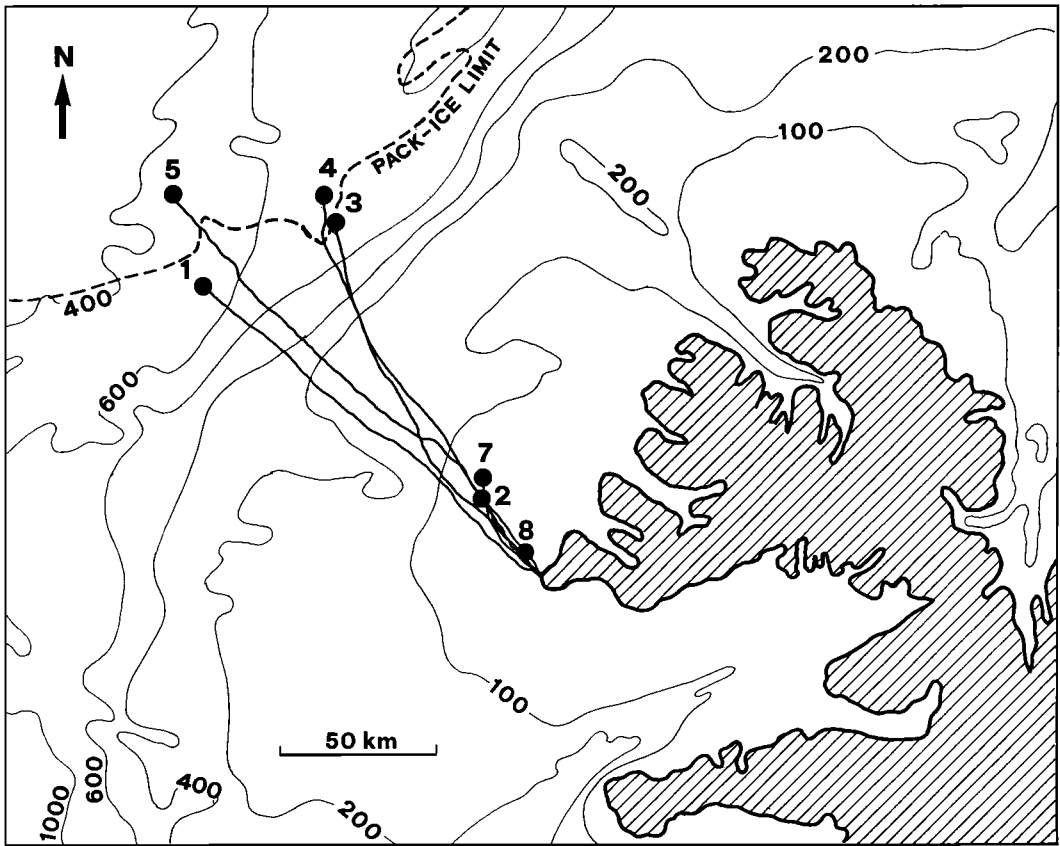


FIG. 4. Complete outbound routes together with the goals (filled symbols) of the Thick-billed Murres during foraging flights. Sea depth is given in meters and indicated by isometric lines. Dashed line indicates the pack-ice limit as revealed a reconnaissance flight of the Icelandic Coast Guard on 7 July 1995 (data from the Icelandic Meteorological Institute).

Another implicit difficulty related to the use of bird-borne devices is evaluating the effects of attaching the device and the load that may alter a bird's behavior (see Wanless et al. 1988). The added mass of the recorder increases wing loading and thereby decreases flight efficiency, whereas the added frontal area of the device may increase drag during both swimming and flight. The effects of an additional burden on the diving behavior of Thick-billed Murres were considered by Croll et al. (1992). Using an electronic recorder that weighed 35 g and had a frontal area of 4.5 cm², they estimated an increase of 4.6 and 5% in the cost of flight and thrust for swimming, respectively. This increased energy demand was considered to cause only minimal effects on the birds' behavior. We are confident that our instruments recorded the normal foraging behavior of Thick-

billed Murres because: (1) each device represented only 2.8 to 3.1% of body mass, which is below the threshold value of 5% that is considered to cause significant disturbances in behavior (Cochran 1980, Nowak and Berthold 1991, Croll et al. 1992); (2) our device was lighter and had a slightly smaller frontal area than the recorders used by Croll et al. (1992); (3) the number and total duration of stops during outbound journeys were much higher than those during inbound flights after feeding activity (the opposite would be expected if the instrument affected flight performance to any significant degree); and (4) experimental birds exhibited no significant or consistent patterns of mass loss.

The birds' tracks were divided into two rather homogeneous categories, short-distance and long-distance routes, which may reflect two

TABLE 1. Statistics for nine foraging routes of five different breeding Thick-billed Murres (each bird centered in bold) from Latrabjarg, northwestern Iceland, July 1995. Data in parentheses are incomplete routes.

Route no.	Capture/recovery	Beeline dist. (km) ^a	Route dist. (km) ^b	T _{cliff} (min) ^c	T _{out} (min) ^d	T _{in} (min) ^e	No. stops out	No. stops in	Capture mass (g)	Recapture mass (g)
323984										
1	7 July/9 July	139	288	870	646	120	5	1	1,025	970
5	9 July/10 July	168	308	261	601	357	8	4	970	—
B2802										
2	7 July/9 July	31	80	460	94	19	4	3	970	—
3	7 July/9 July	128	294	71	670	84	8	2	—	925
6	9 July/11 July	(19)	(19)	525	(19)	—	(1)	—	925	925
B2803										
4	8 July/9 July	137	312	97	452	25	6	2	925	905
323889										
7	10 July/12 July	(37)	(88)	662	69	—	7	—	995	—
8	10 July/12 July	10	46	643	1,033	29	3	1	—	990
323960										
9	10 July/12 July	(74)	(82)	(73)	(308)	—	2	—	925	935

^a Distance between colony and end of outbound flight.

^b Total length of foraging trip.

^c Time from release to first foraging flight, or time between successive trips.

^d Total time on sea during stops on outward journey.

^e Total time on sea during stops on homeward journey.

different strategies of foraging activity rather than the influence of a nonspecific factor. We do not know, however, which factors may have induced the choice of nearby versus distant feeding areas. The distance to feeding areas as recorded by our devices was highly variable (10 to 168 km) but fell within the range estimated by Gaston and Nettleship (1981) using aerial surveys at Prince Leopold Island (foraging flights of up to 200 and 100 km during prelaying and chick rearing, respectively).

The most relevant aspect of our results is the identification of the murres' foraging grounds. The birds tended to make rectilinear flights to sites that were included in a narrow sector of the surrounding areas. Owing to the rectilinear nature of the flights, an estimate of the direction of foraging areas might also be obtained from the headings of murres as they left the colony. Conversely, foraging locations could not be estimated based on trip duration due to high variability in the number and duration of stops. The pattern of foraging activity, as revealed by our recorders, was rather constant: the birds flew to the northwest and made several brief stops during the outbound journey (usually <20 min), the first of which was within 30 km of the colony. Because winds typically came

from the southeast during the study period, we could not verify whether the birds' directional preferences were influenced by wind direction or by other elements, such as variation in prey abundance. All of the flights appeared to be directed toward the pack ice, and longer flights actually ended close to the edge of the ice. Perhaps brief stops during outbound journeys enabled birds to evaluate prey availability along the route (cf. Gaston and Nettleship 1981), whereas sustained foraging occurred during longer stop(s) at the end of outbound flights. This idea is supported by recent experiments, conducted in the same study area, in which recorders were equipped with a depth meter (Benvenuti et al. unpubl. data). According to these preliminary results, during brief stops on outbound flights birds make low numbers (1 to 8) of dives at variable depths, whose pattern is similar to a V-shape (nonstop downward and upward movements), after which they resume flight in the same direction as the previous leg. This dive profile is very different from that recorded during true feeding activity, in which the birds descend steadily to a certain depth at which they remain for most of the dive duration (flattened U-shape). Foraging activity includes a long sequence of these dives, with each

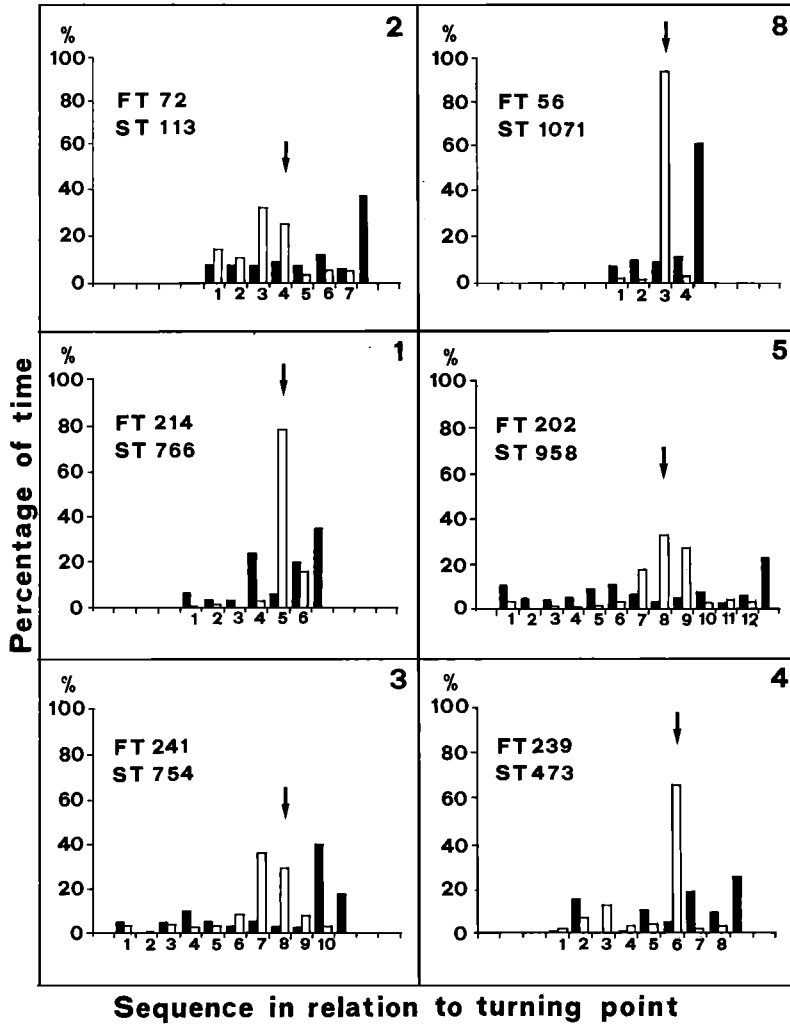


FIG. 5. Sequence of flights and stops during foraging flights of Thick-billed Murres. Black bars indicate the percentage of total flying time (FT, min) during each flight, and open bars indicate the percentage of total time spent on the sea surface (ST, min) during each stop. Numbers in top right indicate routes in Table 1. Numbers on the abscissae refer to the sequence of stops; the last stop on the outbound flight is indicated by an arrow.

dive at a similar depth (see Croll et al. 1992). From our preliminary results it also is apparent that the longer stops, in which sustained feeding occurs, include long periods in which the birds apparently are inactive (no flights or diving). Breeding Common Murres have been shown to spend 70 to 85% of the time away from the colony on the sea surface (Cairns et al. 1990).

Determining the methods used by murres to orient while flying to and from foraging areas was beyond the scope of our study. Familiar to-

pographic cues can be used to determine the correct path to the feeding grounds, whereas the pattern of sea waves may be helpful in maintaining it. The inbound journey may be based on true navigational ability or on a "route-reversal" strategy. However, visual cues cannot be ruled out because the coast may be visible from the foraging areas, at least during favorable weather. Because the release sites for the displaced murres were not so distant as to be beyond the birds' familiar range, familiar topographic cues also may have guided the

birds home. The idea that flocks base their orientation on visual cues also was considered by Gaston and Nettleship (1981). These authors, however, suggested an alternative hypothesis by Sergeant (1951), who proposed that out-bound flocks orient by reversing the flight path of incoming flocks and thereby determine the position of currently favorable feeding grounds. This idea suggests that the colony can function as an "information center" for the transfer of information about the location of suitable feeding areas (Ward and Zahavi 1973). However, as a consequence of lateral movement with respect to the direction of the flight path during the foraging activity indicated by our birds (cf. Figs. 2 and 3), this mechanism would not necessarily bring an outgoing bird exactly to the feeding area of an incoming bird.

Our results show that the route recorder, designed by our research group for investigation of pigeon homing, also is useful in studies of the foraging flights of wild birds. The present results pose several interesting questions regarding the pattern of foraging routes during different phases of the breeding cycle, in different meteorological conditions, and in different species (*Uria lomvia* vs. *U. aalge*), which call for further experiments.

ACKNOWLEDGMENTS

We thank Kristjan Lillindahl of the Marine Research Institute in Reykjavik for help at various stages of this study. We also are grateful to Alberto Ribolini for helping to reconstruct foraging routes from the recorder data, Trausti Jonsson and Thor Jakobsson of the Icelandic Meteorological Institute for providing wind data and information about sea-ice distribution, and Adda and Jonas at Breidavik Guesthouse for their hospitality during our stay. The manuscript benefited by valuable comments of the reviewers: A. E. Burger, D. A. Croll, and W. A. Montevecchi. This study was a cooperative project of the University of Pisa and the Icelandic Institute of Natural History; the Italian authors were supported by grants from the Italian Research Council (C.N.R.) and the University of Pisa.

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Associate Editor: J. M. Eadie