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Allocation of Time and Energy

FLEXIBLE TIME BUDGETS IN BREEDING COMMON MURRES: BUFFERS AGAINST VARIABLE PREY ABUNDANCE

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Abstract. We report on a 4-year study of the relationships between parental behavior of Common Murres (*Uria aalge*) and the relative abundance of their principal prey, capelin (*Mallotus villosus*), at Witless Bay, Newfoundland. Capelin comprised 89% of the prey fed to murre chicks. Capelin abundance and the density of their schools, measured with hydroacoustic surveys, varied significantly within and between each of the murre's breeding seasons, by up to 10-fold. Despite this, the feeding rates of chicks (average 0.28 fish chick^{-1} h^{-1}) did not vary significantly between years, and were not depressed by intraseasonal capelin variations. Adult murres compensated for periods of low capelin abundance by taking more of other fish, particularly sandlance (*Ammodytes* sp.), and by spending more time at sea. Chick survival (average 93%) did not vary significantly between years. Chick feeding rates and parental resting time at the colony were not strongly affected by weather, sea conditions or chick age. We suggest that with moderate prey abundance, variable time budgets of adult murres would buffer the effects of temporal and spatial prey variability so that chick feeding rates would remain relatively constant. Under such conditions chick growth and survival might not reflect food availability.

Key Words: Seabird; fish abundance; time budgets; energetics; murre; capelin.

Herbers (1981) and Southern and Moss (1985) suggested that inactive periods in mobile animals might represent time buffers to compensate for variable food levels. The effects of periodic, unpredictable food shortages can be ameliorated if the animals have a reserve of time, available for foraging when necessary, in lieu of activities like resting or preening. Flexible time budgets might be particularly useful to seabirds feeding on pelagic prey, where the environment and prey availability are often highly variable in time and space. This would be most evident during the breeding season, when foraging ranges are restricted and time and power demands on adults are greatest (Ricklefs 1984, Gaston 1985a).

Several characteristics of breeding seabirds have been shown to vary with food availability, e.g., clutch size (Springer et al. 1986), chick growth (Gaston 1985b, Gaston et al. 1983) and brood size (Braun and Hunt 1983, Shaw 1985). Many seabirds, including murres (*Uria*), lay a clutch of one and thus cannot adjust clutch or brood size. Variations in egg size (e.g., Birkhead and Nettleship 1982) are unlikely to compensate for large variations in food availability. There are comparatively few data on the effects of food availability on parental time budgets in seabirds (Cairns 1988). At one extreme, parents may work at maximum capacity so that chick growth and breeding success are thought to reflect levels of food availability (Ashmole 1963, Diamond 1978, Gaston 1985a). In other cases, successful breeding seabirds appear to have time to spare (Pearson 1968, Furness and Barrett 1985, Cairns et al. 1987).

Following Cairns (1988), we propose that under conditions of moderate to high prey availability, parental time budgets and attendance at the colony should vary, resulting in relatively constant provisioning of chicks, despite fluctuations in prey availability. The chicks might therefore be buffered from the effects of variable food availability. An alternative possibility is that parents always maximize their foraging time and effort, perhaps constrained only by physiological limitations (Drent and Daan 1980) or digestive bottlenecks (Diamond et al. 1986).

We studied the activity-time budgets of Common Murres (*Uria aalge*) rearing chicks at a colony on Gull Island (47°16′N, 52°46′W) in Witless Bay, Newfoundland, over four consecutive breeding seasons. The abundance and distribution of the murre's principal prey, capelin (*Mallotus villosus*), were estimated from hydroacoustic surveys made in and near Witless Bay in each season (Piatt and Methven 1986, Piatt 1987). These data allowed us to assess inter- and intraseasonal variations in chick diets, chick feeding rates, and parental activities at the colony, relative to independent assessments of prey abundance on the birds' foraging grounds. To our knowledge, this has never been done with pelagic seabirds.

METHODS

DETERMINATION OF CAPELIN ABUNDANCE

Relative capelin abundance was determined from hydroacoustic surveys made as part of a study of seabird-capelin interactions (Piatt and Methven 1986, Schneider and Piatt 1986, Piatt 1987). The vessel's

survey routes were 16–28 km long, required 2–2.5 h travelling and encircled Gull Island. Survey routes varied slightly between some years (Piatt 1987), but were always within 10 km of the study colony, within the average foraging range of the murres from Gull Island (Cairns et al. 1987, Piatt 1987).

Hydroacoustic echograms were divided into blocks representing 1 min of travel (approx. 250 m) and 10 m of water depth, and the intensity of the traces of fish within each block were visually graded (scale 0–9). Because fish abundance is proportional to the square of the intensity of the echo signal (Forbes and Nakken 1972), all grades were squared before averaging to obtain a relative abundance index (mean intensity grade per min of transect, see Piatt and Methven 1986, Piatt 1987 for details). The frequencies of capelin schools per min of transect were also calculated from the hydroacoustic traces, and these were the only estimates of capelin abundance available from 1985. In 1982 through 1984 the frequencies of schools were highly correlated with the relative abundance index (Piatt 1987). In 1982, hydroacoustic surveys were sparse and only three surveys coincided with observations at the murre colony. Consequently, data from 1982 were omitted from intraseasonal analyses.

Observations at the Colony

Observations were made from a blind positioned 8–17 m above a cliffside colony of Common Murres on Gull Island (sites 4 and 5 used by Mahoney, 1979). In each season, 20–25 pairs of murres were marked with picric acid dye squirted from the clifftop. Observations of the marked birds provided data on the following: the parental resting time (PRT), defined as the % time that the off-duty (non-brooding) bird was present at the colony, i.e., the pair was together at the colony; the chick feeding rate (CFR), defined as the rate at which fish were delivered by both parents (fish chick^{-1} hour^{-1}); the type and size of prey delivered to the chick; and the duration of the adults' foraging trips at sea.

Observation shifts ranged from four to 17.5 hours, the latter covering the entire day from first light (ca. 04:00, Newfoundland Daylight Saving Time) to dark (21:00–21:30). Observations commenced 30 min after the observer entered the blind. Arrivals and departures of adults were recorded to the nearest minute. The presence of each marked adult was recorded at 5 min intervals to ensure that marked birds that wandered away from their breeding site were not overlooked. Daily means of parental activities and chick feeding rates were compared with estimates of capelin abundance made on the same day, or where that was not possible, with three-day averages covering the day of observation. Growth rates of chicks were not measured.

The birds were close enough for the observer, using binoculars, to identify 88% of the 1150 fish delivered to chicks over four years. Mature capelin were sexed on the basis of the shape of the anal fin, which has an enlarged base in males, or the presence of eggs exuding from the cloacas of females. Fish lengths were estimated relative to the gape lengths of adult murres (mean gape length = 70.3 ± 3.6 mm, N = 21). In 1982, 1983 and 1984, fish were collected by fitting chicks at nearby sub-colonies on Gull Island with collars to prevent them from swallowing for 3-h periods. Comparisons within each year showed no significant differences between visual identifications and samples of fish from collared chicks, in the proportions of prey species, mature and immature capelin or in the sex ratios of mature capelin (A. E. Burger, unpubl. data). Visual observations are thus presented here as valid estimates of prey composition.

Shaded air temperatures, visibility (ability to see landmarks of known distance), sea conditions (calm, moderate or rough seas), windspeed (Beaufort scale later converted to km h^{-1}), wind direction and the occurrence of clouds, fog and rain, were recorded hourly at the colony. Data from 4-hr observations (12:00–16:00) were used to test the effects of weather and sea conditions, because these factors can change dramatically during longer watches.

The non-parametric Kruskal-Wallis analysis of variance and Mann-Whitney tests were used to analyze behavioral and dietary data, using QSTAT programs (Biderman 1985). Throughout, means are given ± one SD.

RESULTS

Factors Affecting Parental Activities of Murres

Before examining the effects of capelin abundance on the parental activities of murres, it is necessary to determine which periods of observation may be used for valid comparisons, and to examine possible confounding influences, such as chick age, weather and sea conditions.

Selecting an appropriate observation period

All observations were made during daylight, and there was no evidence that the murres fed their chicks at night (see also Verspoor et al. 1987). A 4-h subsample was selected from each day of observation, to allow comparisons between days of unequal observation time. Careful selection of the time of this period was needed, because the frequency of many activities, including chick feeding (Fig. 1), varied through the day. Using data from dawn-to-dark watches, we found that feeding rates (CFR) and resting times (PRT) measured in most 4-h subsamples were significantly correlated with the dawn-to-dark values, but only in the period 12:00–16:00 were the magnitudes of both CFR and PRT sufficiently similar to the dawn-to-dark values (Table 1). Consequently, data from this period were selected, and identified as CFR-P3 and PRT-P3 to distinguish them from dawn-to-dark values, designated CFR-DD and PRT-DD.

Effects of environmental conditions

No clear trends or significant correlations were found between either feeding rates (CFR-P3) or resting times (PRT-P3) and visibility, windspeed, wind direction, temperature and sea state in 1983 (N = 8 observation days), 1984 (N =

10) or 1985 (N = 10), possibly due to small sample sizes in each season.

With data from all years pooled, CFR-P3 was not markedly affected by prevailing weather conditions affecting visibility (Table 2). CFR-P3 was not correlated with air temperature at the colony ($r = 0.123$, $df = 27$, $P > 0.05$), or sea condition ($r = -0.162$, $df = 24$, $P > 0.05$), but was negatively correlated with windspeed ($r = -0.376$, $df = 27$, $P < 0.05$), due largely to reduced feeding rates during two days of moderately strong offshore winds. Overall, CFR-P3 was similar on days with onshore (mean 0.25 ± 0.07 fish chick^{-1} h^{-1}, N = 6), longshore (0.30 ± 0.07, N = 5) or offshore (0.26 ± 0.08, N = 17) winds (Kruskal-Wallis test, $H = 1.91$, $df = 2$, $P > 0.05$).

Parental resting time (PRT-P3) appeared unaffected by weather and visibility (Table 2). PRT-P3 was not correlated with windspeed ($r = -0.132$), or sea condition ($r = 0.071$, $df = 27$, $P > 0.05$ in both tests), but was negatively correlated with air temperature ($r = -0.390$, $df = 27$, $P < 0.05$). This reflected occasional periods of intense insolation when heat-stressed off-duty adults left the colony. PRT-P3 was not significantly different on days with onshore (mean 38.9 ± 16.4%, N = 6), offshore (24.9% ± 11.1, N = 17) or longshore winds (21.9% ± 14.1, N = 5; Kruskal-Wallis test, $H = 3.989$, $df = 2$, $P > 0.05$).

Effects of chick age

Within each year there were no consistent correlations between chick age and daily measures of feeding rate, parental resting time, duration of foraging trips or proportion of adult capelin in the diet (Table 3). Fish size was positively correlated with chick age in each year (significant in two years, Table 3), because chicks 1–2 d old are fed a higher proportion of small, immature capelin than older chicks (A. E. Burger, unpubl. data).

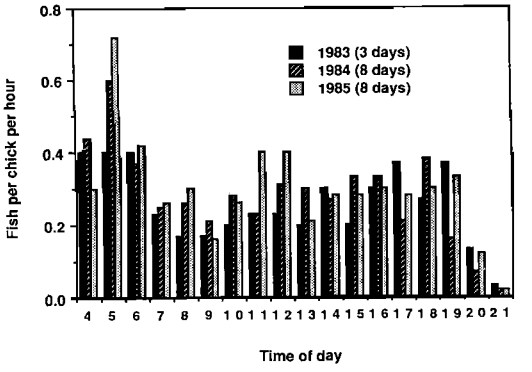

FIGURE 1. Mean hourly chick feeding rates of Common Murres at Gull Island in 1983, 1984 and 1985. The time intervals are labelled with the starting time of each interval (i.e., 4 = 04:00–05:00). Data from complete dawn-to-dusk days only.

The correlation between chick age and proportions of adult capelin in their diets in 1984 probably reflected the scarcity of capelin in the early part of that season (see below), when many chicks were newly hatched.

Variations among Years

Variations in capelin abundance

Schools of capelin first appeared in Witless Bay in late May. Their abundance usually peaked in the last ten days of June and first two weeks of July, and declined markedly by early August (Figs. 2 and 3). The annual means of relative capelin abundance varied by an order of magnitude during the study, showing a significant decline between 1982 through 1984 (Fig. 4, One-way ANOVA, $F_{2,57} = 28.2$, $P < 0.001$). Frequency of capelin schools followed a similar trend, but in-

TABLE 1. Comparison of Chick Feeding Rates (Fish Chick^{-1} H^{-1}) and Parental Resting Times (% Daylight Time with Off-Duty Adult at the Colony) for Various Periods of Observation, including the Middle Eight Hours (MD) and the Whole Dawn-to-Dark Day (DD). All Data from 17 Days of Complete Dawn-to-Dark Observations in 1983 (3 d), 1984 (7 d) and 1985 (7 d), with an Average of Nine Pairs Observed per Day

Observation period (time)	Chick feeding rate (CFR)			Parental resting time (PRT)		
		Comparison with DD rate[1]			Comparison with DD rate[1]	
	Mean ± SD	t	r	Mean ± SD	t	r
P1 (04:00–08:00)	0.41 ± 0.10	6.25***	0.519*	16.5 ± 9.3	3.52**	0.691**
P2 (08:00–12:00)	0.26 ± 0.09	1.55 NS	0.578*	15.4 ± 7.5	6.88***	0.846**
P3 (12:00–16:00)	0.26 ± 0.08	1.81 NS	0.692**	22.6 ± 10.5	0.16 NS	0.678**
P4 (16:00–dark[2])	0.23 ± 0.07	3.28**	0.425 NS	31.9 ± 10.9	5.90***	0.796**
MD (08:00–16:00)	0.26 ± 0.07	2.07 NS	0.734**	19.7 ± 8.4	2.35*	0.846**
DD (04:00–dark[2])	0.28 ± 0.05	—	—	22.3 ± 7.4	—	—

[1] Two-tailed paired t-test; Pearson correlation (r); *** P < 0.001, ** P < 0.01, * P < 0.05, NS not significant (P > 0.05).
[2] Darkness occurred between 21:00 and 21:30.

TABLE 2. EFFECT OF WEATHER AND VISIBILITY ON CHICK FEEDING RATE (CFR-P3) AND PARENTAL RESTING TIME (PRT-P3) IN COMMON MURRES. MEANS ± SD FROM 4-H OBSERVATIONS (12:00–16:00), 1983–1985 POOLED

Weather	Visibility (km)	CFR-P3 (fish chick^{-1} h^{-1})	PRT-P3 (% of 4 h)	N
Clear, sunny	Excellent (>10)	0.28 ± 0.09	32 ± 13	8
Overcast but bright	Good (5–10)	0.24 ± 0.08	22 ± 9	8
Heavy overcast, rain	Moderate (1–5)	0.27 ± 0.08	23 ± 20	3
Moderate fog	Moderate-poor (0.3–1)	0.31 ± 0.07	26 ± 14	6
Thick fog	Poor (<0.30)	0.22 ± 0.02	38 ± 20	3
Kruskal-Wallis H-value		3.82 (P > 0.05)	3.65 (P > 0.05)	

creased slightly in 1985 (Fig. 4, ANOVA, $F_{3,86} = 36.3$, $P < 0.001$).

Diets of the chicks

The diets of Common Murre chicks at Gull Island in 1982–1985 comprised 72% mature capelin (91% females), 11% immature capelin, 6% unclassified capelin, 9% sandlance *Ammodytes* sp. and 2% other fish (N = 1017 fish in visual observations). Diets differed significantly between years, with fewer capelin, particularly mature females, delivered in 1984 (Fig. 5; $\chi^2 = 85.33$, df = 12, $P < 0.001$).

The size/frequency distributions of fish delivered to chicks, estimated visually, differed significantly between years (Fig. 6; χ^2 test with Yate's correction, $\chi^2 = 50.23$, df = 12, $P < 0.01$). This was due to increased numbers of large sandlance and fewer small female capelin in 1984, and more small fish in 1982. Mature female capelin obtained intact from collared chicks were, on average, heavier in 1984 (17.1 ± 3.4 g, N = 13) than in 1982 (13.7 ± 2.4 g, N = 17) and 1983 (13.8 ± 4.1, N = 25; Mann-Whitney tests, $P < 0.05$ in each case). Mature capelin caught in traps were generally also larger in 1984 than 1982 or 1983 (Piatt 1987). Samples of other fish from collared chicks were too small for inter-year comparisons. The mean masses of immature capelin and sandlance were 6.7 ± 3.2 g (N = 5) and 14.5 ± 6.6 g (N = 10), respectively.

Feeding rates and parental activities

For 17 dawn-to-dark watches in 1983, 1984 and 1985 the mean chick feeding rate (CFR-DD) was 0.28 ± 0.05 fish chick^{-1} h^{-1} (4.8 ± 0.9 fish chick^{-1} per 17-h day), and the mean resting time (PRT-DD) was 22 ± 7% (3.7 h d^{-1}). Each off-duty adult thus averaged 1.9 h per day at the colony. Feeding rates (CFR-P3) and resting times (PRT-P3) from the partial day 4-h watches included more days, from all four years, and averaged 0.25 ± 0.07 fish chick^{-1} h^{-1} and 30 ± 14%, respectively (N = 41 days, average 9 chicks per day). Mahoney (1979) reported a feeding rate of 0.23 fish chick^{-1} h^{-1} for the same sites in 1977, but did not sample the most active period between 04:00 and 06:00.

The mean chick feeding rates (CFR-DD and CFR-P3) did not vary significantly among years (Table 4), despite the significant changes in capelin abundance. Feeding rates were higher in 1984, when capelin were least abundant. Parental resting time measured in dawn-to-dark watches did not differ among years, but the sample sizes were small (Table 4). The larger samples from 4-h watches (PRT-P3) did differ significantly, showing that murres spent less time resting at the colony in seasons when fewer capelin were detected on hydroacoustic surveys (Table 4).

The durations of foraging trips preceding fish deliveries were compared using dawn-to-dark

TABLE 3. CORRELATION COEFFICIENTS OF CHICK AGE COMPARED TO PARENTAL BEHAVIOR AND CHICK DIET IN COMMON MURRES AT GULL ISLAND. DATA FROM VISUAL DAWN-TO-DARK OBSERVATIONS ONLY

Parameter	Year 1983	1984	1985
Chick feeding rate (CFR-DD)	−0.408*	−0.168	0.009
Parental resting time (PRT-DD)	0.165	0.136	−0.157
Duration of foraging trips	0.045	0.114	0.243
Percentage of adult capelin fed to chicks	−0.085	0.425**	−0.216
Size of fish fed to chicks	0.479*	0.210	0.401*
No. bird-days	26	68	39

** $P < 0.01$, * $P < 0.05$, all other correlations not significant ($P > 0.05$).

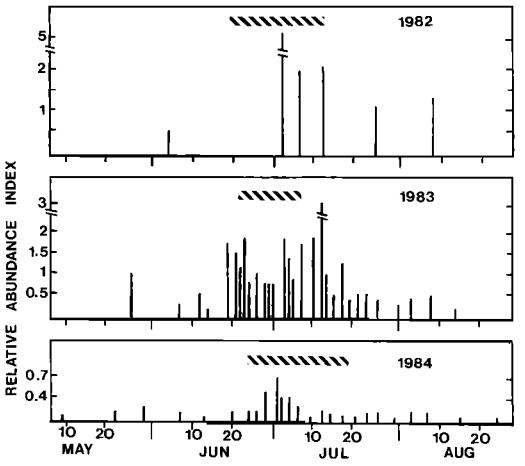

FIGURE 2. Relative abundance indices of capelin in Witless Bay, estimated from hydroacoustic surveys (from Piatt 1987). Horizontal hatched bars indicate the periods of observations of Common Murres at Gull Island. Capelin were recorded on all days surveyed.

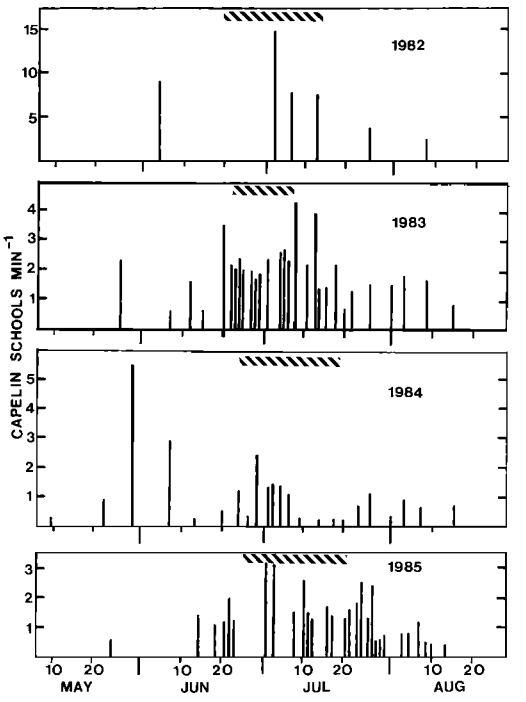

FIGURE 3. Estimates of the frequency of capelin schools in Witless Bay made from hydroacoustic surveys (J. F. Piatt and D. A. Methven, unpubl.). Horizontal hatched bars indicate periods of observations of Common Murres at Gull Island. Schools were detected on all days surveyed.

data and showed no significant differences between years (Fig. 7, Kolmogorov-Smirnov Test, $P > 0.05$).

By combining estimates of feeding rates, proportions of prey in the diet and mean mass and energy content of prey, we calculated the average mass and caloric intake of murre chicks in each year (Table 5). Differences among the years did not correspond to differences in estimated capelin abundance, and the highest intake was in 1984, the year of lowest capelin abundance.

Survival of eggs and chicks

Survival of eggs, excluding those which had not hatched at the end of the field season, was 76% (N = 29), 73% (N = 33), 80% (N = 35) and 67% (N = 15) in 1982 through 1985, respectively. These were maximum survival rates since observations commenced 2–3 weeks after the peak of laying. No mortality occurred among chicks >13 d old, and only two chicks died when >3 d old. Chicks that were >15 d old at the end of each year's field season were therefore assumed to have a high probability of fledging. Survival of chicks to fledging, or to >15 d old at the end of each year's field season, was 82% (N = 17), 100% (N = 21), 92% (N = 25) and 100% (N = 9) for 1982 through 1985, similar to that in other murre colonies in the Atlantic (Harris and Birkhead 1985). There was thus no evidence that egg or chick survival was affected by changes in capelin abundance in these years.

Variations within Seasons

Daily variations in murre activities and capelin abundance

Daily variations in feeding rates (CFR-P3) were significantly correlated with resting times (PRT-P3) in 1984 ($r = 0.671$, $df = 10$, $P < 0.05$), but not in 1982 ($r = 0.135$, $df = 10$, $P > 0.05$), 1983 ($r = 0.097$, $df = 8$, $P > 0.05$), 1985 ($r = -0.571$, $df = 9$, $P > 0.05$), or in the pooled data from all years ($r = -0.276$, $df = 40$, $P > 0.05$). We calculated correlation coefficients to test whether daily averages of relative capelin abundance (1983 and 1984) and the frequency of capelin schools (1983 through 1985) might be related to changes in daily values of feeding rate (CFR-P3), resting time (PRT-P3), mean fish size and % adult capelin in the chicks' diets. Out of 20 pairs of comparisons, only one (CFR-P3 and frequency of schools) showed a statistically significant relationship. Since this result might be obtained by chance alone, we concluded that there was too much variation or "noise" in the daily estimates of both murre behavior and capelin abundance to detect short-term trends with small samples.

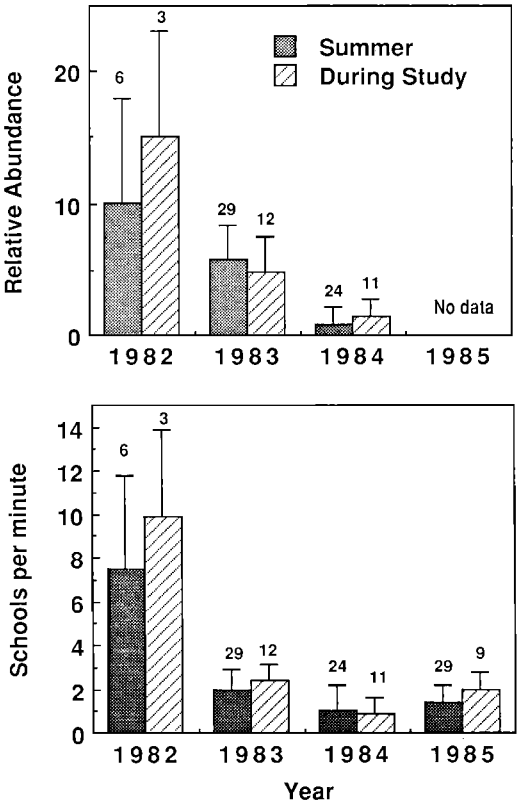

FIGURE 4. Mean ± SD (error bars) measures of the relative abundance index, and the frequency of schools of capelin in Witless Bay during the entire summer (shaded bars) and during the study of murres at Gull Island (hatched bars, see Fig. 2 for duration of study in each year). The number of surveys in each sample is shown. Data from J. F. Piatt and D. A. Methven (unpubl.).

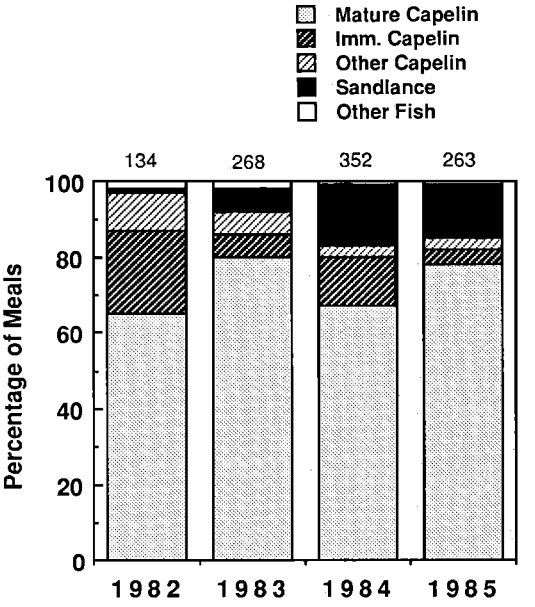

FIGURE 5. Proportions of fish types in the diets of Common Murre chicks at Gull Island, based on visual observations. Fish were classified as mature capelin, immature (imm.) capelin, other (unclassified) capelin, sandlance and other species. The number of meals sampled is shown.

Relationships were therefore examined by grouping data into periods of several days with notably different estimates of capelin abundance. There were three of these periods in 1984 (Figs. 1 and 8) and two in 1985 (Figs. 2 and 9) but none during observations in 1982 or 1983. In 1984 the relative abundance of capelin was initially very low (Fig. 8, 20–26 June), increased seven fold (28 June–6 July), and then decreased

TABLE 4. ANNUAL MEANS (±SD) OF CHICK FEEDING RATES (FISH CHICK^{-1} H^{-1}) AND PARENTAL RESTING TIMES (% DAYLIGHT TIME WITH OFF-DUTY ADULT AT THE COLONY), CALCULATED FROM THE MEAN OF EACH DAY OF OBSERVATION FOR DAWN-TO-DARK AND 4-H (12:00–16:00) PERIODS OF OBSERVATIONS

Measure	Year 1982	1983	1984	1985	Kruskal-Wallis test
Chick feeding rates					
CFR-DD (dawn–dark)	–	0.26 ± 0.04	0.28 ± 0.03	0.29 ± 0.06	H = 0.333 (P > 0.05)
CFR-P3 (12:00–16:00)	0.22 ± 0.05	0.24 ± 0.06	0.29 ± 0.06	0.26 ± 0.10	H = 6.012 (P > 0.05)
Parental resting time					
PRT-DD (dawn–dark)	–	21.5 ± 4.2	18.8 ± 6.0	26.1 ± 8.6	H = 2.879 (P > 0.05)
PRT-P3 (12:00–16:00)	41.2 ± 10.8	33.5 ± 15.6	19.4 ± 9.7	28.4 ± 13.0	H = 14.557 (P < 0.01)
Sample sizes (days)					
Dawn-to-dark watches	0	3	7	7	
Four hour watches	11	9	11	10	

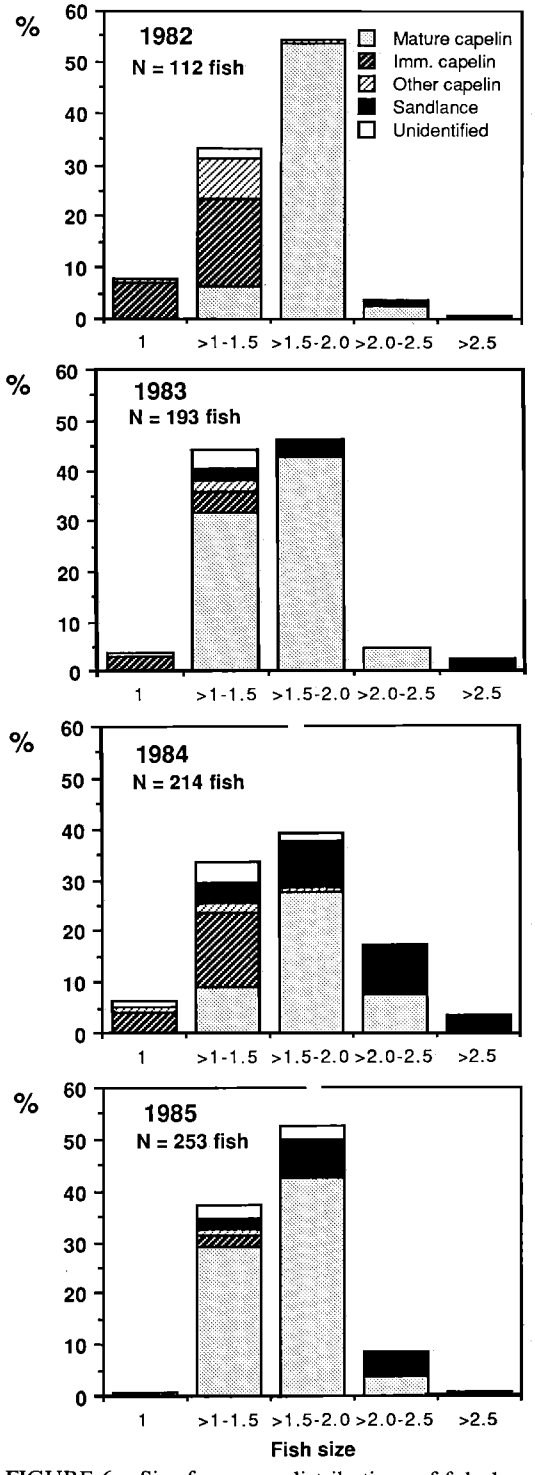

FIGURE 6. Size-frequency distributions of fish delivered to Common Murre chicks at Gull Island. Fish sizes were estimated visually and are presented in units of gape length in adult murres.

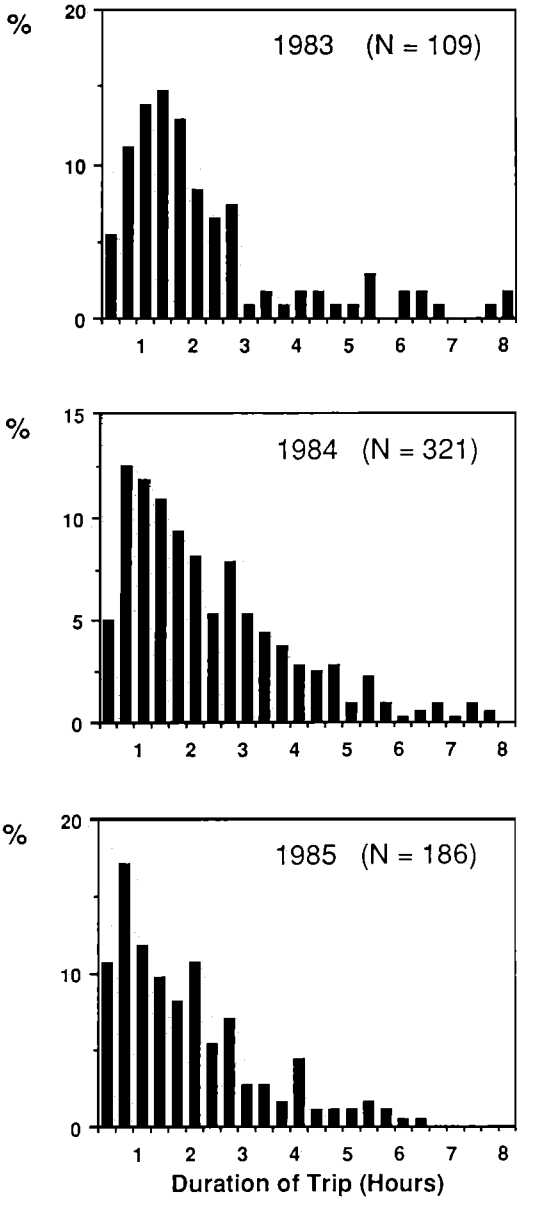

FIGURE 7. Variations between seasons in the durations of foraging trips preceding deliveries of fish to chicks, by Common Murres at Gull Island. Data from dawn-dark observation periods only.

again (9–20 July). Chick feeding rates (CFR-DD) were not significantly affected by these large changes (Fig. 8; Kruskal-Wallis test, $H = 3.07$, $df = 2$, $P > 0.05$), but there were significant differences in the parental resting times (Fig. 8, $H = 11.31$, $df = 2$, $P < 0.05$) and proportions of prey in chicks' diets (Fig. 8, Chi-squared test,

TABLE 5. ESTIMATES OF THE DAILY FEEDING RATE, MEAL SIZE, FOOD AND ENERGY INTAKE PER CHICK OF COMMON MURRES AT GULL ISLAND

Measure	1982	1983	1984	1985	Mean
Chick feeding rate (meals d^{-1})[1]	3.74	4.08	4.93	4.42	4.29
Mean meal size (g)[2]	12.1	13.7	13.4	14.1	13.3
Total food intake (g)	45.3	55.9	66.1	62.3	57.4
Energy intake (kJ)[3]	339	417	485	460	425

[1] From CFR-P3 (Table 4) assuming 17 h daylight.
[2] Calculated using proportions (Fig. 5) and mean weights (A. E. Burger unpubl. data) of fish types delivered to Gull Island chicks.
[3] Calculated using the method and caloric values of fish given in Birkhead and Nettleship (1987), and food intake data from Gull Island.

$P < 0.05$). The most likely explanation for these results is that capelin were generally scarce during the first period, forcing murres to take more sandlance, which demanded increased foraging time. During the third period, capelin were scarce within the surveyed areas, but appeared to have been available elsewhere, since mature capelin made up the bulk of the chick meals and the adults spent only slightly less time at the colony.

In 1985 (Fig. 9), during the late-season period of low capelin abundance, the feeding rate was significantly higher (Mann-Whitney test, $U_{14,26} = 315$, $P < 0.01$), and the resting time significantly lower ($U_{14,26} = 255$, $P < 0.05$), but the chicks' diets did not change (χ^2 test, $P > 0.05$). Again, the parents appeared to work harder when capelin were less abundant locally, but in this year the feeding rates were also affected. The duration of foraging trips preceding fish deliveries was not affected by changes in relative abundance of capelin in 1984 or 1985 (Kolmogorov-Smirnov tests, $P > 0.05$ in each year).

DISCUSSION

EFFECTS OF OBSERVATION PERIODS, WEATHER, AND CHICK AGE

Hourly variations in chick feeding rates and parental activities occur in many seabird populations (e.g., Gaston and Nettleship 1981; Harris and Wanless 1985; Birkhead and Nettleship 1987, this study). Despite this, it is standard practice to determine breeding activities from observation subsamples of 2–8 h per day (e.g., Birkhead 1976; Birkhead and Nettleship 1981, 1987; Gaston and Nettleship 1981; Wehle 1983). We have shown that rates determined in 4-h subsamples were generally strongly correlated with complete dawn-to-dark rates, which would justify some intrastudy comparisons, but rates from subsamples and complete days did not always have the same magnitude. Careful selection of representative sampling periods, as we have done, would facilitate comparisons between studies where observation times differ.

Common Murres at Gull Island were relatively unaffected by most weather and sea conditions at the time of breeding. Chick feeding rates were maintained even in thick fog and fairly strong winds. These findings are consistent with other studies of murres (Birkhead 1976, 1978; Slater 1980; Gaston and Nettleship 1981; Piatt and McLagan 1987). High seas were found to reduce the chick feeding rates of Common Murres in one study (Birkhead 1976) but not in another (Harris and Wanless 1985). The trends in feeding rates and resting times in our data could not therefore be attributed to short-term influences of the weather.

Parental activities and chick feeding rates were relatively unaffected by chick age, except that a greater proportion of small, immature capelin was fed to chicks of 1–2 d old. Gaston and Nettleship (1981) found a similar trend among Thick-billed Murres (*Uria lomvia*). The energy intake of murre chicks studied over two seasons in Labrador increased with chick age in both seasons among Thick-billed Murres, but in only one season among Common Murres (Birkhead and Nettleship 1987). Other studies of Common Murres showed no significant changes in provisioning rates with increasing chick age (Birkhead 1977, Hedgren and Linnman 1979, Harris and Wanless 1985). The lack of consistent evidence for increased parental effort as the chick grows is surprising, because the maintenance requirements of Common Murre chicks are thought to increase about six fold while they are at the colony (Coulson and Pearson 1985). Since murres at Gull Island maintained high feeding rates but usually had time to spare at sea (Cairns et al. 1987) or at the colony (this paper), these results do not support the hypothesis that murre chicks fledge at <30% of adult mass due to the inabilities of parents to provision them adequately at the colony (Tuck 1961, Sealy 1973, Birkhead 1977, Gaston 1985b).

RESPONSES OF COMMON MURRES TO VARIABLE PREY ABUNDANCE

Large scale variations in capelin abundance are normal off Newfoundland (Carscadden 1984), and some of the effects of these variations on

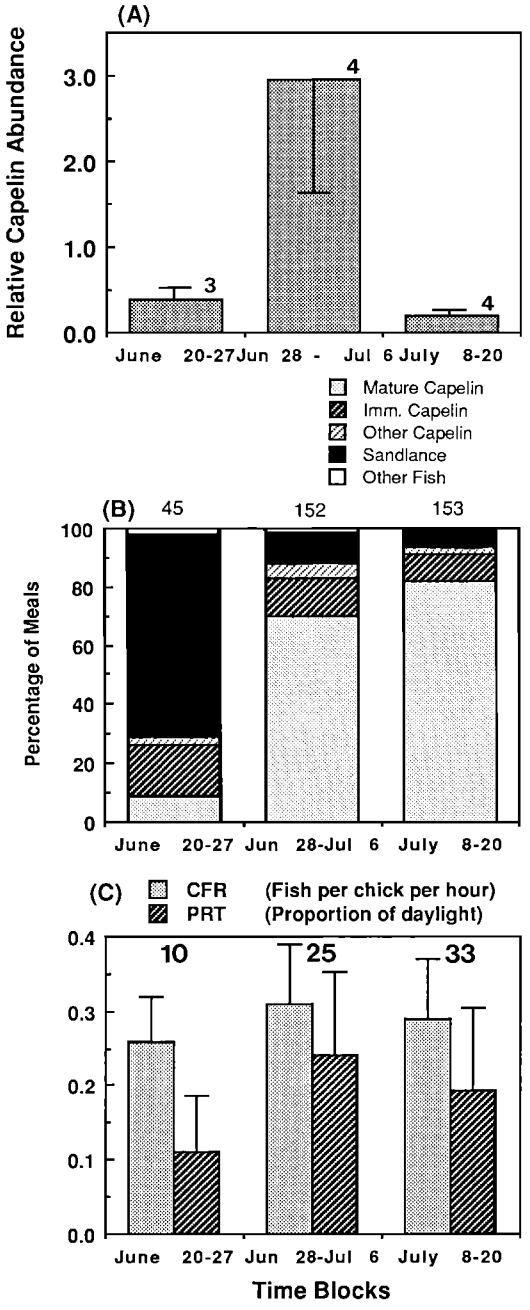

FIGURE 8. Intraseasonal changes in 1984, including: A) the relative abundance index of capelin in Witless Bay (N = number of surveys); B) the proportions of fish types in diets of Common Murre chicks (N = number of meals); and, C) chick feeding rates and parental resting times of Common Murres at Gull Island (N = pair-days). Error bars show SD.

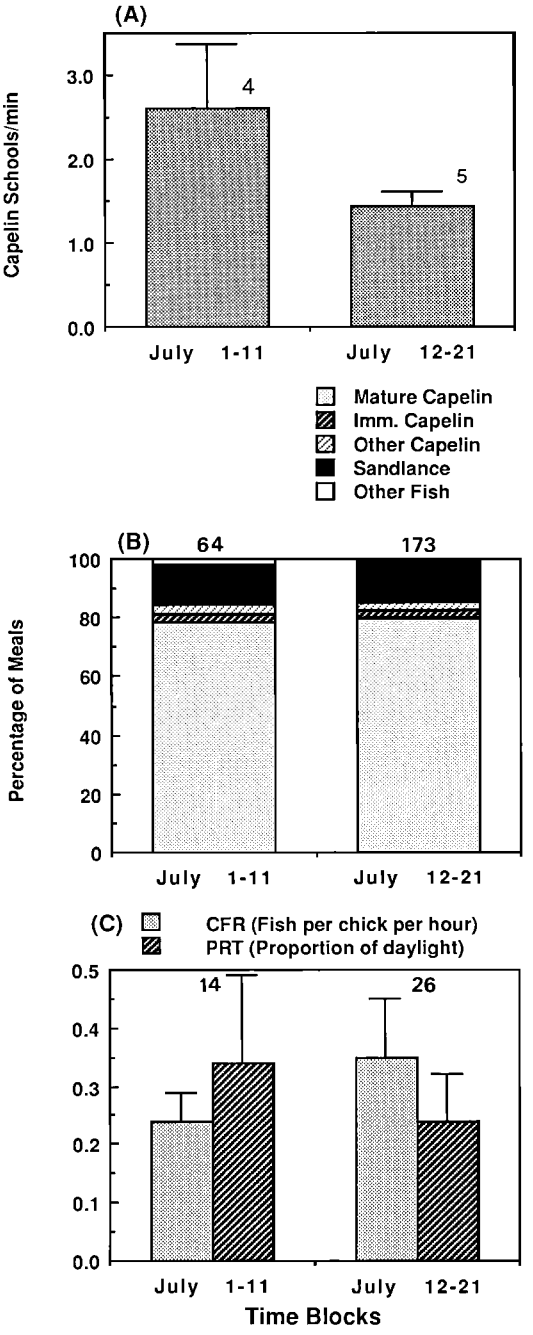

FIGURE 9. Intraseasonal changes in 1985, including: A) the frequency of capelin schools per minute of transect; B) the proportions of fish in the diets of Common Murre chicks; and C) chick feeding rates and parental resting times of murres (N = pair-days). Error bars show SD. Numbers indicate sample size, as in Figure 8.

TABLE 6. ESTIMATES OF THE TIME SPENT AT THE COLONY BY OFF-DUTY PARENTS (PRT) BY MURRES AT VARIOUS LOCATIONS

Species	Location	Day-length (h)	PRT (% day-light)	PRT (h d^{-1})	Reference
Common Murre	Witless Bay, Newfoundland	17	22	3.7	This study
Common Murre	Isle of May, Scotland	18	32[1]	5.9	Wanless et al. (1985)
Thick-billed Murre	Pr. Leopold I., High Arctic	24	4	1.0	Gaston and Nettleship (1981)
Thick-billed Murre	Hornøy/Reinøy, North Norway	24	53	12.7	Furness and Barrett (1985)

[1] Each adult was at the colony for 66% of the day, so the time when both would be ashore together should average 32%.

seabirds have been reviewed (Brown and Nettleship 1984, Piatt 1987). Capelin abundance off Newfoundland during this study (1982–1985) was intermediate (Carscadden et al. 1987, Carscadden in litt. 1987, Piatt 1987), and higher than in 1981, when the breeding success of Atlantic Puffins (*Fratercula arctica*) in Witless Bay was markedly poor (Brown and Nettleship 1984). Analysis of commercial catches of inshore spawning capelin off eastern Newfoundland (averaging 12.3, 19.5, 22.2, 17.2, and 21.0 t d^{-1}, for 1981–1985, respectively) also shows that fewer capelin were available in 1984 than in the other years of our study (Carscadden et al. 1987).

Common Murres at Gull Island varied their activities in response to variations in capelin abundance, and thereby ameliorated the effects on the chicks. Chick feeding rates were relatively invariable within and between seasons, despite variations in relative capelin abundance and frequency of schools of up to 10 fold, near the colony. The estimated food and energy intake of the chicks was not markedly affected by these changes either. The murre parents compensated for reduced capelin availability in two ways: by including a greater proportion of large mature sandlance in their catches, and by spending more time per day at sea.

Significant interactions between capelin abundance and murre activities were evident at time scales ranging from several days to complete seasons. Trends were less obvious when day-to-day variations were analyzed, but this was not unexpected, since the food demands of the chicks and adults on any day would be affected by foraging success on previous days. In addition, the "snapshot" estimates of capelin abundance, made during shipboard surveys, covered only a small portion of the space and time normally available to the murres at the colony. Murres at sea in Witless Bay have been found to respond rapidly to small scale temporal and spatial variations in capelin abundance (Schneider and Piatt 1986; Piatt 1987; Piatt, this volume).

IMPLICATIONS OF FLEXIBLE TIME BUDGETS

The time spent ashore by off-duty, breeding seabirds is very variable, ranging from 0.4% of the trip time in Grey-headed Albatrosses (*Diomedea chrysostoma,* Prince and Francis 1984) to over 90% of the day in the Shag (*Phalacrocorax aristotelis,* Pearson 1968). Among murres, where one parent almost always remains on duty at the nest site, resting at the colony by the off-duty bird (PRT) varied between 4 and 53% of the daylight time (Table 6). Pearson's (1968) estimate of only 16% of the day spent at sea by Common Murres at the Farne Islands was not well supported by data and seems too low, even though food was apparently abundant.

Seabirds spend part of their time ashore preening and interacting with chicks, mates or neighbors. The extent to which such activities are essential to survival or breeding success is not known for any seabird, and would be very difficult to assess. The murres we watched used very little time ashore in overt activity. Digestive bottlenecks affect time budgets of some birds (Diamond et al. 1986), and might affect the activities of murres feeding large fish to small chicks. Energy and physiological limitations also constrain activities (Drent and Daan 1980, Walsberg 1983). Flight and diving are energetically very demanding in murres (Gaston 1985a), and some recuperation time might be essential following long flights or bouts of diving. Cairns et al. (1987) showed that the Gull Island murres spent 4–5% of their total day in flapping flight, which is much higher than expected for a 990 g bird (Walsberg 1983).

Despite these potentially confounding factors, our data from four years, and comparisons between colonies, indicates that breeding murres do have discretionary time ashore, which varies inversely with food availability. Where colonies were large and birds fed on distant prey stocks, time at the colony was low (Gaston and Nettleship 1981, 1982; Gaston 1985a), but where food

was apparently abundant near the colony, murres spent more time ashore (Furness and Barrett 1985, this study).

Thick-billed Murres at Prince Leopold Island and Digges Island, in the Canadian Arctic, foraged far from their colonies and appeared to work much harder than Common Murres at Gull Island (Gaston and Nettleship 1981, Gaston 1985a). Adults with chicks spent ca. 36% of their time away from the colony in flight, and appeared to be functioning near their maximum sustainable limit (Gaston 1985a). In contrast, murres rearing chicks at Gull Island spent 10.5% of their trip times in flight and were not considered to be stressed (Cairns et al. 1987). Because of the distant distribution of food, and possible intraspecific competition at the large colonies, the murres in the high Arctic, unlike those in Newfoundland, seemed unable to adjust their time budgets to buffer environmental effects on their reproductive performance. At Prince Leopold Island, the parental resting time averaged about 1 h d^{-1} (Table 6), and did not vary much between and within seasons, but food intake, chick growth and maximum chick mass at the colony all varied between years and within seasons (Gaston and Nettleship 1981, 1982).

Birkhead and Nettleship (1987) studied murres breeding in Labrador in two seasons. The average daily energy intake of chicks (296 and 336 kJ in 1982 and 1983, respectively) indicated less favorable conditions than at Gull Island (Table 5). In 1982, a poor year, adult Common Murres made about 20% more, but shorter, feeding trips, delivered smaller capelin and a greater proportion of poor quality alternative fish, and left their chicks unattended more frequently than in 1983. By working harder, the adults appeared to compensate for poor conditions in 1982. Mortality of chicks was similar in the two years, and fledging weights were only 6% lower in 1982 than in 1983.

The activities of murres at sea are largely unknown but are obviously critical parts of time and energy budgets. Cairns et al. (1987) used gauges to determine time on or under water, and estimated that Common Murres with chicks at Gull Island in 1985 spent 10.5% of their time away from the colony in flight and 16.8% actively foraging. Thus, 73% of the time at sea was spent swimming or resting on the sea surface. It is not known what proportion of this time was used in essential activities, but Cairns et al. (1987) hypothesized that time at sea was flexible and could be adjusted with changing fish availability.

Among other seabirds, there is both evidence for (Pugesek 1981, Shea and Ricklefs 1985) and against (Ricklefs 1987) the concept that parental effort varies with changing conditions while breeding. Attempts to increase feeding rates in seabirds by experimentally adding a second chick to the brood have been successful in a few species, but have failed in others (Ricklefs 1987). We anticipate that time budgets would be most flexible in seabirds that lay a single egg clutch, since clutch and brood size adjustments are precluded.

CONCLUSIONS

The role of flexible time budgets of seabirds as buffers against variable food resources is not clear, but needs to be considered. In our view, growth rates or survival of chicks should not be assumed to be strongly correlated with food availability (e.g., Gaston et al. 1983, Ricklefs et al. 1984) until the buffering role of variable time budgets has been considered (cf. Cairns et al. 1987, Cairns 1988). Deleterious effects of food shortage on chick growth and survival might occur only in situations where adults have inflexible time budgets, or face excessive energy demands. Furthermore, our data show that parental time budgets might provide a sensitive indicator of prey stocks under conditions of moderate prey abundance. More rigorous examinations of behavioral time buffers are required, with simultaneous measurements of prey availability, diets, provisioning rates, and reproductive performance. Such studies are essential if seabird breeding activities are to be considered as valid indicators of the local abundance and distribution of commercial fish stocks.

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