TIME ALLOCATION AND FORAGING PATTERN OF CHICK-REARING RAZORBILLS IN NORTHWEST ICELAND

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Abstract. A newly modified, bird-borne data-logger was used to investigate the flight activity and diving behavior of foraging Razorbills (*Alca torda*) breeding at Latrabjarg, northwest Iceland. The recorders allowed us to determine with high time-resolution all relevant movements in 47 complete foraging trips of 29 different Razorbills during two successive breeding seasons, 1997 and 1998. In 1998, direction recorders equipped with a compass recorded 19 foraging routes of 10 different Razorbills. The trips consisted of a number of flights interrupted by short series of diving bouts by which the birds seemingly explored areas for prey availability. Foraging occurred at sites where Razorbills stopped, dived, and rested for a long time before returning to the nest by a single flight or a sequence of a few flights. The majority of dive profiles ($n = 17\ 095$ dives) consisted of nonstop downward and upward movements to depths rarely greater than 35 m, and never exceeding 41 m. There was considerable diurnal variation in foraging behavior, expressed by more frequent and shallower dives around midnight. The Razorbill's diving pattern turns out to be very different from that reported for Thick-billed Murres (*Uria lomvia*) breeding in the same colony. Considerable differences in duration of trips, average number of dives, and time allocation were observed between the two breeding seasons, suggesting differences in foraging conditions for the birds.

Key words: Alca torda, breeding, data-loggers, diving pattern, Iceland, Razorbill, time-budget.

Asignación de Tiempo y Patrones de Forrajeo durante la Crianza de los Pichones en *Alca torda* en el Noroeste de Islandia

Resumen. Un archivador de datos recientemente modificado que se acopla a las aves fue utilizado para investigar la actividad de vuelo y el comportamiento de buceo de individuos reproductivos de *Alca torda* en Latrabjarg, noroeste de Islandia. Los equipos nos permitieron determinar con una alta resolución de tiempo todos los movimientos relevantes en 47 viajes de forrajeo de 29 individuos diferentes durante dos temporadas reproductivas sucesivas (1997 y 1998). En 1998, equipos registradores de dirección equipados con una brújula, registraron 19 rutas de forrajeo de 10 individuos diferentes. Los viajes consistieron en un número de vuelos interrumpidos por pequeñas series de sesiones de buceo por medio de las cuales las aves aparentemente investigaban la disponibilidad de presas en distintas áreas. El forrajeo tuvo lugar en sitios donde las aves se detuvieron, bucearon y descansaron por un período prolongado antes de regresar al nido en un solo vuelo o en una secuencia de pocos vuelos. La mayoría de perfiles de buceo ($n = 17\ 095$ inmersiones) consistieron en movimientos ininterrumpidos hacia abajo y hacia arriba a profundidades rara vez mayores de 35 m y nunca superiores a 41 m. Hubo una variación considerable en el comportamiento de forrajeo a lo largo del día, con inmersiones más frecuentes y menos profundas alrededor de la medianoche. Los patrones de buceo de *A. torda* resultan ser muy diferentes de los que se han reportado para individuos de *Uria lomvia* que se reproducen en la misma colonia. Se observaron diferencias considerables en la duración de los viajes, el número promedio de inmersiones y la asignación del tiempo entre las dos épocas reproductivas, lo que sugiere que existieron diferencias en las condiciones de forrajeo para las aves.

INTRODUCTION

Seabirds exploit marine niches using a variety of species- and family-specific foraging tech-

niques (Furness and Monaghan 1987, Montevecchi 1993). Penguins and auks pursue their prey using wing-propelled dives (Burger 1991). The Razorbill (*Alca torda*) is an example of a ''pursuit-diving'' auk that forages on a variety of marine fish and invertebrate species, with fish largely predominating over invertebrates (Lilliendahl and Solmundsson 1997). Both mem-

bers of a pair provision their chick with loads composed of a single fish or several fish (up to 20 minute or larval fishes, usually about 3–4 times per day; Harris and Wanless 1986, 1989, Benvenuti et al., in press). Compared to penguins and other large birds, there have been few studies of the pelagic behavior of Razorbills (Harris and Wanless 1986, 1989, Barret and Furness 1990, Benvenuti et al., in press), due to their small body mass and high wing loading which imposes severe restraint on the weight and size of recording devices with which they can be fitted.

We used minute electronic data-loggers, devised and manufactured in our lab, on breeding Razorbills in northwestern Iceland. The objectives of our study were to (1) quantify the duration and timing of flight activity and foraging trips; (2) estimate the spatial distribution of foraging sites; (3) quantify the number, duration, and profile of dives carried out during foraging trips; and (4) compare the pattern of foraging activity and time allocation recorded at the same colony in two consecutive breeding seasons.

METHODS

STUDY AREA AND BIRDS

The 58 Razorbills used in our field tests (19 in 1997 and 39 in 1998) were captured at Latrabjarg, northwestern Iceland (65°30′N, 24°32′W). This huge sea cliff, 11.5 km long, supports an estimated breeding population of 230 000 pairs of Razorbills (the largest known colony of this species in the world), 118 000 pairs of Thick-billed Murres (*Uria lomvia*), and 298 000 pairs of Common Murres (*Uria aalge*; Gardarsson 1995). The study was carried out between 4 and 17 July 1997 and between 3 and 14 July 1998. During this period at Latrabjarg, the sun is below the horizon for only 2 hr day^{-1}, and fair light conditions exist even around midnight.

Birds were snared on the ledges from the cliff edge using a 7-m noose-pole and immediately weighed, measured, banded, and equipped with a data-logger. All the birds we used were attending a chick (1–11 days old at the time of capture of the adult). When the exact age of a chick was unknown, it was estimated by comparing the chick's level of development with that of known-age chicks. The instrument was fastened by soft brass wire to a patch of fine-meshed netting glued on the back feathers (de-

TABLE 1. The types of data-loggers used in 1997 and 1998 on breeding Razorbills at Latrabjarg, northwest Iceland, the number of tagged birds from which we obtained data, and the number of complete foraging trips recorded. ER = Event recorder, FR = Flight recorder, DR = Direction recorder. Different individuals were tagged each year.

Year	Type	Mass (g)	Flight sensor	Depth sensor	Compass	No. of birds	No. of trips
1997	ER	28.0	×	×		11	13
	FR	18.5	×			4	6
1998	ER	28.0	×	×		18	34
	DR	25.0	×		×	10	20[a]

[a] Due to failure of one compass, DR recorded 20 trips and 19 routes.

tailed attachment method in Benvenuti et al. 1998). The average time from capture to release was 14 min (range 4–32), depending on whether the birds were transported to the nearby lighthouse or manipulated at the cliff edge. We stopped the indoor manipulation of the birds as soon as we realized that chicks, left alone in the nest, were attacked by prospecting, nonbreeding adult Razorbills, which usually perch near the nests. Further manipulations in 1998 involved injection with doubly labeled water prior to the release of 14 of the 39 tagged birds, to measure the field metabolic expenditure (Hansen et al., unpubl.). After capture and subsequent manipulations, the great majority of the birds returned to the nest within 5 min from release, and resumed the normal brooding behavior.

For the purpose of avoiding excessive disturbance to the birds, which might have affected the recovery rate of recorders, we limited our visits to the colony to the time necessary for recapturing the tagged birds one or more days after they were equipped with the recorders. Therefore, we refrained from making observations on prey types carried to the chicks and other aspects of the birds' breeding biology.

DATA-LOGGERS AND BIRD MANIPULATIONS

The instruments used in our tests (see Table 1) were modified versions of a direction recorder designed by researchers at the Istituto di Elaborazione dell'Informazione, C.N.R., Pisa, Italy (Dall'Antonia et al. 1993), and used in a series of tests on the homing strategies of pigeons and of Cory's Shearwaters (*Calonectris diomedea*)
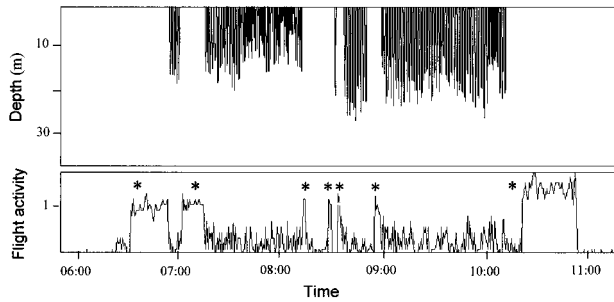
FIGURE 1. Data collected by event recorder (ER in Table 1) during one foraging trip of a Razorbill breeding at Latrabjarg, northwest Iceland, from 06:31 to 10:49 on 15 July 1997. In the lower section flight activity recorded by one microphone is shown. Flight (indicated by asterisks) is clearly distinguishable from swimming and diving. During the stops, a depth meter recorded the diving profile of the foraging bird (top section).

(Papi et al. 1991, Ioalé et al. 1994, Dall'Antonia et al. 1995, 1999).

The data-loggers used in 1997 (ER in Table 1) were equipped with a depth meter (operative range 0–70 m, resolution 0.3 m), and a flight sensor (a small modified microphone) in order to distinguish flight activity from activities at the nest or sea (Fig. 1). The memory capacity was 128 kB, and the time between successive recordings was set at 4 sec for the depth meter and 40 sec for the flight sensor. This schedule allowed continuous recording for 5 days. The external width of the streamlined container was 22–33 mm, height 13–18.5 mm, and total length 80 mm. The instruments, including the water-proof container and the batteries, weighed 28 g (about 4–5% of the bird's body mass). Five birds were equipped with a smaller type of data-logger (FR in Table 1) in which the depth meter was replaced by two short electric wires emerging from the container. These wires were designed to short-circuit while submerged in sea water, but due to frequent shallow dives with a brief surface time in between (sometimes shorter than 4 sec), this switch was not entirely effective, inducing us to rely only on diving data from ER-type instruments (data from the flight sensor in FR units, however, were included in our analysis). The external width of the streamlined container was 22–26 mm, height 13–18.5 mm, and total length 62 mm. The instruments weighed 18–19 g (about 3% of the bird's mass).

In 1998 we again used two types of instruments. One was identical to the event recorders (ER in Table 1) used in 1997, except that the sampling frequencies of the flight sensors were set at 6 sec. The other type was a direction re-corder (DR in Table 1) supplied with a compass (see Dall'Antonia et al. 1993, 1995, Benvenuti et al. 1998, for details) and a flight sensor, but no depth meter. Sampling frequencies of both the compass and the flight sensor were 6 sec. The compass of each device compensated for the effect of deviation from horizontal positions (see details in Benvenuti et al. 1998). We tagged 14 Razorbills with direction recorders in order to study the birds' foraging routes and directional preferences. The direction recorders, including the waterproof container and the batteries, weighed 25 g (about 4% of the bird's mass). The external width of the streamlined container measured 22–31 mm, the height was 13–22 mm, and the total length 90 mm. All containers of ER, FR, and DR devices were made of epoxy and carbon fibers. They had all been tested in the lab to a pressure of 5 atm (the lighter versions used in 1997) or 10–20 atm prior to application, and none of the recovered containers was damaged by excessive pressure.

Whenever possible, we tagged both mates of a pair (4 pairs in 1997 and 9 in 1998). In one case only, both members of a pair carried data-loggers simultaneously (30.1 hr). Four out of 58 birds equipped with recorders were never recaptured. Due to technical failures, a further four of the tagged birds did not produce data and, for a direction-recorder-equipped bird, we have the timing of the trip, but not the route. Data recorded for seven individuals were excluded from analyses either due to loss of the chick after the release of the tagged bird (killed by nonbreeders) or because the birds did not carry out foraging trips while tagged. None of the devices fell off. The total material presented here there-

fore comprises 47 trips performed by 29 individuals equipped with depth meter and flight sensor (event recorder), and 20 trips (19 routes) of 10 individuals carrying a compass and flight sensor (direction recorder). For a further 4 individuals carrying flight sensors only we recorded 6 trips which provided data on timing and duration of the foraging trips.

STATISTICAL ANALYSIS

The data from the recorders were downloaded in the field to a portable computer, and later analyzed in the lab by a specially designed software package (A. Ribolini, unpubl.). Data from flight sensors allowed us to reconstruct the foraging trips as a series of flights and stops of known duration. During the stops, the birds dived or rested; the time on the sea surface, therefore, included dive time, interdive intervals (time between dives) and post-dive intervals (time between dive bouts, or between a dive bout and a flight when birds were swimming or resting). The return to the nest was clearly detected from compass tracks followed by a long period of inactivity or, for the loggers without compasses, from the pattern of flights and stops in combination with diving activity. Data from direction-recorders confirmed that birds do not pay very short visits to the nest. The only likely exception was one bird tagged in 1997, which may have visited the nest after a foraging trip and subsequently left again on a very long trip (68.7 hr; excluded from analyses), as the chick was lost soon after we released the tagged bird.

During stops, diving activity was computed as number of dives, dive depth, dive duration, mean and maximum descent and ascent rate, and bottom time (time between the end and start of uninterrupted descent and ascent profiles). Time spent at the surface within and between dive bouts was also computed. Two series of dives were considered to belong to different bouts when the surface interval between them was 90 sec or longer. During surface intervals, sensors did not distinguish between active swimming or simple sitting on the sea surface. A detailed analysis of parameters related to diving behavior is in preparation and will be reported in another paper specifically dealing with the birds' diving performance. In order to compensate for small oscillations of the zero line reported by the depth sensor, we excluded all dives shallower than 1 m when analyzing dive depth.
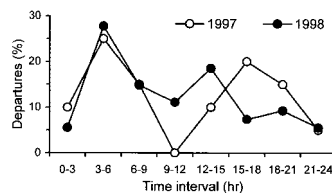

FIGURE 2. Percentage of Razorbill departures for foraging trips, from Latrabjarg, northwest Iceland, in three-hour intervals during the day.

Time of day in this paper is reported as the correct celestial time (UTC − 90 min). Between-year differences in body mass, duration of foraging trips, duration of flight during trips, number and duration of stops, and number and duration of dives during the stops were tested by the two-tailed t-test, or Mann-Whitney U-test when a normality test failed. Tested data were independent from each other: data recorded in two or more trips performed by the same bird were used as mean values in subsequent analysis. The only exception regards the comparison between trips performed in low-light conditions (around midnight) and in full-light conditions: some birds accomplished both low-light and full-light trips, which were included and analyzed in two separate groups. The Watson U^2 test (Batschelet 1981) was used to evaluate differences in the directional preferences between Razorbills and Thick-billed Murres. Mean values are given $\pm$ SD, and statistical significance is recognized at $P < 0.05$.

RESULTS

FORAGING TRIPS

In both breeding seasons studied, departures to foraging trips peaked in the early morning, with a second peak occurring in the afternoon (Fig. 2). In 1997 the overall mean trip duration was 17.1 $\pm$ 7.4 hr, ranging from 4.0 to 30.8 hr. In 1998, the mean overall duration of foraging trips was significantly shorter at 13.1 $\pm$ 6.3 hr, ranging from 1.6 to 30.4 hr (Mann-Whitney test, U = 2.1, n_1 and n_2 = 15 and 28 in 1997 and 1998, respectively, $P < 0.05$).

During the trips carried out in 1997, the birds spent on average 2.3 $\pm$ 0.7 hr (range 0.7–3.8 hr) flying. Based on an assumed flight speed of 58 km hr^{-1} (Pennycuick 1990), this corresponds to a 133 $\pm$ 41 km flight (range 40–220 km), or to a maximum one-way foraging distance ranging between 20 and 110 km. The average flight du-
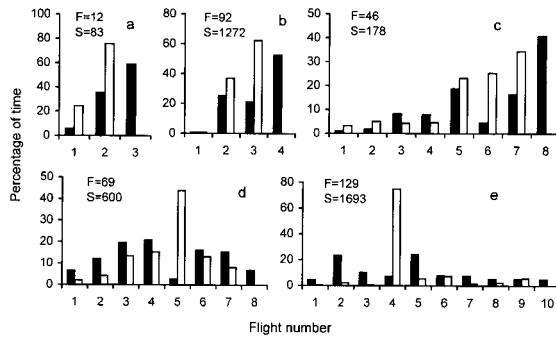
FIGURE 3. Examples of flight and stop sequences during foraging trips of five Razorbills (a–e). Solid bars indicate the percentage of total flight time during each trip, and unfilled bars indicate the percentage of total stop time (on the sea surface or diving) during each trip. Numbers on the x-axis refer to the sequence of flights during a single foraging trip. F and S refer to the total flight and stop times (min).

ration in 1998 was significantly shorter than in the previous year (1.3 ± 0.7 hr, range 0.2–3.1 hr; t_{41} = 4.8, P < 0.001), corresponding to 70 ± 41 km, or to a one-way flight range of up to 4–90 km.

The number of stops per foraging trip was highly variable and different between years. The mean number of stops in 1997 (11.4 ± 4.9, range 6–25) was significantly higher than in 1998 (6.5 ± 3.8, range 1–20, t_{41} = 3.6, P < 0.001). In most cases, the longest stops, where the most foraging activity occurred, were the last stops of the whole trip. From there the bird returned home by a single nonstop flight or a small number of flights (examples of this typical pattern are shown in Fig. 3a–c). Deviations from this pattern occurred, e.g., with the longest flight in the middle of the trip (Fig. 3d), or the longest stops made at the beginning of the trip (Fig. 3e). If we divide the total flight time into two equal parts, it should correspond approximately to the outbound and inbound flights. Comparison of the number of stops in each half shows that the number of stops in the first half was greater than that in the second in 71 out of 72 trips (1997 and 1998 pooled, binomial test, P < 0.001). The average number of stops in the first and second half of the trips was 8.2 and 4.2 in 1997, and 4.3 and 2.0 in 1998, respectively.

In 1997, the birds' average body mass at capture was 591 ± 33 g, (range 535–650). During the time they were carrying the recorders, four birds increased their weight, whereas all others lost weight. Average body mass at recapture was 570 ± 27 g, and the average mass loss was 10.1 g day^{-1} (1.7%), ranging between +19 and −31

g day^{-1} for individual birds. In 1998, the birds' average body mass at capture and recapture was 619 ± 37 g (range 555–705 g) and 582 ± 38 g, respectively. The average mass loss in 1998 was 22.1 g day^{-1} (3.5%; range +5 to −52 g). The between-year difference in the initial body mass was statistically significant (t_{46} = 2.5, P < 0.02). In 1998 the daily mass loss, as a percentage of the initial mass, was significantly larger than in 1997 (t_{44} = 2.4, P < 0.02, two recaptured birds were not weighed).

TIME ALLOCATION

The analysis of time spent on different activities during the trips is based only on birds bearing event recorders equipped with depth-meters (Table 1). The event recorders allowed us to reconstruct the daily time allocation of chick-rearing Razorbills (Table 2). In 1997 the birds spent on average 15% of their time flying (0.7–3.8 hr), 32% diving (1.5–10.6 hr) and 53% on the sea surface (1.5–15.8 hr) during the foraging trips, which lasted on average 14.8 hr. The time on the sea surface includes both the interdive surface intervals (13%, 0.6–4.2 hr), which actually are a part of the foraging behavior, and post-dive intervals (swimming or resting, 40%, 0.5–14.2 hr). The corresponding figures for 1998 (Table 2), for foraging trips which lasted an average of 11.2 hr, were the following: 11% of the time was spent flying (0.1–3.1 hr), 20% diving (0.2–7.3 hr) and 69% on the sea surface (0.9–25.8 hr); the interdive surface time was 11% (0.1–3.2 hr) of the total, and post-dive intervals 58% (0.6–24.1 hr).

For 23 birds we recorded two or three con-

TABLE 2.   Time allocation of breeding Razorbills at Latrabjarg, northwest Iceland in July 1997 and 1998. Only data related to foraging trips of birds supplied with instruments with both flight sensors and depth meter (ER in Table 1) are summarized. Duration of various activities each year are given as mean values (hr ± SD) per trip, and as percentages of total trip duration.

	1997	Percent of trip	1998	Percent of trip
No. of foraging trips	13		34	
No. of birds tested	11		18	
Duration of foraging trips	14.8 ± 7.1		11.2 ± 6.6	
Flight time	2.3 ± 0.8	15	1.2 ± 0.8	11
Diving time	4.7 ± 2.5	32	2.3 ± 1.7	20
Interdive surface time	2.0 ± 1.0	13	1.2 ± 0.9	11
Post-dive time	5.9 ± 4.0	40	6.5 ± 4.8	58

secutive trips, thus providing 29 measurements of the time spent at the cliff between foraging trips (data pooled across both years and all recorder types). The birds spent about 50% of their time at the cliff and 50% on trips (average 11.6 ± 6.6 hr at the cliff and 11.4 ± 6.4 hr on trips). Assuming that the two mates provision their chick similarly (see Wagner 1992), and that they never leave the chick alone in the nest, this result indicates that partners spend almost no time together at the nest site. This could be tested by simultaneously equipping both mates with recorders, which we did only once. During 30.1 hr that the two mates were monitored simultaneously, each bird accomplished one complete and one incomplete trip, and in all cases the mate on duty departed on a foraging trip within minutes after the arrival of the partner.

Based on conversion equations proposed by Diamond et al. (1993) and assuming that the two mates contribute equally to chick provisioning,

FIGURE 4.   Duration of trips and time spent flying by foraging Razorbills compared to the estimated age of their chick ($r = 0.39$ and 0.43, respectively, $F_{1,52} = 9.0$ and 11.3, $P < 0.01$).

the energy expenditure of Razorbills at Latrabjarg during the chick rearing phase can be calculated for the 1997 and 1998 seasons. These calculations give the following average daily energy expenditure per bird: 1183.3 and 1065.6 kJ, respectively. The average trip duration, 17.1 and 13.1 hr in 1997 and 1998, respectively, indicate that the Razorbill chicks received a total of 1.4 and 1.8 feeds day^{-1}.

For data collected in 1998 ($n = 54$ trips, Table 1), the duration of trips and the flying time were positively and significantly correlated with the estimated age of the chick (Fig. 4). Because the timing of breeding of Razorbills at Latrabjarg is fairly well synchronized, the duration of the trips and flights and the progress of the breeding season (as number of days from the start of the field tests) also gave weak but significant positive correlation ($r = 0.35$ and 0.28, respectively; $F_{1,52} = 7.1$ and 4.3, $P < 0.02$ and 0.05). In order to distinguish between the influence of chick age and progress of the season on the flight time and trip duration, partial correlations were computed; a significant effect of chick age on flight time ($r = 0.36$, $P < 0.02$), but not on trip duration ($r = 0.22$, $P > 0.1$), was found. Considering the birds equipped with depth meters, a statistically significant positive correlation also emerged between the underwater time in foraging trips and chick age ($r = 0.41$, $F_{1,32} = 6.4$, $P < 0.02$).

DIRECTIONAL PREFERENCES

Our direction recorders yielded 19 foraging routes from 10 different birds. The birds' directional preferences are shown in Figure 5, which reports the approximate position of the 19 feeding sites (the last stop on the foraging route). The birds showed a clear tendency to forage to the north of home (mean direction 6°); the dis-
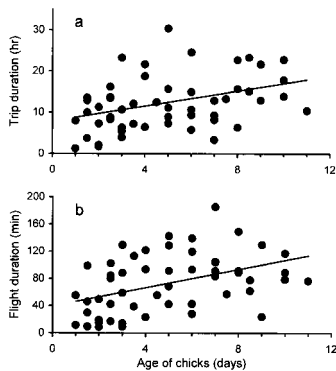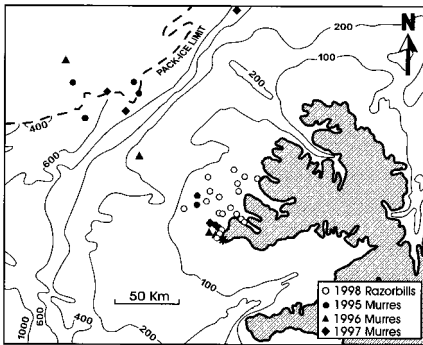
FIGURE 5. Foraging sites of Razorbills (unfilled circles; 1998) and Thick-billed Murres (solid symbols; 1995–1997), as revealed by bird-borne direction recorders. Symbols indicate the approximate position of the last stop sites in the outbound legs of foraging trips, where most foraging occurred. The asterisk indicates the location of the breeding colonies at Latrabjarg, northwest Iceland. The pack-ice limit, indicated in the top right sector, was recorded by the Icelandic Coast Guard in July 1995; in subsequent breeding seasons, the pack-ice limit could have been at a different distance from the colony. The ice covered only a fraction of the sea surface where feeding sites beyond the pack-ice limit are located.
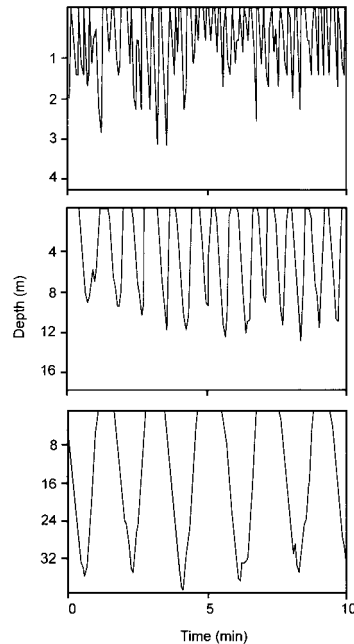

FIGURE 6. Three examples of diving profiles of Razorbills diving to different depths, approximately 2, 10 and 30 m. They were all recorded on the same sampling interval (4 sec) and are drawn on the same time scale.

tribution of the feeding sites is different from a random distribution (Reyleigh test, $P < 0.001$), and significantly different from that exhibited by Thick-billed Murres breeding at the same colony site in previous years (327°, Watson U^2 test, $P < 0.01$, Benvenuti et al. 1998, Gudmundsson et al., unpubl.). The mean distance of Razorbill feeding sites from the colony, as represented by the farthest point in the outbound leg of each foraging route, was 29.0 ± 17.3 km.

DIVING BEHAVIOR

Razorbills dived in bouts, where consecutive dives were to similar depths (Fig. 1). The majority of the dive profiles were V-shaped (76% and 81%, in 1997 and 1998, respectively, Fig. 6), with nonstop downward and upward movement at a mean velocity of about 1 m sec^{-1} (both maximum recorded descent and ascent velocity were 2.4 m sec^{-1}). In contrast to Thick-billed Murres (Croll et al. 1992), Razorbills spent a very short time at the bottom; the mean bottom time was 8.9 and 7.7 sec in 1997 and 1998, respectively.

In 1997, the birds made on average 515 ± 219 dives in each foraging trip. In 1998, the number of dives per foraging trip was lower, but not sig-

nificantly different from that recorded the year before (mean 339 ± 260; $t_{27} = 1.9$, $P < 0.08$). The mean immersion time in trips performed in 1998 was 147 ± 86 min, significantly shorter than in the previous season (226 ± 79 min; $t_{27} = 2.5$, $P < 0.02$). The frequency distribution of dive depths was very similar in both years (Fig. 7). Over 70% of the dives were shallower than 15 m, with most dives between 5 and 10 m deep. Dives exceeding 35 m were rare (1997 and 1998
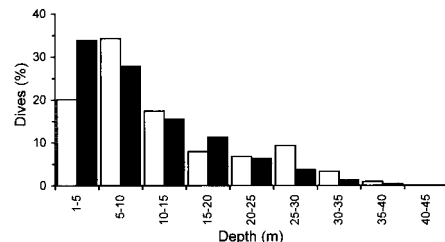

FIGURE 7. Percentage of dives by depth for breeding Razorbills carrying data-loggers in 1997 (open bars, $n = 6650$) and 1998 (solid bars, $n = 10\ 445$), in Latrabjarg, northwest Iceland.
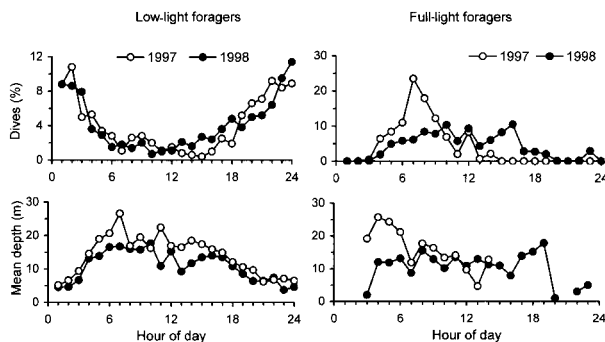
FIGURE 8. Percentage of dives and average depth by hour of day during foraging trips of breeding Razorbills. Left panel refers to low-light foraging (most dives occur around midnight) and right panel to full-light foraging (foraging does not include midnight). 1997 low-light and full-light foraging: $n = 5626$ and 1024 dives, respectively; corresponding figures for 1998 data: $n = 7268$ and 3177.

pooled, 103 out of 17 095 (0.6%) of recorded dives) and the deepest was 41 m.

Diving activity was not randomly distributed over the day, but tended to follow two quite different patterns. The birds that started the foraging trip in the morning, with very few exceptions, concentrated their foraging activity between 05:00 and 09:00 (in 1997) or around noon (in 1998), whereas the great majority of those which left in the afternoon tended to be most active in the hours around midnight (Fig. 8). It is worth noting that fair light conditions are available around midnight, as a consequence of the fact that the sun is below the horizon for only 2.5 hr day^{-1} during the study period. Low-light foragers, during the trips performed in 1997, accomplished a higher number of dives (703 ± 131) than diurnal full-light foragers (205 ± 121). The corresponding figures for 1998 are 519 ± 291 and 159 ± 130 dives. Pooling the data from the two seasons, it turns out that low-light and full-light foragers performed 610 ± 242 and 184 ± 140 dives, respectively ($t_{35} = 6.7$, $P < 0.001$). There was also a clear diurnal pattern in dive depth; dives occurring around midnight were much shallower than those occurring around noon (Fig. 8).

DISCUSSION

BIRD REACTION TO MANIPULATION

The use of bird-borne devices should always be coupled with an evaluation of possible negative reactions and consequent effect on the birds' normal behavior (Wilson et al. 1986, Wanless et al. 1988, Calvo and Furness 1992). Effects may include: (1) alteration of the normal sequence of events related to nest attendance and foraging behavior; (2) increased wing loading and thereby decreased flight efficiency; or (3) increased drag during both swimming and flight.

Although we cannot exclude that the devices may have affected the time allocation results, we believe that the instruments recorded normal foraging behavior of Razorbills for the following reasons: (1) The mass of the instruments was only 3–5% of total body mass of the birds tested; loads less than 5% of body mass are generally considered to cause negligible constraints on birds' behavior (Cochran 1980, Croll et al. 1992). We are however conscious that alcids, due to their high wing loading, may be more vulnerable than other birds to the effects of extra loads. It is therefore worth noting that the devices did not cause significant cumulative effects; no significant relationship was found between body-mass variation and the time carrying the devices ($r = 0.24$, $F_{1,40} = 2.4$, $P > 0.10$). (2) The number of stops during the first half of the total flight duration was significantly higher than that in the second half (the inbound flight). The opposite would be expected if the instruments affected the flight ability and diving performance to any significant degree; in fact, during the inbound flight, which occurs after such energetically expensive activities as flying and diving, the birds carry the food for their chick. The higher number of stops in the outbound trip than in the inbound trip cannot be considered a simple 'adjustment' to the device, because the same pattern was also recorded for the second or third trips of the same birds. This indicates that the stops are the expression of a strategy

aimed at testing the area for prey availability. (3) Our study is based on a comparison between birds' behavior recorded in two successive breeding seasons. Both years, the birds were carrying the same or similar devices, which should have produced similar disturbance. Therefore, the significant differences which emerged in several aspects of the foraging patterns are unlikely to have been caused by non-specific disturbance due to the instruments. (4) Some of the birds increased their body mass while carrying the recorders, and the average mass loss (as a percentage of the pre-test body mass) is similar to that reported in similar investigations on Thick-billed Murres (Croll et al. 1992). In addition, the loss of body mass could be a normal event for Razorbills during the chick rearing phase, as reported for Thick-billed and Common Murres (Gaston 1985, Croll et al. 1991, Gabrielsen 1996).

FORAGING BEHAVIOR AND TIME ALLOCATION

Our instruments allowed us to record the timing of a number of behavioral events throughout the foraging trips of breeding Razorbills. These events are performed as a sequence of flights, stops, and bouts of dives. This pattern suggests that the birds interrupt their flights to test prey availability, until a favorable area is found where main foraging activity occurs. The return to the colony is more or less straight, as indicated by the fact that, in most cases, the flight-stop sequence ends with a single long flight or a few flights. Data from direction recorders confirm this pattern, which is similar to that described for Thick-billed Murres breeding at the same colony (Benvenuti et al. 1998, Gudmundsson et al., unpubl.) and in high-arctic Greenland (Falk et al. 2000). Thick-billed Murres exhibited a strong northwestern directional preference, the shortest way to the pack-ice edge, where plankton is usually abundant. In 1997, our measurements indicated for Razorbills a potential foraging range of 20 to 110 km, but directional preferences were not registered. The foraging routes recorded in 1998 show that Razorbills have a directional preference significantly different from that in Thick-billed Murres. Their routes tended to be directed in a wide range north of the home colony, leading them to coastal areas and the mouths of the large fjords which characterize the coast north of the colony. It is

worth noting, however, that this comparison between Razorbill and Thick-billed Murre directional preferences is based on data recorded in different years for the two species. Therefore, we cannot rule out the possibility that directional preferences of these two species are the same within breeding seasons.

Our data showed a tendency for the birds to begin foraging trips either in the early morning or afternoon, but in successive trips individuals did not consistently leave at one of these times. Therefore, departure times do not seem to be controlled by a sex-related pattern of nest attendance as reported for Thick-billed Murres (Gaston and Nettleship 1981). Due to the aggressiveness of nonbreeding prospectors, the chick cannot be left alone at the nest, despite favorable weather conditions. Therefore, the return of the partner regulates the departure time.

For more than half of the time spent on each foraging trip the Razorbills were at the sea surface (53% and 69% in 1997 and 1998, respectively). This time includes the interdive intervals (13% and 11% of the total duration of trip) during which the birds catch their breath and recover from the strain of the previous dives. The remaining part of the surface time (40% and 58% of the time spent in a trip) is seemingly spent inactive, possibly to digest and to restore normal physiological conditions before performing the inbound trip to the nest. A similar pattern can be inferred from data on Common and Thick-billed Murres (Cairns et al. 1990, Benvenuti et al. 1998).

The duration of the trips and the distance flown correlate positively with the age of the chicks and the progress of the breeding season. Partial correlation indicates that the age of the chick is the more important factor. It is an interesting observation that the birds with larger chicks carried out longer trips to more distant foraging areas, and dived for an increasingly long time than birds caring for small chicks. Whether this change is due to depletion of profitable prey in the vicinity of the colony, or changed prey choice, we have no means of saying.

A comparison of the data collected in 1997 and 1998 indicates that the 1998 breeding season was more favorable than the 1997 season. The following arguments support this conclusion: in 1998 (1) the birds were significantly heavier at capture than in 1997, despite the same

timing and similar stage of the breeding cycle; (2) the flight duration (distance flown) was significantly shorter; (3) the duration of foraging trips was significantly shorter; (4) the number of dives per trip was only 60% of that recorded in 1997; and (5) a smaller proportion of each foraging trip was spent on diving activity. According to our analysis, the Razorbills in the 1998 breeding season seem to have fed their chicks 43% more often and with only 90% of the energy expenditure as compared to the previous year. Furthermore, in 1997, due to seemingly poorer conditions, the fledging time may have been longer, thereby resulting in even greater energy expenditure.

Our data indicate that the two mates spend a very short time together at the nest site during chick rearing. This is confirmed by our non-systematic observations at the cliff and by the data recorded for the two mates that were tagged simultaneously.

DIVING BEHAVIOR

The Razorbill's diving profile is different from that of the flattened U-shape usually exhibited by murres (Croll et al. 1992, Falk et al. 2000, Gudmundsson et al., unpubl.); the majority of the dive profiles have a V-shape, with nonstop downward and upward movements. Similar devices used in 1997 at the same site on chick-rearing Thick-billed Murres (Gudmundsson et al., unpubl.), reported that only a minority of the dive profiles were V-shaped. The bottom time for Razorbills is very short, and significant deviation from the descending or ascending paths is infrequent. In addition, dives are shallower than those reported for the Common and Thick-billed Murres (Croll et al. 1992, Falk et al. 2000, Gudmundsson et al., unpubl.), and the surface recovery time shorter than that reported for murres following dives to comparable depths. This interspecific difference between species characterized by similar ecological adaptation could suggest that short bottom times in Razorbills is due to disturbance caused by the devices. This is contradicted by the fact that all tagged Razorbills showed the same diving pattern, including those which were able to increase their body mass during the time they carried the recorder. The different shapes of the diving profiles between Razorbills and murres is probably based on different foraging techniques or prey selection by the two bird species: murres often prey on crustaceans (except when chick rearing), whereas Razorbills seem to depend on fish (Croll et al. 1992, Lilliendahl and Solmundsson 1997).

The time when foraging trips started appeared to determine the subsequent diving behavior: birds that left in the afternoon or evening (low-light foragers) were hampered by poor light conditions which precluded deep foraging. This disadvantage was probably counterbalanced by an increased availability of prey at shallow depths during the darkest part of the day (vertically migrating prey is at its minimum depth during the darkest part of the day, Croll et al. 1992). Light conditions allowed birds that left in the morning to forage at deep levels in the water column and to reach prey at its maximum depth. The need for deep dives to reach vertically migrating prey was however counterbalanced by the smaller number of dives required for diurnal foraging. Whether low-light or full-light foraging is more favorable is difficult to evaluate as we do not know the prey chosen and the amount or energy content of prey taken. Low-light foraging, despite the possible availability of prey at shallow depth, seems to require higher energy expenditure than diurnal foraging, as shown by the diving time reported for low-light and full-light foragers. Low-light foragers dived for a time significantly longer (79 min, on average) than that recorded for full-light foragers.

Our results show that dives deeper than 35 m are quite rare, and no dives exceeded 41 m. This depth, however, cannot be considered a limit imposed by physiological constraints, as reports of incidental catches in fishing nets (Piatt and Nettleship 1985) and observations from a submersible (Jury 1986) have shown that Razorbills are capable of diving to depths of 120–140 m. Their ability is not likely to exceed far beyond this range, as diving capabilities are strongly influenced by body mass, and significant allometric relationships have been reported (Piatt and Nettleship 1985, Prince and Harris 1988, Barret and Furness 1990, Burger 1991). The fact that the maximum depth recorded in our study is drastically shallower than that allowed by the birds' physiological capabilities might suggest the devices impaired the diving performance of the tagged birds. Our data, however, are in agreement with those recorded by Harris et al. (1990) on Razorbills breeding in the Isle of May (Scotland), where birds equipped with small capillary

tubes (1 g) never dived deeper than 32 m (the sea depth in this area reaches 60 m). In addition, in studies carried out at other colony sites (Benvenuti et al., in press), the maximum depth reached by Razorbills equipped with the same devices as those used in this study was similar to that reported here (43 m). Apart from the dive depth, Razorbills at different colony sites, or in successive breeding seasons, exhibited significantly different foraging strategies, despite the fact that the same types of devices had been used (Benvenuti et al., in press). This indicates that the birds' behavior recorded by our data-loggers is not related to the effects of the manipulations, but is the expression of adaptations to contingent local factors which influence the availability and spatial distribution of prey.

ACKNOWLEDGMENTS

LITERATURE CITED

BARRET, R. T., AND R. W. FURNESS. 1990. The prey and diving depth of seabirds on Hornøy, North Norway, after a decrease in the Barents Sea capelin stock. Ornis Scandinavica 21:179–186.

BATSCHELET, E. 1981. Circular statistics in biology. Academic Press, New York.

BENVENUTI, S., F. BONADONNA, L. DALL'ANTONIA, AND G. A. GUDMUNDSSON. 1998. Foraging flights of breeding Thick-billed Murres in Iceland as revealed by bird-borne direction recorders. Auk 115:57–66.

BENVENUTI, S., L. DALL'ANTONIA, AND P. LYNGS. In press. Foraging behaviour and time allocation of chick-rearing Razorbills Alca torda at Græsholmen, central Baltic Sea. Ibis.

BURGER, A. E. 1991. Maximum diving depth and underwater foraging in alcids and penguins. Canadian Wildlife Service Occasional Paper 68:9–15.

CAIRNS, D. K., W. A. MONTEVECCHI, V. L. BIRT-FRIESEN, AND S. A. MACKO. 1990. Energy expenditures, activity budgets and prey harvest of breeding Common Murres. Studies in Avian Biology 14:84–92.

CALVO, B., AND R. W. FURNESS. 1992. A review of the use and the effects of marks and devices on birds. Ringing and Migration 13:129–151.

COCHRAN, W. W. 1980. Wildlife telemetry, p. 507–520. In S. D. Schemnetz [ED.], Wildlife management techniques manual. The Wildlife Society, Washington, DC.

CROLL, D. A., A. J. GASTON, A. E. BURGER, AND D. KONNOF. 1992. Foraging behavior and physiological adaptation for diving in Thick-billed Murres. Ecology 73:344–356.

CROLL, D. A., A. J. GASTON, AND D. G. NOBLE. 1991. Adaptive mass loss in Thick-billed Murres. Condor 93:496–502.

DALL'ANTONIA, L., P. DALL'ANTONIA, S. BENVENUTI, P. IOALÈ, B. MASSA, AND F. BONADONNA. 1995. The homing behaviour of Cory's shearwaters (Calonectris diomedea) studied by means of a direction recorder. Journal of Experimental Biology 198:359–362.

DALL'ANTONIA, P., L. DALL'ANTONIA, AND A. RIBOLINI. 1993. Flight path reconstruction of birds by a route recorder, p. 544–549. In P. Mancini, S. Fioretti, C. Cristalli, and B. Bedini [EDS.], Biotelemetry XII, Proceedings of the XII international symposium on biotelemetry. Litografia Felici, Pisa, Italy.

DALL'ANTONIA, P., L. DALL'ANTONIA, A. RIBOLINI, P. IOALÈ, AND S. BENVENUTI. 1999. Pigeon homing: site simulation experiments with bird-borne direction recorders. Behavioural Processes 44:331–339.

DIAMOND, A. W., A. J. GASTON, AND R. G. B. BROWN. 1993. Studies of high-latitude seabirds. 3. A model of the energy demands of the seabirds of eastern and Arctic Canada. Canadian Wildlife Service Occasional Paper 77:1–36.

FALK, K., S. BENVENUTI, L. DALL'ANTONIA, K. KAMPP, AND A. RIBOLINI. 2000. Time allocation and foraging behaviour of chick-rearing Brünnich's Guillemots Uria lomvia in high-arctic Greenland. Ibis 142:82–92.

FURNESS, R. V., AND P. MONAGHAN. 1987. Seabird ecology. Blackie, Glasgow, UK.

GABRIELSEN, G. W. 1996. Energy expenditure of breeding Common Murres. Canadian Wildlife Service Occasional Paper 91:49–58.

GARDARSSON, A. 1995. Numbers and distribution of Common Murre Uria aalge, Thick-billed Murre U. lomvia and Razorbill Alca torda in Iceland. Bliki 16:47–65.

GASTON, A. J. 1985. Energy invested in reproduction by Thick-billed Murres (Uria lomvia). Auk 102:447–458.

GASTON, A. J., AND D. N. NETTLESHIP. 1981. The Thick-billed Murres of Prince Leopold Island. 1981. Canadian Wildlife Service Monograph Series, No. 6.

HARRIS, M. P., H. TOWLL, A. F. RUSSEL, AND S. WANLESS. 1990. Maximum dive depth attained by auks feeding young on the Isle of May. Scottish Birds 16:25–28.

HARRIS, M. P., AND S. WANLESS. 1986. The food of young Razorbills on the Isle of May and a comparison with that of young Guillemots and Puffins. Ornis Scandinavica 17:41–46.

HARRIS, M. P., AND S. WANLESS. 1989. The breeding biology of Razorbills Alca torda on the Isle of May. Bird Study 36:105–114.

IOALÉ, P., P. DALL'ANTONIA, L. DALL'ANTONIA, AND S. BENVENUTI. 1994. Flight path of homing pigeons studied by means of a direction recorder. Ethology Ecology & Evolution 6:519–517.

JURY, J. A. 1986. Razorbill swimming at depth of 140 m. British Birds 79:339.

LILLIENDAHL, K., AND J. SOLMUNDSSON. 1997. An estimate of food consumption of six seabird species in Iceland. ICES Journal of Marine Science 54: 624–630.

MONTEVECCHI, W. A. 1993. Birds as indicators of marine prey stock conditions. In R. W. Furness and J. J. D. Greenwood [EDS.], Birds as monitors of environmental change. Chapman & Hall, London.

PAPI, F., P. IOALÉ, L. DALL'ANTONIA, AND S. BENVE- NUTI. 1991. Homing strategies of pigeons investigated by clock shift and flight path reconstruction. Naturwissenschaften 78:370–373.

PENNYCUICK, C. J. 1990. Predicting wingbeat frequen- cy and wavelength of birds. Journal of Experi- mental Biology 150:171–185.

PIATT, J. F., AND D. N. NETTLESHIP. 1985. Diving depth of four alcids. Auk 102:293–297.

PRINCE, P. A., AND M. P. HARRIS. 1988. Food and feed- ing ecology of breeding Atlantic alcids and pen- guins. Proceedings of the International Ornitho- logical Congress 19:1195–1204.

WAGNER, R. H. 1992. Confidence of paternity and pa- rental effort in Razorbills. Auk 109:556–562.

WANLESS, S., J. A. MORRIS, AND M. P. HARRIS. 1988. Diving behaviour of Guillemot Uria aalge, Puffin Fratercula arctica and Razorbill Alca torda as shown by radio-telemetry. Journal of Zoology 216:73–81.

WILSON, R. P., W. S. GRANT, AND D. C. DUFFY. 1986. Recording devices on free-ranging marine ani- mals: Does measurement affect foraging perfor- mance? Ecology 67:1091–1093.