ENERGY EXPENDITURES, ACTIVITY BUDGETS, AND PREY HARVEST OF BREEDING COMMON MURRES

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Abstract. We used doubly labeled water and electronic timers to measure field metabolic rates (FMRs) and activity budgets of Common Murres (*Uria aalge*) breeding in eastern Newfoundland. Mean FMR (1789 ± 265 kJ·day⁻¹) was about 50% higher than predictions for seabirds. The high FMR may be related to thermal costs in a cold ocean environment and to high locomotion costs associated with a wing structure that is a compromise between flying and diving needs. Basal metabolic rates ($\bar{X}$ = 360 ± 69 kJ·day⁻¹) were also higher than allometric predictions. While absent from the colony birds spent most (70.2–84.9%) time on the sea surface. Potential foraging range as estimated by flight time was greater during incubation than during chick rearing in two study years. Rates of prey exploitation were highest near the colony, but high exploitation rates may also have occurred about 60–70 km from the colony during incubation. Murres associated with the Witless Bay colony consumed an estimated 7579 tonnes of food, primarily capelin (*Mallotus villosus*).

Key Words: Common Murre; field metabolic rate; energy budget, activity budget; seabird prey harvest.

Seabird biology has traditionally been practiced either on land, where the activities of individual animals can be recorded in detail, or at sea, where shipboard observers tally bird distributions in relation to oceanographic features. The cross-product of these approaches is an understanding of the ecology and behavior of individual birds at sea. Until recently, technological limitations effectively precluded the study of individual birds at sea. Innovative techniques have now opened the subject to scientific scrutiny. These include the doubly-labeled water (DLW) method of measuring metabolism (Nagy 1980), activity timers (Prince and Francis 1984), maximum depth recorders (Burger and Simpson 1986, Burger and Wilson 1988), time-depth recorders (Wilson and Bain 1984a) and swimming speed meters (Wilson and Bain 1984b).

We developed a new type of activity timer that allows seabird time budgets to be measured non-intrusively during consecutive foraging trips (Cairns et al. 1987b). The present paper reports field metabolic rates (FMRs) of Common Murres (*Uria aalge*) breeding in eastern Newfoundland and extends earlier activity measurements of murres in the same area (Cairns et al. 1987c). Activity and energy data are integrated in a bioenergetics model that estimates the magnitude and location of the murres' prey harvest. Accurate characterization of food exploitation by murres in eastern Newfoundland is important because of their large population (ca. 500,000 pairs, Cairns et al. 1989) and their dependence on capelin (*Mallotus villosus*). Capelin migrate in large numbers to inshore Newfoundland waters in June and July, where they are a primary food source for many seabirds, marine mammals, and commercially harvested fish, and are

themselves subject to an important commercial fishery (Carscadden 1984, Birkhead and Nettleship 1987, Piatt 1987).

METHODS

ENERGY AND ACTIVITY MEASUREMENTS

This study was conducted at Gull (47°16′N, 52°46′W) and Great (47°11′N, 52°49′W) islands, Witless Bay, Newfoundland. These islands and nearby Green Island are the site of a multi-species seabird community that includes some 77,000 pairs of Common Murres (Cairns et al. 1989). On Gull Island in 1985 murres were captured from breeding ledges by noose-pole. On Great Island in 1986 birds were captured at a cliff-top subcolony with a noose-pole or wire neck-hook. All study birds were breeders; we observed them from distances of 15–18 m on Gull Island and 1–3 m on Great Island. The close observations at Great Island were made possible by a 30-m tunnel (Cairns et al. 1987a) that allowed undetected access to blinds fitted with one-way glass (Purdy 1985).

In 1986, we injected 0.3 mL of ³HH¹⁸O containing 95 atom % $H_2^{18}O$ and 0.051 MBq·mL⁻¹ ³HHO into the pectoral muscles of four chick-rearing murres. Birds were weighed, banded, fitted with timers, and individually color-marked on the breast with airplane dope. They were then confined in cotton sacks for 2–3 h to allow equilibration of isotopes with body fluids. Following this, 1–2 mL of blood was sampled from the brachial vein, and the bird released. Birds were recaptured about two days later, when a second blood sample was taken. Water distilled from the blood was assayed for levels of tritium and ¹⁸O on a Beckman LS7500 scintillation counter and a Micromass 903E mass spectrometer, respectively (Birt-Friesen et al. 1989).

CO_2 production rate (mL·g⁻¹·day⁻¹) was calculated for each bird, assuming that changes in body water volume were negligible (Nagy 1980). Total body water was estimated from ¹⁸O dilution space (Nagy 1983). FMR (kJ·day⁻¹) was calculated assuming an energy equivalent of 0.025 kJ·mL⁻¹ CO_2 for a diet of capelin

TABLE 1. INPUT PARAMETERS FOR POPULATION MODEL OF COMMON MURRE ENERGETICS AND FORAGING AT WITLESS BAY, NEWFOUNDLAND

Parameter	Value	Source
Breeding population	77,487 pairs	Cairns et al. 1986
Egg mass	108.4 g	Mahoney and Threlfall 1981
Assimilation efficiency	76%	Montevecchi et al. 1984
Pre-breeding period	40 days	personal observation
Incubation period	31 days	Mahoney 1979
Chick-rearing at colony	23 days	Mahoney 1979
Post-nesting period	7 days	personal observation
Non-breeding population as a		
percent of breeding population	30.5%	see text
Yolk as a percent of egg	32	Montevecchi unpubl.
Hatching success	74%	Burger and Piatt 1990
Fledging success	94%	Burger and Piatt 1990
Chick fledging mass	241 g	Mahoney and Threlfall 1981
Adult field metabolic rate	1789 kJ·day^{-1}	present study
Chick metabolic rate	425 kJ·day^{-1}	Burger and Piatt 1990
Adult diet by mass		Piatt 1987
Ovid female capelin	50.7%	
Spent female capelin	4.8%	
Adult male capelin	26.3%	
Immature capelin	0.9%	
Total capelin	83.0%	
Atlantic cod	7.6%	
Sand lance	9.7%	
Chick diet by mass		Piatt 1987
Ovid female capelin	56.3%	
Spent female capelin	20.8%	
Adult male capelin	9.2%	
Immature capelin	4.4%	
Total capelin	90.7%	
Atlantic cod	0.2%	
Sand lance	8.0%	
Other	1.0%	
Energy density of prey		
Ovid female capelin	4.6 kJ·g^{-1}	Montevecchi and Piatt 1984
Spent female capelin	3.9 kJ·g^{-1}	Montevecchi and Piatt 1984
Adult male capelin	3.8 kJ·g^{-1}	Montevecchi and Piatt 1984
Immature capelin	3.8 kJ·g^{-1}	Montevecchi and Piatt 1984
Atlantic cod	4.5 kJ·g^{-1}	Birkhead and Nettleship 1987
Sand lance	7.3 kJ·g^{-1}	Montevecchi et al. 1984
Other	4.0 kJ·g^{-1}	mean of other fish
Flight speed	64.4 km·h^{-1}	Pennycuick 1987a

(Montevecchi et al. 1984). Mean values are given ± SD.

Basal metabolic rates (BMRs) were measured at Great Island in 1987 by the closed-system respirometry method of Ricklefs et al. (1984). Drierite® and soda lime were placed beneath a plastic mesh floor in 11.5 and 16.3 L chambers to absorb water and CO_2, respectively. Birds were captured at dusk and held in chambers for 2–3 hours before trials. Murres digest food rapidly; Gaston and Noble (1985) suggested that stomachs empty in 1–2 hours, and an X-ray experiment indicated that all food reached the rectum within 95 min of ingestion (Partridge 1986). We therefore believe that little if any food remained in the gut during the metabolism trials. O_2 uptake was calculated from water displacement in a manometer during two 15 min tests during which the manometer showed smoothly decreasing fluid levels. Trials in which manometer levels changed irregularly or in which birds moved vigorously were discarded. Mean chamber temperature during trials, monitored by Yellow Springs Instruments telethermometers, was 18.7 ± 0.4°C. BMR was calculated using the equation of Ricklefs et al. (1984).

All captured birds were fitted with electronic activity timers (Cairns et al. 1987b) on the tail and a leg. When used in conjunction with continuous colony watches, these devices permit a bird's time budget to be partitioned into colony, flying, sea surface, and diving times. Unit mass of timers was 12.5 g in 1985 and 7.5 g in 1986. Timers represented 2.7 and 1.6% of body mass for the two years, respectively. Timers appeared to have little effect on birds' behavior and locomotion (Cairns et al. 1987c).

Potential foraging ranges were calculated from flight

1985
INCUBATION

5.2% 10.0%
diving flying

84.9% surface

1985
CHICK-REARING

13.4% 9.4%
diving flying

77.3% surface

1986
INCUBATION

16.6% 13.4%
diving flying

70.2% surface

1986
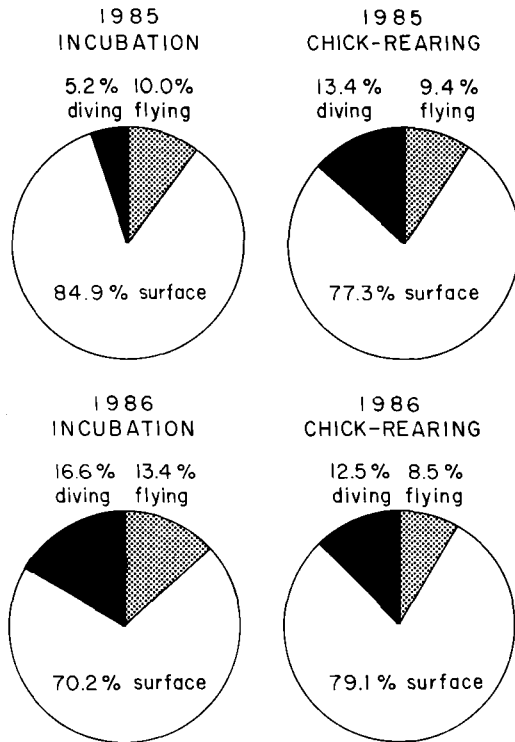CHICK-REARING

12.5% 8.5%
diving flying

79.1% surface

FIGURE 1. Time allocation of breeding Common Murres during absence periods from the colony at Witless Bay in 1985 and 1986. Diving, flying, and surface times were calculated from 1, 16, and 1 trips for incubation in 1985; from 38, 48, and 30 trips for colony-based chick-rearing in 1984; from 29, 23, and 18 trips for incubation in 1986; and from 8, 6 and 6 trips for colony-based chick-rearing in 1986 (all numbers given respectively).

times during individual trips, assuming that birds flew at 64 km·h⁻¹ (Pennycuick 1987a) and flew to and returned from feeding sites along straight lines radiating from the colony.

BIOENERGETICS MODEL

We modeled prey consumption and harvest distribution of Common Murres during the breeding season

at Witless Bay using measured FMRs and activity data and literature values for breeding and other parameters. The model was written on VP-Planner, a microcomputer spreadsheet package. Input parameters are listed in Table 1. Although non-breeders are exempt from the demands of incubation and chick-feeding, we assigned them energy expenditures equal to breeders because they are probably less efficient food-gatherers (Gaston 1985). Activity patterns were also assumed to be equivalent between the two groups.

To estimate numbers of non-breeders associated with the Witless Bay colonies we assumed age of first breeding and annual adult survival as five years and 0.9, respectively (Hudson 1985). Using these values, we iterated a life table with various values of pre-breeding survival until population stability was reached. Non-breeders represented 67.8% of the breeding population (individuals) at this point. Pre-breeding murres are generally absent from the colony area at age one, and gradually increase their attendance until breeding age is attained (Piatt et al. 1984, Hudson 1985). We assumed presence at the colony of 0, 40, 80, and 90% of non-breeders of ages one through four, respectively. This yielded an estimate that total non-breeder numbers at the colony were 30.5% of breeder numbers.

We assumed that murre numbers near the colony increase linearly from zero at the beginning of the pre-breeding period until the full breeding population is reached at the start of incubation, and that the reverse occurs following nest-leaving. Non-breeding immature birds tend to arrive in the colony area later than breeders (Hudson 1985), and we assumed that non-breeders are present only during incubation and chick-rearing at the colony.

Egg production cost was estimated from percentage yolk composition by Carey et al.'s (1980) formula for semi-precocial chicks. Chick energy requirements were summed over the nestling period from mean daily consumption derived from observations of food deliveries (Burger and Piatt 1990). Based on the tendency for chick mortality to occur soon after hatching (Burger and Piatt 1990), chicks that die were assumed to receive no food from the parent.

RESULTS

ENERGY EXPENDITURES

We obtained simultaneous DLW and activity measurements on four murres rearing chicks at the colony. FMRs ranged from 1542 to 2054 kJ·

TABLE 2. ENERGY EXPENDITURES AND ACTIVITY BUDGETS OF FOUR COMMON MURRES BREEDING AT GREAT ISLAND, NEWFOUNDLAND, IN 1986

Bird	Mass (g)	Days	Field metabolic rate		FMR[a]	Percent time allocation			
			ml CO₂·g⁻¹·day⁻¹	kJ·day⁻¹	BMR	At colony	Flying	Surface	Diving
Orange	927	2.24	2.84	1580	4.61	25.2	5.0	57.8	12.0
Green	972	1.71	3.40	1979	5.50	43.8	4.9	51.3[b]	
Purple	898	1.85	3.82	2054	6.18	10.8	16.6	66.6	6.1
Black	963	1.87	2.67	1542	4.33	41.4	4.2	48.2	6.2
Mean	940	1.92	3.18	1789	5.16	30.3	7.7	57.5	8.1
SD	34	0.23	0.53	265	0.85	15.4	6.0	9.2	3.4

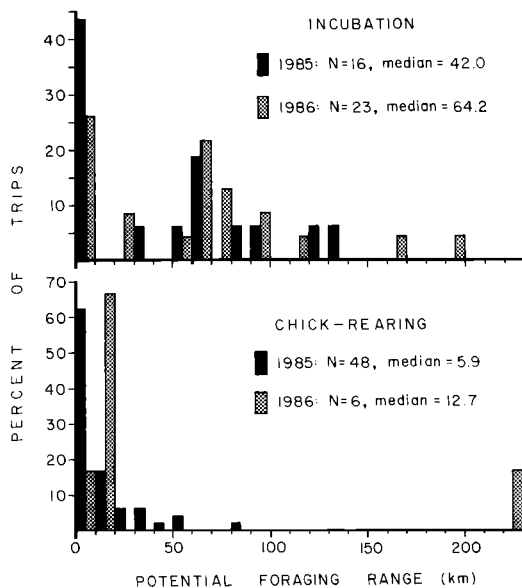[a] Based on BMR of 0.370 kJ·g⁻¹·day⁻¹ (present study).
[b] Sum of surface and diving time.

FIGURE 2. Frequency distributions of potential foraging ranges of Common Murres at Gull Island in 1985 and Great Island in 1986.

FIGURE 3. Relationship between potential foraging ranges and percent diving time during absence periods from the colony.

day^{-1} ($\bar{X}$ = 1789 ± 265) (Table 2). Mass-specific FMR was 1.90 ± 0.31 kJ·g^{-1}·day. During trials birds spent a mean of 57.5 ± 9.2% of their time on the surface of the water, with the remainder of their time divided among flying, diving, and colony (Table 2).

BMRs of three murres of mean body mass 972 ± 24 g were 283, 381, and 416 kJ·day^{-1} ($\bar{X}$ = 360 ± 69 kJ·day^{-1}). Mass-specific BMR averaged 0.370 ± 0.078 kJ·g^{-1}·day^{-1}. Using this value of BMR, the ratio of FMR to BMR varied from 4.33 to 6.18 ($\bar{X}$ = 5.16 ± 0.85, Table 2).

TIME ALLOCATION

Proportions of time spent flying, on the sea surface and diving are shown in Figure 1. In all periods, most (70.2–84.9%) time away from the colony was spent on the surface. The proportion of time spent diving did not vary significantly among the four time periods (incubation and colony-based chick-rearing, 1985 and 1986; Kruskal-Wallis H = 3.7, P < 0.3), but the proportion of time flying varied significantly among these periods (H = 12.8, P < 0.01).

Modal potential foraging range was <20 km in all time periods (Fig. 2). During incubation, a secondary mode appeared at 60–70 km, but during colony-based chick-rearing few foraging trips could have exceeded 20 km in range. Potential foraging range was significantly greater during chick-rearing in 1986 than during chick-rearing
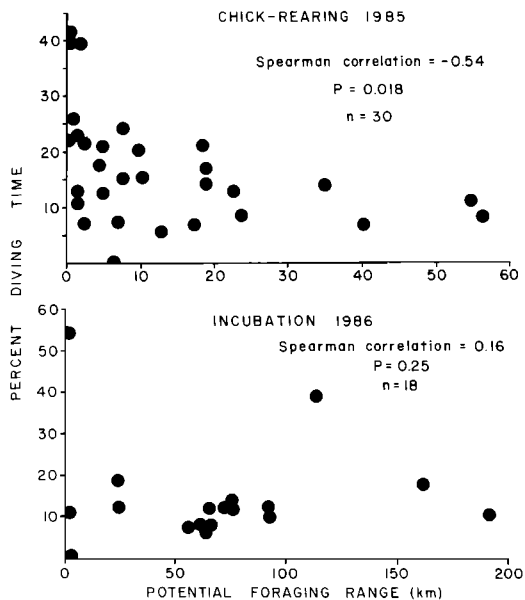
in 1985 (Mann-Whitney test; z = 1.72, P = 0.043), but was not significantly different between incubation in 1985 and 1986 (z = 0.86, P = 0.2). Proportion of time diving decreased significantly with potential foraging range during chick-rearing in 1985, but not during incubation in 1986 (Fig. 3).

PREY CONSUMPTION

Common Murres associated with the Witless Bay colony were estimated to require 7579 tonnes of food per breeding season (Table 3). Based on diet composition reported by Piatt (1987), capelin comprised 83% of this requirement, and Atlantic cod (*Gadus morhua*) and sand lance (*Ammodytes* spp.) accounted for most of the remainder. About 68% of estimated food harvest was directed to maintenance and activity of breeders. Food harvest required for egg production (0.3%) and chick feeding (2.7%) was a very small portion of total consumption.

The model estimated that Common Murres at Witless Bay require 103 tonnes of food·day^{-1} during incubation and 110 tonnes·day^{-1} during chick-rearing at the colony. If we assume that birds take prey only at their most distant point from the colony during a foraging trip, the geographic distribution of predation intensity can be calculated from the distribution of potential foraging ranges (Fig. 2). We have done this under two foraging regimes. Noting that the Witless
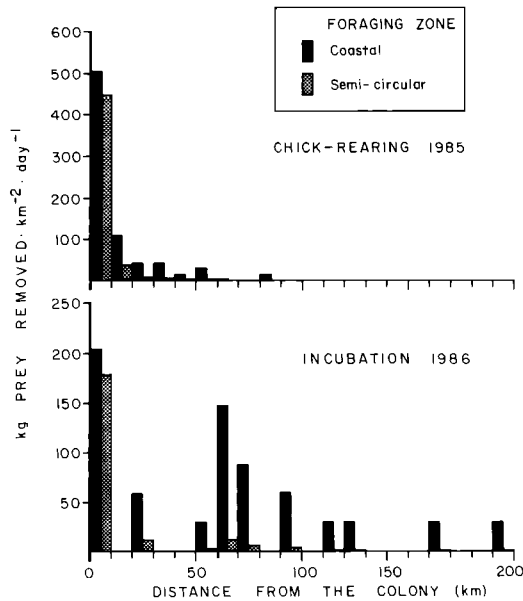
FIGURE 4. Potential prey harvest intensities in kg of prey·km^{-2}·day^{-1} by Common Murres during the breeding season in relation to distance from the colony. Harvest intensities for coastal foraging zones assume that birds feed only in an 8 km wide strip running north and south of the colony. Harvest intensities for semi-circular zones assume that birds use semi-circular foraging zones centered at the colony. See text for additional assumptions.

Bay breeding sites are located just off the straight eastern face of Newfoundland's Avalon Peninsula, we first assumed that murres foraged only in a coastal strip 8 km wide running north and south of the islands. This assumption is supported by distributions of murres recorded during boat transects, which show higher densities on long-shore than offshore transects (Piatt 1987). However, murres from Witless Bay also feed offshore (Schneider et al. 1990). We therefore postulated a second regime in which feeding occurred in a semi-circular area centered at the colony.

Figure 4 plots predation intensity in kg of prey removed·km^{-2}·day^{-1} under these regimes. When a coastal feeding zone was assumed, the pattern of prey removal·km^{-2}·day^{-1} with respect to distance from the colony closely paralleled the distribution of potential foraging ranges (Fig. 2). However, when feeding was assumed to occur in semi-circular zones, predation intensity was relatively high only near the colony, and very low beyond 10 km.

DISCUSSION

ENERGY EXPENDITURES

FMRs of Common Murres tested at Witless Bay fall well above the allometric regression line of other seabirds, which tend to have higher FMRs than birds in general (Nagy 1987, Birt-Friesen et al. 1989). Mean FMR was 1789 ± 265 kJ·day^{-1}, compared to the predicted 993 kJ·day^{-1} for seabirds in general (Nagy 1987) and 1661 kJ·day^{-1} for seabirds with flapping flight occurring in cold oceans (Birt-Friesen et al. 1989; all calculations assume a mass of 940 g).

The high value of FMR may be related to locomotory inefficiencies caused by a wing structure that allows both aerial flight and wing-propelled diving, but which is optimal for neither (Storer 1960, Pennycuick 1987b). It may also be related to the high cost of thermoregulation in cold, windswept marine environments (see Kersten and Piersma 1987, Birt-Friesen et al. 1989).

FMRs of Common Murres overlapped with those of three Thick-billed Murres (*Uria lomvia*) measured in the eastern Canadian arctic (1432–1763 kJ·day^{-1}, Gaston 1985). These findings suggest that Thick-billed Murres may not have higher FMRs than Common Murres, despite their colder environment (Birt-Friesen et al. 1989).

BMR measurements ($\bar{X} = 360 ± 69$ kJ·day^{-1}) exceeded allometric predictions for non-passer-

TABLE 3. ESTIMATED FOOD CONSUMPTION BY COMMON MURRES AT WITLESS BAY DURING THE BREEDING SEASON

Prey	Estimated consumption (tonnes)					
	Breeders	Non-breeders	Egg formation	Chicks	Total	Percent of total
Ovid female capelin	2624	1104	10.0	116	3854	50.9
Spent female capelin	248	104	0.9	43	397	5.2
Adult male capelin	1361	572	5.2	19	1958	25.8
Immature capelin	47	20	0.2	9	75	1.0
Total capelin	4280	1800	16.0	187	6284	83
Atlantic cod	393	165	1.5	0.4	561	7.4
Sand lance	502	211	1.9	16	732	9.7
Stichaeidae	0	0	0	2	2	0.03
Total	5176	2177	19.8	206	7579	
Percent of total	68	29	0.3	2.7		

ines (313 kJ·day^{-1}, Lasiewski and Dawson 1967) and birds in general (231 kJ·day^{-1}, Bennett and Harvey 1987), but were similar to those for seabirds in general (374 kJ·day^{-1}, Ellis 1984). BMRs reported here (0.370 kJ·g^{-1}·day^{-1}) were considerably lower than those reported for Common and Thick-billed Murres in the Bering Sea (0.626 kJ·g^{-1}·day^{-1}, Johnson and West 1975) and Thick-billed Murres in Svalbard (0.535 kJ·g^{-1}·day^{-1}, Gabrielsen et al. 1988).

The FMR:BMR ratio calculated from our data ($\bar{X}$ = 5.16, Table 2) exceeds the proposed avian ceiling of 4.0 (Drent and Daan 1980), which has been recently supported by the empirical and theoretical arguments of Kersten and Piersma (1987). However, the ratio of 4.0 cannot be considered an absolute ceiling for seabirds, as FMR:BMR ratios of four of 18 seabird species reviewed by Birt-Friesen et al. (1989:table 1) exceed this value.

It must be noted that sample sizes in our energetic trials are small, and further FMR measurements should be made to test the generality of our results. Reported metabolic rates also depend on the reliability of measurement techniques. We have confirmed the validity of our DLW procedures through cross-comparison with isotopic assays performed by two other labs (see Birt-Friesen et al. 1989). Similar comparisons among closed-system respirometry techniques (Ricklefs et al. 1984) used in this study, open system techniques, and DLW would also be useful.

THE MAGNITUDE AND DISTRIBUTION OF PREY HARVEST

Brown and Nettleship (1984) estimated that Common Murres at Witless Bay consume 3246 tonnes of food each year between 1 July and 15 August. Chick-rearing begins approximately 1 July, and their estimate therefore applies both to the time when chicks are reared at the colony and to the time they spend on the water following nest-leaving. Our model estimates consumption at 2774 tonnes for this period. The difference between the two estimates is due chiefly to large differences in two input parameters. Brown and Nettleship (1984) assumed that murres consume 200 g·day^{-1} of food, which is much lower than the 511 g·day^{-1} we derived from DLW measurements. Their lower consumption rate was offset by their assumption that all murres remain in the colony area until 15 August. However, desertion by murres of the colony area proceeds rapidly following the third week in July (personal observations), so that most birds are present in the area during only about half the 1 July–15 August period.

Bioenergetics models that compare estimates of harvest by breeding seabirds with fishery landings and stock size (e.g., Furness 1978, Furness and Cooper 1982) require information on the area over which seabird predation occurs. The foraging areas used in models are usually based on sparse and anecdotal data (Bourne 1983). In addition, the models generally assume that predation is equally intense throughout the foraging area, although foraging effort is often spatially heterogeneous (e.g., Cairns and Schneider 1990). The use of activity timers to calculate flight times and therefore potential foraging ranges during individual trips can aid in clarifying the geographical pattern of resource exploitation around colonies.

Figure 4 shows that predation intensity by Common Murres around Witless Bay may be high at substantial distances from the colony during incubation, but that intensity decreases rapidly with distance from the colony during chick-rearing. It is important to note that predation intensities calculated from potential foraging ranges give maximum distances at which given foraging intensities may occur, and are subject to other limitations. To the extent that foraging birds deviate from straight line courses radiating from the colony, and to the extent that they feed during transit to and from the end-points of these courses, foraging intensities in distant zones will be overestimated. The assumption of straight flight paths seems generally valid; with the exception of birds within 1–2 km of the colony, murres seen in flight during the breeding season are nearly always flying directly toward or away from the colony (Schneider et al. 1990, DKC and WAM pers. obs.). It is not known how frequently murres feed en route to or from their most distant stopping points.

Seabird prey and seabird feeding effort are generally patchily distributed in space and time (e.g., Brown 1980, Schneider and Duffy 1985). Predation intensities calculated from potential foraging ranges apply to concentric rings around colonies, and these intensities indicate local conditions better than do feeding rates that apply to a colony's entire foraging range (e.g., Furness 1978). However, these calculated intensities will not reflect variation within rings. Detailed mapping of foraging intensity is possible only when modeling approaches are combined with fine-scale surveys of distributions at sea (e.g., Cairns and Schneider 1990, Schneider et al. 1990). These two approaches to the study of distribution of foraging intensity around colonies are complementary, because flight time measurements give a picture for the colony as a whole but lack geographic precision, whereas at-sea surveys may precisely locate feeding "hot spots" but are rarely

extensive enough to cover more than a fraction of potential feeding area. A third method of mapping foraging intensity, that of long-range telemetry (Trivelpiece et al. 1986, Anderson and Ricklefs 1987) also has potential, although the transmitters now available usually lack sufficient power to allow tracking of offshore and pelagic seabirds to the limit of their foraging range.

Several lines of indirect evidence (Furness 1978, Gaston et al. 1983, Furness and Birkhead 1984, Cairns 1989) and recent direct measurements of prey density around colonies (Birt et al. 1987) have been invoked to suggest that seabirds may deplete prey around colonies. The simultaneous availability of foraging range and dive time data on individual foraging trips suggests a test of this hypothesis. If seabird predation reduces prey density in waters around a colony in which initial prey density is uniform, then foraging success should rise with distance from the colony as successively less-depleted waters are encountered. Central place foraging theory (Orians and Pearson 1979) also predicts that foraging success should rise with distance, because long trips are economical only if they lead to better feeding areas which allow predators to recoup additional transportation costs. In the case of breeding seabirds, prey depletion near the colony should produce an inverse correlation between foraging range and proportion of diving time during individual trips, since birds should require fewer dives to meet food requirements in distant, less-depleted waters.

Potential foraging range and percentage of time diving were inversely correlated during colony-based chick-rearing in 1985, but not during incubation in 1986 (Fig. 3). Although the negative correlation found in chick-rearing in 1985 is consistent with the prey depletion hypothesis, other explanations cannot be ruled out. Capelin, the major food for breeding murres and their chicks at Witless Bay, undergo a spawning migration to coastal beaches in June and July. Migratory or advective flow of food (Cairns and Schneider 1990) will not prevent prey depletion effects if predation is large in comparison with prey influx. However, the arrival of large schools of capelin at sites distant from the Witless Bay colonies could produce a negative correlation between foraging range and dive time in the absence of near-colony prey depletion.

The demonstration of prey depletion by seabirds will remain problematic until difficulties in the measurement of prey distribution and abundance are resolved. However, new techniques such as those used in this study will help clarify the patterns and magnitude of seabird predation and focus questions for future investigation. These are essential steps towards understanding the role of seabirds in marine food webs.

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