

ENERGY INVESTED IN REPRODUCTION BY THICK-BILLED MURRES (*URIA LOMVIA*)

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ABSTRACT.—Pelagic seabirds that lay single-egg clutches have been thought to invest less energy in reproduction than inshore-feeding species that rear more than one young. To examine this idea I calculated time and energy budgets for Thick-billed Murres (*Uria lomvia*) breeding at two large arctic colonies and compared their energy expenditure with that of a hypothetical group (shirkers) that was capable of feeding at the same rate but did not attempt any reproductive activity. The difference in energy investment between breeders and shirkers was strongly dependent on the average foraging range. I also compared my results with similar estimates for inshore-feeding Black Guillemots (*Cephus grylle*). For the two Thick-billed Murre colonies, energy allocated to reproduction represented 30% and 24% of total energy expenditure during the breeding season. These values exceed the estimates for Black Guillemots. The amount of energy invested by Thick-billed Murres at the colonies considered probably is similar to that invested by other seabirds laying larger clutches and rearing heavier young. Received 8 December 1983, accepted 3 July 1984.

THE allocation of resources to reproduction, as a fraction of total energy budgets, has been regarded as an important component of life-history strategy (Cody 1966, Gadgil and Solbrig 1972, Goodman 1974, Wiens and Scott 1975, Dunn 1979, Hails and Bryant 1979). Techniques for quantifying such investment vary (Calow 1979). Previous studies of seabirds have depended mainly on estimating the energetic cost of egg production and chick rearing, although the authors acknowledged that the additional flying and feeding involved in reproduction must add significantly to the total energy cost (Wiens and Scott 1975, Dunn 1979).

Oceanic seabirds, which lay small clutches and have slow-growing chicks, have been thought to make a relatively small investment in reproduction compared with most birds (Dunn 1979), and hence considered to fall at the "K" end of the r-K strategy continuum (Goodman 1974). The assumption implicit here is that smaller clutches and slower-growing chicks indicate a lower annual energetic investment by the parents. This in turn is assumed to increase their residual reproductive value by increasing survival and the number of subsequent breeding attempts.

To examine the amount of energy invested by a long-lived pelagic seabird with a single-egg clutch, I calculated the cost of reproduction for the Thick-billed Murre (*Uria lomvia*), an arctic-nesting alcid that feeds, during the breeding season, on fish and crustacea obtained

mainly in offshore waters (Bradstreet 1980, Gaston and Nettleship 1981).

I adopted a new approach to calculate the amount of energy expended on reproduction. The energy expenditure of breeding birds was compared with that of a category of non-existent birds that hypothetically lived in the same area and had the same food-collecting ability as the breeders, but made no effort to breed. I have coined the term "shirkers" for this group to distinguish them from the true nonbreeding population, which carries out many activities associated with breeding (flying to and from the breeding colony, occupying breeding sites) and therefore makes some investment toward reproduction in future years. My intention was not to test the predictions of r- and K-selection theory, but to demonstrate that our ideas of "reproductive investment" may depend heavily on the way in which we choose to measure it.

To provide some material for comparison, I estimated the reproductive investment of Black Guillemots (*Cephus grylle*) in the same way. This is an inshore-feeding species that breeds in the same area as Thick-billed Murres, normally lays two eggs, and frequently rears two chicks.

METHODS

Information on time budgets and foraging ranges of Thick-billed Murres was drawn from data accumulated during Canadian Wildlife Service studies on

the large colonies at Prince Leopold Island, N.W.T. (86,000 pairs, 74°02'N, 90°00'W; Gaston and Nettleship 1981) and Digges Island, N.W.T. (180,000 pairs, 62°34'N, 77°43'W; Gaston et al. 1985). Data on Black Guillemots were obtained at Nuvuk Islands, N.W.T. (62°23'N, 78°05'W; Gaston et al. 1985, Cairns unpubl. data) about 25 km from the murre colony at Digges Island. Calculations of energy budgets are based on the energetics model used by Furness (1978).

Time budgets.—Information on time budgets was obtained during 24-h watches carried out every 5–10 days from before laying until most chicks had left, on study plots where the position of each breeding site was mapped and numbered. Thick-billed Murres incubate and brood continuously, so one member of each breeding pair was always present on each site. The arrival of the other member of the pair was marked by a recognizable greeting display (Gaston and Nettleship 1981), and the timing of arrivals and change-overs was recorded at all sites. The frequency of change-overs/24 h was used to estimate the mean number of visits to the colony by each bird.

Foraging range.—Information on distances traveled away from the colony was obtained from aerial surveys carried out during the chick-rearing period at Prince Leopold Island (Nettleship and Gaston 1978) and during the incubation and chick-rearing periods at Digges Island (Gaston et al. 1985, Gaston unpubl. data). Additional information for the prelaying and incubation periods at Prince Leopold Island was obtained from helicopter surveys of important feeding areas conducted by Bradstreet (1979).

Energy expenditure for breeders.—To calculate the energy expenditure of adult murres, their daily activities were divided into five categories:

(1) Time spent occupying the nest site, including incubation, brooding, and guarding the chick (T_1). Typically, birds occupying sites sat immobile; they sometimes slept. Preening and interacting with mates or neighbors occupied less than 10% of the total time. The duration of this behavior was determined by direct observation.

(2) Time spent in flight traveling between the colony and the feeding area (T_2). This was estimated from mean foraging range (L), flight speed (S), and mean number of visits made to the colony (V) using the equation $T_2 = 2VL/S$.

(3) Time spent flying between different locations within the feeding area (T_3). Most murres seen during aerial surveys were flying either toward or away from their colonies; hence, movement between feeding areas appears to be small. I estimated 0.33 h/day, adopted as a constant, for all classes of birds throughout the season.

(4) Time spent resting (T_4). I could not estimate what proportion of time away from the colony was spent resting. Birds relieved at the nest site usually flew to the water close to the colony to bathe and rest. Numbers on the water sometimes amounted to

as much as 10% of the entire breeding population. Some time on the feeding grounds also may be spent resting. The time during which both members of a pair were present at the site simultaneously amounted to less than 1 h/day and declined as the season progressed, suggesting that less time could be spared for rest in the chick-rearing period than during incubation. I therefore estimated time spent resting during daylight as 2 h during the incubation periods and 1 h during chick rearing. At Digges Island, where darkness imposes inactivity for a period, I assumed that one member of each pair was resting during darkness (T_5) and that the other was on the colony. I assumed that nonbreeders and shirkers spent the dark period resting.

(5) Time spent feeding (T_6). The remainder of the day I assumed was devoted to feeding. Hence, $T_6 = 24 - (T_1 + T_2 + T_3 + T_4 + T_5)$.

Energy expenditure was calculated for each category, using estimates based on equations given by Kendeigh et al. (1977; hereafter referred to as KDG) and observed mean weights (900 g for Prince Leopold Island and 936 g for Digges Island). The rate for T_1 and T_2 was assumed to be the same. Because birds occupying sites (T_1) were inactive, I considered their rate of energy expenditure equivalent to the mean of Standard and Existence Metabolism (KDG: Eqs. 5.15 and 5.35, Table 1). For resting during daylight (T_4), which included bathing and other maintenance activities, I assumed a rate equal to Existence Metabolism (KDG: Eq. 5.35). Birds resting away from the colony during darkness were assumed to have the same rate of energy expenditure as for incubation (T_1). Expenditure in flight (T_2, T_3) was calculated from KDG Eq. 5.43. The resulting approximation ($11.3 \times \text{BMR}$) is close to the rate measured for a $1,026\text{-g}$ American Black Duck (*Anas rubripes*), a bird with a rapid, flapping flight similar to that of a murre (Berger et al. 1970), but well below the rate predicted by Pennycuik's (1969) formula for the power requirements of a bird of the murre's dimensions. Details of input parameters are given in Appendix 1.

Estimates for energy expenditure during feeding present a problem because murres feed by pursuing prey underwater, using their wings for propulsion. For the Mallard (*Anas platyrhynchos*), Prange and Schmidt-Nielsen (1970) found the maximum rate of energy expenditure required for swimming was only one-third of that used in flight. However, the duck was using only its leg muscles for propulsion. In the case of the murres, because of the type of muscular activity involved, we may anticipate a rate of energy expenditure similar to that for flight. Between dives, which lasted 1–2 min, murres spent a similar length of time on the surface, usually being fairly inactive. I therefore estimated energy expenditure while feeding as $6 \times \text{BMR}$, which is about half the rate of expenditure in flight. This is $3.7 \times \text{SMR}$ for a 900-g bird, which is within the range of the $2\text{--}4 \times \text{SMR}$

TABLE 1. Rates of energy expenditure used in calculating daily energy budgets for Thick-billed Murres at Prince Leopold Island (PLI) and Digges Island (DI).

| | Brooding/ incubation (e_i) ^a | Flying (e_v, e_a) | Resting (e_r) | Feeding (e_f) |
|--------------------------------------------------------|---------------------------------------------------|--------------------------|----------------------|----------------------|
| Energy expenditure (kcal/h) for body wt of 900 g (PLI) | 6.151 | 36.420 | 7.003 | 19.338 |
| Energy expenditure (kcal/h) for body wt of 936 g (DI) | 6.286 | 37.430 | 7.154 | 19.902 |
| Multiple of BMR | 1.9 | 11.3 | 2.2 | 6.0 |

^a Also resting away from the colony at night.

estimated by Kooyman et al. (1982) for King Penguins (*Aptenodytes patagonica*). Their estimates presumably included some resting time. Final estimates for energy expenditure on different activities are given in Table 1.

Calculations of energy expenditure assume an ambient temperature of 0°C. At Prince Leopold Island, the mean air temperature for the entire season was very close to 0°C. At Digges Island it was 8°C, but the sea water, on which murres spent about half of their time, was constantly about 0°C, so the approximation probably remains valid.

Additional energy expended by the female in producing the egg and by both sexes in incubating was calculated from KDG Eqs. 5.51, 5.52, and 5.56. However, the cost of incubation estimated in this way was less than 2% of daily average energy expenditure, and it therefore has been ignored. Energy expended in catching food for the chick was introduced by adding the energy content of fish delivered to chicks to the estimate of total energy consumed and then using this figure to calculate the rate at which energy was captured during feeding (feeding time being constant). The cost of transporting meals and lifting them to the nest site was considered negligible.

The general equation used to calculate average daily energy expenditure (ADEE) was:

$$ADEE \text{ (kcal)} = T_e e_i + (T_i + T_a) e_a + T_v e_v + T_f e_f + x \tag{1}$$

where T = time (h), e = rate of energy expenditure (kcal/h), and x represents daily expenditure on egg production. Expressing all e 's in terms of BMR, this is equivalent to:

$$ADEE \text{ (kcal)} = 3.22 [1.91T_i + 11.30(T_v + T_a) + 2.17T_v + 6.00T_f] + x \tag{2}$$

for a 900-g bird.

The rate at which food is captured (R) can then be calculated from the total energy expenditure and the time spent feeding:

$$R = ADEE (K + Y) / T_f \tag{3}$$

where K = a constant representing the efficiency with which the bird converts food energy to output energy and Y = the amount of food fed to the chick

(kcal/day). I assumed a value of 1.18 for K throughout, following Dunn's (1975) estimate for a cormorant feeding on fish.

Energy expenditure for shirkers and nonbreeders.—For shirkers I assumed a rate of feeding equal to that calculated for breeders at the same period and assumed that they flew only the 0.33 h required to move between feeding places. The remainder of their time I assumed was spent resting. The time spent feeding was calculated by solving the simultaneous equations:

$$0.33e_v K + T_v e_v K + T_f e_f K = R_b T_f \tag{4}$$

and

$$T_r + T_f = 23.67, \tag{5}$$

where R_b = the rate of energy intake of breeders while feeding. Hence, substituting,

$$T_f = (0.33e_v + 23.67e_r) / (R_b / K + e_r - e_f) \tag{6}$$

and

$$T_r = 23.67 - T_f \tag{7}$$

Because nonbreeders did not occupy fixed sites on the colony and were not marked, I could not determine time budgets for these birds by observation. I have estimated their time and energy budgets using the following assumptions:

- (1) The most capable nonbreeders could achieve a feeding rate equal to that of the breeders without the additional cost of egg formation and incubation.
- (2) The least capable nonbreeders were barely able to maintain their condition in the breeding area at the median date of laying (i.e. all their time was spent feeding, except the basic 2 h for resting and 0.33 h for flying).
- (3) The mean feeding rate for nonbreeders was the median value for the most and least capable.
- (4) The ratio of the mean feeding rate of nonbreeders to that of breeders remained constant over the season.
- (5) Nonbreeders visited the colony only once every two days.
- (6) The rate of energy expenditure of birds on the

colony was equal to e_r (EMR) rather than e_i because they spent more time than breeders moving about and interacting with other birds (Gaston and Nettleship 1981).

Because the time budget is fixed except for time spent on the colony (T_c) and time spent feeding (T_f), these two parameters can be derived from the simultaneous equations:

$$T_c e_c K + (T_i + 0.33) e_r K + 2e_r K + T_f e_f K = R_{nb} T_i \quad (8)$$

and

$$T_i + T_f = 21.67 - T_c \quad (9)$$

where R_{nb} = median rate of energy intake of nonbreeders while feeding and $T_i = L/S$, where L is the same as for breeders.

The assumption that nonbreeders did not travel to and from the colony as often as breeders rests on the hypothesis that their fitness is maximized by maximizing the amount of time spent on the colony. Because traveling involves a high rate of energy expenditure, they should try to minimize the amount of traveling that they do. The lowest rate of exchange of breeders observed was 0.5 visits/day, so I assumed that nonbreeders maintained this schedule throughout the season at both colonies.

Observed values for parameters.—Observers were present at Prince Leopold Island from the start of the season in 1976. Birds were seen at the colony for the first time (D_1) 50 days before the median date of laying (D_c), but for the first 20 days after D_1 numbers never exceeded 25% of the breeding population. From 30 days before D_c , 7 1–2-day peaks of about 50–80% attendance alternated with periods when numbers were low. The mean number counted at the colony during the 30 days prior to median laying was 40% of the total breeding population. Once laying had begun, however, 50% of the breeders nearly always were present. During incubation the rate of changeovers at Prince Leopold Island rose from 1 to about 2 changes \cdot egg $^{-1} \cdot$ day $^{-1}$ between D_c and median hatching. At Digges Island the corresponding figures were 0.5 and 0.8 changes \cdot egg $^{-1} \cdot$ day $^{-1}$. During the chick-rearing period food was delivered to chicks 3–5 times daily ($\bar{x} = 4$) at Prince Leopold Island and twice daily at Digges Island.

The number of birds attending both colonies declined from about the median date of chick departure onwards, so that less than 10% of breeding sites were occupied 2 weeks later. During this period a marked diurnal change in attendance suggested that the remaining birds were visiting the colony once a day.

The mean foraging range of birds from Prince Leopold Island was 110 km during the prelaying and incubation periods (Bradstreet 1979) and 56 km during the chick-rearing period (Nettleship and Gaston 1978, Gaston and Nettleship 1981). At Digges Island

the mean foraging range was estimated as 100 km during both incubation and chick-rearing (Gaston et al. 1985, Gaston unpubl. data). The flight speed of Thick-billed Murres flying between their colony and feeding area is 58 km/h (Bradstreet 1982).

At Prince Leopold Island birds were active throughout the 24-h day up to the date when 50% of chicks had fledged (Gaston and Nettleship 1981). At Digges Island darkness imposed almost total inactivity for an average of 3 h during the early part of incubation, 4 h near the end of incubation, and 5 h by the middle of the chick-rearing period.

Values adopted for energy estimates.—During the prelaying period I considered time spent at the colony (T_c) and traveling (T_i) to be negligible up to D_{20} . Thereafter, I calculated the mean duration spent at the colony from:

$$T_i = \frac{\text{Mean number counted at the colony } D_{20}-D_c}{\text{Total number of breeders}} \times 24 = 9.6 \text{ h/day.}$$

This indicates that birds averaged about 41 h at the colony at each visit.

I assumed that, on average, breeders made 7 trips from the feeding area to the colony before the median date of laying. Hence, the mean time spent traveling during the period $D_{20}-D_c$ can be estimated from:

$$T_i = 2VL/[58(D_c - D_{20})] = 0.89 \text{ h/day.}$$

I assumed that the rate of energy intake while feeding during the prelaying period was a little lower than that calculated for the start of the incubation period (45 kcal/day).

For the incubation period I used observed rates of exchange to calculate the frequency of visits to the colony by breeders and estimated the rate of visits by nonbreeders to be once every two days. I assumed that from the median date of fledging onwards, the mean daily energy expenditure of breeders took 16 days to fall to the level of shirkers.

Fresh egg weights averaged 96.5 g at Prince Leopold Island and 109 g at Digges Island. The mean weight of fish delivered to chicks was 12.5 g at Prince Leopold Island and 8.9 g at Digges Island (Gaston and Nettleship 1981, Gaston unpubl. data). Only one fish was delivered on each visit to the colony. I assumed an energy content for fish of 1.14 kcal/g fresh weight (Dunn 1975). Colony-specific input parameters are summarized in Appendix 2.

RESULTS

Energy expenditure.—Estimated time budgets are shown in Table 2. Estimated daily energy expenditure by breeding murres based on these

TABLE 2. Time budgets used in estimating average daily energy expenditure for Thick-billed Murres ($\text{h} \cdot \text{bird}^{-1} \cdot \text{day}^{-1}$).

| | On colony | Traveling | Flying | Feeding | Resting (daylight) | Resting (night) |
|-------------------------------|-----------|-----------|--------|---------|-----------------------|--------------------|
| Prince Leopold Island | | | | | | |
| Breeders | | | | | | |
| Prelaying male | 9.60 | 0.89 | 0.33 | 7.59 | 5.59 | 0 |
| Prelaying female ^a | 9.60 | 0.89 | 0.33 | 8.08 | 5.10 | 0 |
| Early incubation | 12.00 | 1.90 | 0.33 | 7.77 | 2.00 | 0 |
| Late incubation | 12.00 | 3.79 | 0.33 | 5.88 | 2.00 | 0 |
| Chick rearing | 12.00 | 3.86 | 0.33 | 6.81 | 1.00 | 0 |
| Nonbreeders (average) | | | | | | |
| Early incubation | 11.25 | 1.90 | 0.33 | 8.52 | 2.00 | 0 |
| Late incubation | 11.25 | 1.90 | 0.33 | 8.52 | 2.00 | 0 |
| Chick rearing | 12.76 | 0.97 | 0.33 | 7.94 | 2.00 | 0 |
| Shirkers | | | | | | |
| Prelaying | 0 | 0 | 0.33 | 6.89 | 16.28 | 0 |
| Early incubation | 0 | 0 | 0.33 | 6.19 | 17.48 | 0 |
| Late incubation | 0 | 0 | 0.33 | 3.74 | 19.93 | 0 |
| Chick rearing | 0 | 0 | 0.33 | 3.96 | 19.71 | 0 |
| Digges Island | | | | | | |
| Breeders | | | | | | |
| Early incubation | 12.00 | 1.72 | 0.33 | 6.45 | 2.00 | 1.5 |
| Late incubation | 12.00 | 2.76 | 0.33 | 4.91 | 2.00 | 2.0 |
| Chick rearing | 12.00 | 3.45 | 0.33 | 4.72 | 1.00 | 2.5 |
| Nonbreeders (average) | | | | | | |
| Early incubation | 4.96 | 1.72 | 0.33 | 11.99 | 2.00 | 3.0 |
| Late incubation | 7.59 | 1.72 | 0.33 | 8.35 | 2.00 | 4.0 |
| Chick rearing | 7.50 | 1.72 | 0.33 | 7.44 | 2.00 | 5.0 |
| Shirkers | | | | | | |
| Prelaying | | | | | | |
| Early incubation | 0 | 0 | 0.33 | 5.20 | 15.47 | 3.0 |
| Late incubation | 0 | 0 | 0.33 | 3.46 | 16.21 | 4.0 |
| Chick rearing | 0 | 0 | 0.33 | 2.96 | 15.71 | 5.0 |

^a During last 15 days, assuming egg formation extends over 15 days at a cost of 15 kcal/day.

time budgets ranged from 295 to 365 $\text{kcal} \cdot \text{bird}^{-1} \cdot \text{day}^{-1}$ at Prince Leopold Island and from 304 to 333 $\text{kcal} \cdot \text{bird}^{-1} \cdot \text{day}^{-1}$ at Digges Island (excluding the prelaying period, for which no data were available). Maximum rates represent 2.9 and $2.6 \times \text{SMR}$ or 4.7 and $4.2 \times \text{BMR}$. Minimum rates occurred during the prelaying period and maximum rates during chick rearing (Fig. 1).

Corresponding figures for nonbreeders ranged from 306 to 395 $\text{kcal} \cdot \text{bird}^{-1} \cdot \text{day}^{-1}$ at Prince Leopold Island and from 324 to 384 $\text{kcal} \cdot \text{bird}^{-1} \cdot \text{day}^{-1}$ at Digges Island. Rates for "average" nonbreeders were higher than those for breeders at the start of the incubation period at both colonies, falling below them during the chick-rearing period (Fig. 1).

Rates of energy intake.—Rates of energy intake during feeding rose from 48 kcal/h at the time of incubation to 67 kcal/h during chick rearing at Prince Leopold Island and from 56 to 86 kcal/h over the same period at Digges Island. Median feeding rates estimated for nonbreeders ranged from 60 to 70% of the rates for breeders (Table 3).

Energy expenditure by shirkers and the cost of reproduction.—Energy expenditure by breeders and shirkers was assumed to be equal at the beginning of the prelaying period. Thereafter, the daily expenditure of shirkers decreased while that of breeders increased (Fig. 1). The minimum daily energy expenditure of shirkers was 223 $\text{kcal} \cdot \text{bird}^{-1} \cdot \text{day}^{-1}$ at Prince Leopold Island and 215 $\text{kcal} \cdot \text{bird}^{-1} \cdot \text{day}^{-1}$ at Digges Is-

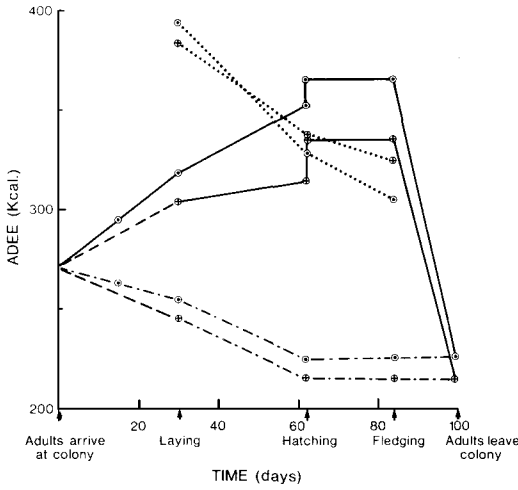


Fig. 1. Estimated average daily energy expenditure (ADEE) by breeding (solid lines), nonbreeding (dotted lines), and shirking (broken lines) Thick-billed Murres at Prince Leopold Island (circles) and Digges Island (crosses).

land, giving maximum ratios of 1.61 and 1.55, respectively, for the energy expenditure of breeders to that of shirkers (Table 4).

I estimated the energy expenditure of breeders and shirkers over the entire breeding season by calculating the areas below the corresponding curves in Fig. 1. I then estimated the proportion of energy expenditure devoted to reproduction by subtracting the area below the shirkers' curve from the area below the breeders' curve. I expressed the difference as a percentage of the area below the breeders' curve. This yielded estimates for the proportion of energy expenditure devoted to reproduction of 30% at Prince Leopold Island and 24% at Digges Island.

The effect of changes in body weight.—I assumed that birds remained in energy balance throughout the season, but this assumption is not precisely correct. In one year at Prince Leopold Island and in two years at Digges Sound, Thick-billed Murres showed significant weight losses between laying and the end of chick rearing. Average weights at Digges Island in 1982 rose by 40 g between egg-laying and the middle of the incubation period (20 days) and then fell by 120 g/bird by the end of chick rearing (40 days); hence, average gains were about 2 g/day, and losses were about 3 g/day.

TABLE 3. Rates of energy intake during feeding (kcal/h).

| Locality/status | Start of incubation | Chick rearing |
|-----------------------|---------------------|---------------|
| Prince Leopold Island | | |
| Breeder | 48.46 | 67.48 |
| Nonbreeder | 34.50 | 41.91 |
| Digges Island | | |
| Breeder | 55.71 | 85.72 |
| Nonbreeder | 39.03 | 53.39 |

Observations on the amount of fat present on birds collected suggested that these weight changes were caused by changes in the amount of stored fat.

One gram of fat is equivalent to approximately 9.5 kcal of energy (Pennycuik 1975, Kendeigh et al. 1977). Therefore, actual rates of energy intake in the first half of incubation may have been a minimum of 19 kcal/day greater than those predicted, and subsequent rates may have been about 29 kcal/day lower. If the food supply within foraging range of the colony remained relatively stable during this period, the observed weight gain and loss would have effectively evened out the rate of feeding necessary to support energy expenditure during reproduction.

Changes in weight also would have affected

TABLE 4. Sensitivity of average daily energy expenditure (ADEE) estimates for breeders and ADEE (breeder) : ADEE (shirker) ratios to variation in input parameters.

| Input parameter | Deviation of output from "best" estimate (%) | | | |
|------------------------------|----------------------------------------------|------------|--------------------------------|------------|
| | ADEE (breeder) | | ADEE (breeder): ADEE (shirker) | |
| | +25% | -25% | +25% | -25% |
| e_a | +11 | -11 | +11 | -11 |
| e_r | +1 | -1 | +19 | -13 |
| e_f | +7 | -7 | 0 | 0 |
| e_i | +7 | -7 | +4 | -4 |
| L | +5 | -5 | +10 | -9 |
| S | -5 | +5 | -9 | +10 |
| V (and corresponding Y) | +5 | -5 | +10 | -10 |
| | 3 h | 0 h | 3 h | 0 h |
| T_r | -9 | +4 | 0 | 0 |
| | 1 h | 0 h | 1 h | 0 h |
| T_s | +4 | -2 | -4 | +3 |

energy expenditure, particularly in flight. Freed (1981) and Norberg (1981) have argued that weight changes during reproduction may be an adaptive response to the increased amount of flying necessitated by chick rearing. In the case of Thick-billed Murres at Digges Sound, the observed decline in weight between mid-incubation and the end of chick rearing would have altered the estimated flight energy expenditure from 40.37 to 37.82 kcal/h. Recalculating ADEE for incubation and chick rearing using the weights observed in 1982 (1,043 and 923 g) gives 395 and 363 kcal/day, a reversal of the trend in daily energy expenditure predicted assuming a constant weight.

If the changes in weight are wholly accounted for by stored fat, the difference in energy expenditure is probably less than these calculations indicate because fat deposits are likely to have little effect on BMR. Also, because the bulk of the fat is stored subcutaneously (pers. obs.), it probably helps to improve insulation and hence decrease energy expenditure on thermoregulation. The exact magnitude of the effect of weight changes on energy expenditure therefore must remain uncertain. However, heavier birds inevitably must expend more energy on flight (Pennycuik 1975).

Sensitivity of the model to variation in input parameters.—The effect of variation in constants derived from energy expenditure equations on a similar model was examined by Furness (1978). He found that output from his model (total energy expenditure of an entire colony) was very strongly affected by variation in these constants. My estimates of ADEE are likely to be similarly affected by these constants and should be treated with caution. However, for comparisons between breeders, nonbreeders, and shirkers, variation in the equation constants has a negligible effect because the same body weights are used for all three classes.

The ratio of energy expenditure by breeders, nonbreeders, and shirkers is affected by the relative rate of energy expenditure on different activities. To examine the sensitivity of the model to variation in the relative values of these parameters, I repeated the model calculations for the chick-rearing period with values of e_r , e_{ar} , e_s , and e_f that were 25% greater and smaller than my best estimates, altering the input values one at a time.

The greatest effect on the ADEE of breeders

was produced by alteration of the rate of energy expenditure on flight, where a 25% variation altered the ADEE of breeders by 11%, nonbreeders by 5%, and shirkers less than 1% (Table 4). A 25% variation in the rate of energy expended while resting (e_r) resulted in a change of 15% in the ADEE of shirkers and hence had a big effect on the ratio ADEE (breeders): ADEE (shirkers). Alterations in the rates of energy expended while feeding and incubating had smaller effects on outputs.

I also examined the sensitivity of the output to other input parameters. Neither time spent resting nor time spent flying in the feeding area had much effect on the output (Table 4). However, a 25% change in flight speed (S) or distance traveled (L) altered the ADEE of breeders by 5% and the ratio breeders: shirkers by 9–10%.

Because foraging range (L) and the energetic cost of feeding (e_f) were poorly estimated, I examined variation in output in relation to these two parameters in greater detail, using three values for each (Table 5). Changing e_f had a large effect on estimated ADEE but had little impact on the ratio ADEE (breeders): ADEE (shirkers). Foraging range had considerable impact on ADEE for the case where e_f was 10 kcal/h but a much smaller effect for the (probably more likely) cases where e_f was higher. It had a large effect on the ratio ADEE (breeders): ADEE (shirkers) for all values of e_f , the ratio increasing with foraging range. This is to be expected because as traveling time is reduced, a greater proportion of time is spent feeding and the energy budgets of breeders and shirkers converge, with incubation and brooding having energy demands similar to those of resting.

Energy expenditure by Black Guillemots.—Black Guillemots cease to brood their chicks about 5 days after hatching, and consequently they are free to feed throughout the daylight period (about 19 h at Nuvuk Islands in August) during the remainder of chick rearing. Although they make many trips to feed their chicks each day ($V = 5-10$), they forage within 5 km of the breeding site. Hence, travel time is small compared to Thick-billed Murres. The combination of these characteristics means that, although daily energy expenditure during chick rearing is 41% greater than during incubation, the rate at which food has to be found is only slightly

TABLE 5. Average daily energy expenditure by Thick-billed Murres at Prince Leopold Island in relation to different estimates of foraging range and energy expenditure while feeding.

| | $e_f = 10$ | | | $e_f = 19.34$ | | | $e_f = 30$ | | |
|-----------------|--------------------|--------|--------|---------------|--------|--------|------------|--------|--------|
| | Close ^a | Mid | Far | Close | Mid | Far | Close | Mid | Far |
| Incubation | | | | | | | | | |
| Breeders | 223.87 | 260.31 | 296.75 | 304.52 | 328.07 | 351.63 | 396.58 | 405.53 | 414.29 |
| Shirkers | 199.88 | 192.82 | 195.23 | 267.12 | 239.47 | 228.33 | 344.85 | 293.86 | 265.57 |
| Breeder/shirker | 1.12 | 1.35 | 1.52 | 1.14 | 1.37 | 1.54 | 1.15 | 1.38 | 1.56 |
| Chick rearing | | | | | | | | | |
| Breeders | 235.97 | 290.63 | 345.30 | 322.73 | 358.07 | 393.42 | 421.79 | 435.07 | 448.35 |
| Shirkers | 198.29 | 191.20 | 185.65 | 264.53 | 232.51 | 209.27 | 340.15 | 278.89 | 237.22 |
| Breeder/shirker | 1.19 | 1.52 | 1.86 | 1.22 | 1.54 | 1.88 | 1.24 | 1.56 | 1.89 |

^a Average foraging ranges for the incubation period: close, 30 km; mid, 70 km; far, 110 km; and for the chick-rearing period: close, 20 km; mid, 50 km; far, 80 km.

greater during the chick-rearing period, once brooding has ceased, than during incubation (Table 6). The figures in Table 6 are based on a nest containing two chicks. For the average nest, containing 1.3 chicks, energy delivered to chicks (Y) is 72.8 kcal/day, and the peak rate of energy intake becomes 21.85 kcal/h, lower than that during incubation.

According to these estimates, shirkers expend practically the same energy as breeders during the incubation period, and even during chick rearing the ratio of ADEE of breeders to that of shirkers is only 1.45. These estimates are lower than the estimates for the Thick-billed Murres, although differences between the species for the chick-rearing period is largely dependent on the difference between the values I have selected for energy expended while foraging (e_f) and flying (e_a). In the terms I have adopted, therefore, the cost of reproduction seems to be lower for the Black Guillemots at Nuvuk Islands than for the neighboring Thick-billed Murres at Digges Island, amounting to only a 19% increase over the level estimated for shirkers (based on a total colony attendance period of 74 days).

DISCUSSION

Four points deserve particular mention from these results. First, the maximum daily energy expenditure of breeding murres, at 4–5 times BMR, is high in comparison with other studies on breeding birds (Utter and Lefebvre 1973, Ricklefs 1974, Hails and Bryant 1979) and may approach the sustainable limit for birds of 4 times BMR (Utter, quoted in King 1974; Drent

and Daan 1980). Measurements of energy expenditure by breeding Thick-billed Murres at Digges Island and breeding Black Guillemots at Nuvuk Islands during the incubation period using the doubly labeled water technique suggest that my estimates are approximately correct (3 incubating Thick-billed Murres, 342–421 kcal/day; 5 incubating Black Guillemots, 124–183 kcal/day; Prÿs-Jones and Gaston in prep.). In terms of SMR these estimates are also similar to those made for King Penguins (Kooyman et al. 1982), another underwater-pursuit predator.

Second, comparison with our hypothetical shirkers suggests that maximum rates of energy expenditure by breeders average 1.5–1.7 times the level that would sustain them if they made no attempt to visit the colony. Assuming that birds remain in energy balance, this suggests an equivalent increase in the amount of food consumed. The Pigeon Guillemot (*Cephus columba*, Koelink 1972) and the Double-crested Cormorant (*Phalacrocorax auritus*, Dunn 1975), two comparable fish-eating seabirds that, on average, rear two young per nesting attempt, had estimated increases in feeding rates during chick rearing twice that of nonbreeders. Third, the estimated rate of energy intake during feeding, which during the chick-rearing period reached 3–5 times the expenditure involved, is normal, or perhaps a little higher than normal, for birds in which the young are fed at the nest (Ricklefs 1974).

Finally, the estimated daily energy expenditure of nonbreeders is not much different from that of breeders. Although this seems counterintuitive, it is quite reasonable if we assume (as the model does) that nonbreeders are

TABLE 6. Time budgets and estimates of energy expenditure for breeding Black Guillemots and shirkers.

| Status | Period | At the nest (T_n, e_n) ^a | Flying ($T_a + T_v,$ e_a) ^b | Feeding (T_f, e_f) ^c | Resting, daylight (T_r, e_r) ^d | Resting, night (T_n, e_n) | Totals (ADEE) | Rate of energy intake (kcal/h) ^e |
|---------|----------------------------|--------------------------------------------|--------------------------------------------------|----------------------------------------|-----------------------------------------------------|-------------------------------------|------------------|------------------------------------------------------|
| Breeder | Incubation | | | | | | | |
| | Time (h) | 12.0 | 1.0 | 7.0 | 2.0 | 2.0 | | |
| | Energy (kcal) | 47.04 | 20.68 | 74.83 | 9.0 | 9.0 | 160.55 | 22.94 |
| | Chick rearing (>5 days) | | | | | | | |
| | Time (h) | 0 | 1.5 | 15.5 | 2.0 | 5.0 | | |
| | Energy (kcal) | | 31.02 | 165.69 | 9.0 | 19.60 | 225.31 | 24.38 |
| Shirker | Incubation | | | | | | | |
| | Time (h) | 0 | 0.5 | 6.93 | 12.57 | 4.0 | | |
| | Energy (kcal) | | 10.34 | 74.08 | 56.56 | 18.0 | 158.98 | |
| | Chick rearing (>5 days) | | | | | | | |
| | Time (h) | 0 | 0.5 | 6.38 | 12.12 | 5.0 | | |
| | Energy (kcal) | | 10.34 | 68.20 | 54.54 | 22.50 | 155.58 | |

^a $e_n = 3.92$ kcal/h.

^b $e_a = 20.68$ kcal/h, "nontravel flying" = 0.5 h.

^c $e_f = 6 \times \text{BMR} = 10.69$ kcal/h.

^d $e_r = \text{EMR} = 4.50$ kcal/h.

^e $R_b = 1.18 \text{ ADEE}/R_i$ (incubation) and $(1.18 \text{ ADEE} + Y)/T_f$ (chick rearing), where $Y = 112$ kcal/day (nest contains 2 full-grown chicks).

less efficient at foraging than breeders (see Burger 1980). The extra efficiency of breeders allows them to invest time in incubation and brooding, which requires a low rate of energy expenditure compared to the additional feeding that nonbreeders must do. If nonbreeders travel from the colony to the feeding area more frequently than once every two days, as assumed by the model, then their energy expenditure almost certainly will exceed that of breeders. The possibility that prebreeders actually might be making a greater investment towards reproduction than breeders emerges, although their efforts yield no immediate output. The model estimates that nonbreeders average about 9 h/day (Digges Island) or 13 h/day (Prince Leopold Island) at the colony during the chick-rearing period. Assuming that all of this is in daylight, this suggests that half the nonbreeding population is present at any one time when we can count them. This accords fairly well with counts made at both colonies and estimates of numbers of nonbreeders as a proportion of the total population (Birkhead and Hudson 1977, Gaston and Nettleship 1981, Gaston et al. 1985).

These observations give slightly conflicting impressions of the investment in reproduction

made by Thick-billed Murres, in comparison with other birds. The maximum rate of energy expenditure for most birds, however, is sustained for only a few days when the nestlings are at their peak weight (Dunn 1975). In the Thick-billed Murre feeding rates hardly vary with the age of the chick, so the maximum rate of expenditure applies for the entire 20–25-day period when the chick is being fed (Gaston and Nettleship 1981). Also, Dunn (1975) and Koelink (1972) calculated reproductive investment in a different manner, including the total energy delivered to the chicks in the adult's energy budget instead of only the energy expended on finding and catching the food. Estimated in such terms, Thick-billed Murres make a very small investment in reproduction.

If we compare the Thick-billed Murre with the Black Guillemot, we find that successful Black Guillemots at Nuvuk Islands reared an average of 1.3 chicks to fledging, with a mean fledging weight of about 350 g (Gaston et al. 1985). In contrast, Thick-billed Murres never reared more than 1 chick, and average weights at fledging at Digges Island were about 150 g. Despite this difference in reproductive output, the energy expenditure of breeders exceeded that of shirkers to a greater degree in Thick-

billed Murres than in Black Guillemots during both incubation and chick rearing. Hence, the murres make a greater energetic investment than the guillemots but achieve a smaller reproductive profit.

In summary, in terms of energy expenditure, the Thick-billed Murre appears to make just as much investment in reproduction as other seabirds that have life-history strategies involving a higher potential intrinsic rate of increase. As indicated in Table 5, this conclusion depends heavily on my estimates of foraging range for the Thick-billed Murres. Although data on the foraging ranges of birds from the two colonies considered are fragmentary, additional evidence from shipboard surveys by Brown (1980) in the vicinity of Digges Island support the figures given here. The figures for close foraging range given in Table 5 are likely to be well below the mean foraging range for colonies the size of Prince Leopold and Digges islands (see also Gaston 1985). Otherwise, the results seem fairly robust to variations in input parameters within reasonable limits.

The very long distances over which Thick-billed Murres travel to find food are probably a consequence of the very large colonies in which these birds congregate (Gaston et al. 1983). This situation is typical of the species. In the western Atlantic, for instance, more than 90% of the population breeds in colonies of more than 10,000 pairs (Gaston 1980).

I conclude that the reproductive investment of seabirds appears to vary with the way that we choose to measure it. Measured by the shirker method, it probably is not closely correlated to reproductive rate. The apparently K-selected attributes of seabirds probably constitute a special case deriving from the fact that breeding sites are restricted and hence food resources for reproduction are constrained, as suggested by Ricklefs (1977).

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LITERATURE CITED

- BERGER, M., J. HART, & O. Z. ROY. 1970. Respiration, oxygen consumption, and heart rate in some birds during rest and flight. *Z. Vergl. Physiol.* 66: 201-214.
- BIRKHEAD, T. R., & P. J. HUDSON. 1974. Population parameters for the Common Guillemot *Uria aalge*. *Ornis Scandinavica* 8: 145-154.
- BRADSTREET, M. S. W. 1979. Thick-billed Murres and Black Guillemots in the Barrow Strait area, N.W.T., during spring: distribution and habitat use. *Can. J. Zool.* 57: 1789-1802.
- . 1980. Thick-billed Murres and Black Guillemots in the Barrow Strait area, N.W.T., during spring: diets and food availability along ice-edges. *Can. J. Zool.* 58: 2120-2140.
- . 1982. Occurrence, habitat use and behavior of seabirds, marine mammals and arctic cod at the Pond Inlet ice edge. *Arctic* 35: 28-40.
- BROWN, R. G. B. 1980. The pelagic ecology of seabirds. *Trans. Linnaean Soc. New York* 9: 15-22.
- BURGER, J. 1980. The transition to independence and post-fledging parental care in seabirds. Pp. 367-448 in *Behavior of marine animals*. Vol. 4, *Marine birds* (J. Burger, B. L. Olla, and H. E. Winn, Eds.). New York, Plenum Press.
- CALOW, P. 1979. The costs of reproduction—a physiological approach. *Biol. Rev.* 54: 23-40.
- CODY, M. L. 1966. A general theory of clutch size. *Evolution* 20: 174-184.
- DRENT, R. H., & S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225-252.
- DUNN, E. H. 1975. Caloric intake of nestling Double-crested Cormorants. *Auk* 92: 553-565.
- . 1979. Time-energy use and life-history strategies of northern seabirds. Pp. 141-166 in *Conservation of marine birds of North America* (J. C. Bartonek and D. N. Nettleship, Eds.). Washington, D.C., U.S. Fish Wildl. Serv., Wildl. Rept. No. 11.
- FREED, L. A. 1981. Loss of mass in breeding wrens: stress or adaptation? *Ecology* 62: 1179-1186.
- FURNESS, R. W. 1978. Energy requirements of seabird communities: a bioenergetics model. *J. Anim. Ecol.* 47: 39-54.
- GADGIL, M., & O. T. SOLBRIG. 1972. The concept of "r" and "K" selection: evidence from wild flowers and some theoretical considerations. *Amer. Natur.* 106: 14-31.
- GASTON, A. J. 1980. Populations, movements and wintering areas of Thick-billed Murres (*Uria lomvia*) in eastern Canada. *Can. Wildl. Serv. Progr. Note* 110.
- . 1985. Development of the young. In *The*

- Atlantic Alcidae (T. R. Birkhead and D. N. Nettleship, Eds.). New York, Academic Press. In press.
- , D. CAIRNS, R. D. ELLIOTT, & D. G. NOBLE. 1985. A natural history of Digges Sound. Can. Wildl. Serv. Rept. In press.
- , G. CHAPDELAINE, & D. G. NOBLE. 1983. The growth of Thick-billed Murre chicks at colonies in Hudson Strait: inter- and intra-colony variation. Can. J. Zool. 61: 2465-2475.
- , & D. N. NETTLESHIP. 1981. The Thick-billed Murres of Prince Leopold Island. Can. Wildl. Serv. Monogr. No. 6.
- GOODMAN, D. 1974. Natural selection and a ceiling cost on reproductive effort. Amer. Natur. 108: 247-268.
- HAILS, C. J., & D. M. BRYANT. 1979. Reproductive energetics of a free-living bird. J. Anim. Ecol. 48: 471-482.
- KENDEIGH, S. C., V. R. DOL'NIK, & V. M. GAVRILOV. 1977. Avian energetics. Pp. 127-204 in Granivorous birds in ecosystems (J. Pinowski and S. C. Kendeigh, Eds.). Cambridge, England, Cambridge Univ. Press.
- KING, J. R. 1974. Seasonal allocation of time and energy resources in birds. Pp. 4-85 in Avian energetics (R. A. Paynter, Jr., Ed.). Publ. Nuttall Ornithol. Club No. 15.
- KOELINK, A. F. 1972. Bioenergetics of growth in the Pigeon Guillemot. Unpublished M.Sc. thesis. Vancouver, British Columbia, Univ. British Columbia.
- KOORYMAN, G. L., R. W. DAVIS, J. P. CROXALL, & D. P. COSTA. 1982. Diving depths and energy requirements of King Penguins. Science 217: 726-727.
- NETTLESHIP, D. N., & A. J. GASTON. 1978. Patterns of pelagic distribution of seabirds in western Lancaster Sound and Barrow Strait, N.W.T. Can. Wildl. Serv. Occ. Pap. No. 39.
- NORBERG, A. 1981. Temporary weight decrease in breeding birds may result in more fledged young. Amer. Natur. 118: 838-850.
- PENNYCUICK, C. J. 1969. The mechanics of bird migration. Ibis 111: 525-556.
- . 1975. Mechanics of flight. Pp. 1-76 in Avian biology, vol. 5 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.
- PRANGE, M. D. & K. SCHMIDT-NIELSEN. 1970. The metabolic cost of swimming in ducks. J. Exp. Biol. 53: 763-777.
- RICKLEFS, R. E. 1974. Energetics of reproduction in birds. Pp. 152-292 in Avian energetics (R. A. Paynter, Jr., Ed.). Publ. Nuttall Ornithol. Club No. 15.
- . 1977. On the evolution of reproductive strategies in birds: reproductive effort. Amer. Natur. 111: 453-478.
- UTTER, J. M., & E. A. LEFEBVRE. 1973. Daily energy expenditure of Purple Martins (*Progne subis*) during the breeding season: estimates using D_2O^{18} and time-budget methods. Ecology 54: 597-603.
- WIENS, J. A., & J. M. SCOTT. 1975. Model estimation of energy flow in Oregon coastal seabird populations. Condor 77: 439-452.

APPENDIX 1. Input parameters for model (energy expenditure estimates and formulae from Kendeigh et al. 1977).

| | BM (5.5) ^a | SM (5.15) | EM (5.35) | Flight (5.43) | Egg production ^b (5.51, 5.52) | Chick food ^c |
|--------------|--------------------------|--------------|--------------|------------------|------------------------------------------------|-------------------------|
| Multiplicand | 0.5224W | 2.624W | 4.142W | 0.3157W | 2.484W | |
| Exponent | 0.7347 | 0.5705 | 0.5444 | 0.698 | 0.9574 | 1.14 (fish wt) |

^a Formula number in Kendeigh et al. (1977).

^b Daily investment in egg production (x) is estimated by dividing this result by the number of days taken to form an egg (15 days, Gaston and Nettleship 1981).

^c Daily energy fed to chicks (Y) is estimated by multiplying this figure by the number of visits during the chick-rearing period (V).

APPENDIX 2. Summary of colony-specific input parameters (EI = early incubation, LI = late incubation, CR = chick rearing).

| | Prince Leopold Island (TBM) | Digges Island (TBM) | Nuvuk Islands (BG) |
|-----------------------------------------------------|--------------------------------------|---------------------------|--------------------------|
| Weight (g) | | | |
| Adult | 900 | 936 | 400 |
| Egg | 96.5 | 110 | — |
| Fish | 12.5 | 8.9 | 12.0 |
| Visits · bird ⁻¹ · day ⁻¹ (V) | | | |
| EI | 0.5 | 0.25 | — |
| LI | 1.0 | 0.4 | — |
| CR | 2.0 | 1.0 | 8.0 |
| Foraging range (L) (km) | | | |
| EI | 110 | 100 | 2 |
| LI | 110 | 100 | 2 |
| CR | 56 | 100 | 2 |
| Daylight rest (T _d) (h) | | | |
| EI | 2.0 | 2.0 | 2.0 |
| LI | 2.0 | 2.0 | 2.0 |
| CR | 1.0 | 1.0 | 2.0 |
| Dark period (T _n) (h) | | | |
| EI | 0 | 3.0 | 3.0 |
| LI | 0 | 4.0 | 4.0 |
| CR | 0 | 5.0 | 5.0 |

On 2 April 1985 the ICZN gave 6 months' notice of the possible use of its plenary power in case #2277, published in Bull. Zool. Nomen. 42(1). Comments are invited and should be addressed to the Secretary ICZN, % British Museum (Natural History), London SW7 5BD, England.

Carpophaga aurorae Peale, 1848, and *Serresius galeatus* Bonaparte, 1855 (Aves): proposed conservation by the suppression of *Columba R. Forsteri* Wagler, 1829.