

RESPONSE OF ADULT LEACH'S STORM-PETRELS TO INCREASED FOOD DEMAND AT THE NEST

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ABSTRACT.—In a colony of Leach's Storm-Petrels (*Oceanodroma leucorhoa*) on Kent Island, New Brunswick, i chicks were rotated on a daily basis through n nests to produce i/n chick-equivalents of food requirement, increasing by small increments from 1 ($i = 6, n = 6$) to 2 ($i = 2, n = 1$), between ages 10 and 50 days. Food delivered each night (SUM) was estimated by 24-h increments in chick mass. In nonexperimental nests SUM varied significantly among pairs, and chick mass varied in direct relation to SUM . Adults tending experimental nests did not respond to increased food demand, and chick mass decreased with increasing chick-equivalent per nest. After rotations were terminated, the mass of most chicks increased quickly to normal levels. These results suggest that the average amount of food delivered daily by each parent is determined independently of food demand and that chicks attain a mass that balances a fixed food intake against food requirement, which varies in direct relation to mass. Received 29 September 1986, accepted 17 June 1987.

PELAGIC seabirds typically rear a single, slowly growing chick. This pattern of reproductive performance characterizes species in several taxonomic orders and in a wide variety of marine environments from the tropics to high latitudes. Two types of explanations have been offered for this low productivity. Lack (1968), Nelson (1977), and others have argued that breeding productivity is limited by the availability of food in the environment or by the ability of adults to transport food between the feeding and nesting sites. Alternatively, some authors have suggested that pelagic seabirds reduce breeding productivity below the level they are capable of supporting either to reduce the stress of reproduction and thereby prolong life (Goodman 1974, Dunn 1979) or to prevent overpopulation (Wynne-Edwards 1962). These two classes of hypotheses can be distinguished by the ability of adults to increase their rate of food delivery to the nest in response to increased demand. Accordingly, if feeding rate were maximized at a level imposed by resource availability or ability to transport food, then feeding rate could not be increased. If, however, feeding rate were optimized at a lower level, parents would be able to respond to increased food demand at the nest.

Several investigators have attempted to increase the food demand of the brood by adding a second chick. Such experiments have met with mixed success, generally failing to elicit marked responses in Procellariiformes (Rice and Kenyon 1962; Huntington 1963; Harris 1966, 1969)

but leading to increased feeding rate and successful rearing of twins in Swallow-tailed Gulls (*Creagrus furcatus*, Charadriiformes; Harris 1970) and gannets (*Sula* spp., Pelecaniformes; Nelson 1964, Jarvis 1974). Cross fostering the chicks of a larger species into the nests of a smaller, related species also has stimulated increased food provisioning by parents in Gray-backed Terns (*Sterna lunata*; Shea and Ricklefs 1985).

The failure of petrels (Procellariiformes) to respond to the presence of twins is difficult to interpret with respect to the contrasting hypotheses of maximized vs. optimized feeding rate. Although the results are consistent with resource limitation, twinned chicks may interact so as to interfere with proper communication with adults. Recent studies have demonstrated the influence of chick-chick interactions within broods on feeding rates (Henderson 1975; Bengtsson and Ryden 1981, 1983; Stamps et al. 1985). Furthermore, storm-petrel parents may not be suitably responsive to the novel family situation created by the twinning experiment. Finally, the feeding rates of parents may be fixed to match average food demand, and not to respond to variation in the nutritional level of the chick. Petrel chicks vocalize when a parent is at the nest, and actively solicit food, but it is not known whether solicitation varies with respect to level of nutrition.

The experiment reported here was designed to chronically increase the food demand of chick rearing for storm-petrels without there being more than one chick in the nest at any time. By

rotating a number of chicks among a smaller number of nests on a daily basis, I created a graded food demand, ranging from 1 to 2 chick-equivalents. This experimental design circumvented some of the potential problems of twinning experiments but raised others. A positive parental response to increased food demand could mean that foraging effort is normally regulated below the maximum possible. But a failure to respond would be consistent with several alternative explanations. Among these are: (1) parents cannot deliver more food, (2) chicks do not increase solicitation when deprived, and (3) the presence of different chicks in the nest from night to night so confuses the parents that they cannot respond appropriately.

METHODS

The study was conducted at the Bowdoin Scientific Station on Kent Island, New Brunswick (66°45'W, 44°35'N), located just south of Grand Manan Island at the mouth of the Bay of Fundy, during July through September 1985. The local breeding biology of Leach's Storm-Petrel (*Oceanodroma leucorhoa*) has been described by Huntington (1963), Wilbur (1969), and Ricklefs et al. (1980a, b, 1985).

Six nests were assigned to each of six rotation schedules, designated as i/n (i chicks rotated on a daily basis among n nests). There was one set of 6/6, one of 7/6, two of 4/3, three of 3/2, two of 5/3, and six of 2/1. The additional chicks needed over and above the 36 in the experimental nests were taken from other burrows in the colony. The rotations presented pairs in the experiment with 1.00, 1.17, 1.33, 1.50, 1.67, or 2.00 chick-equivalents. Chicks were switched among nests during the middle of the day. Those not in an experimental nest on a particular night were held in cardboard containers in an unheated room during the first part of the experiment, and were placed in inactive "holding" burrows during the latter part of the experiment. In the 6/6 treatment, which provided a control for the effects of daily handling, all chicks were moved to the next burrow in the rotation sequence each day. In the 7/6, 4/3, 3/2, and 2/1 treatments, the chick in one nest in each set was exchanged with the chick in the holding burrow each day. The nest involved in the exchange rotated on a regular schedule among those in the set. In the 5/3 rotation, 2 of the 3 nests in each set exchanged chicks with holding burrows. No chick was kept in a holding burrow for more than 1 night in succession.

Nests were placed in rotation sets according to hatching dates, so that the age spread within each set was 2 days or less. Hatching dates of the various sets of chicks were distributed uniformly among the six types of rotations. The rotations were begun when

all chicks in each set were 10 (± 1) days old, and they were continued to at least 50 days of age in all cases. Fledging typically occurs between 65 and 70 days. Body masses and wing lengths of all chicks were recorded each day until fledging or the end of the field season on 4 October. Length of the folded wing was measured from the forward edge of the wrist to the end of the manus or, on older chicks, to the tip of the longest feather.

Chicks in 28 unmanipulated nests were weighed and measured each day to determine the range of growth rates in intact families. In addition, these chicks were weighed at 3-h intervals during one night each week to determine the relationship between mass of food delivered (sum of positive mass increments, *SUM*) and 24-h mass increments of the chicks (*NET*; Ricklefs et al. 1985).

RESULTS

Estimation of SUM from daily weighings.—Because daily mass changes (*NET*) could be influenced by the age and previous feeding history of the chick, I used multiple regression to determine the statistical relationship of *SUM* to age (X), X^2 , wing length (L), initial mass (M), *NET*, and mass increments on the previous 4 nights (*NET1*, *NET2*, *NET3*, *NET4*). Because a preliminary analysis showed that X , X^2 , and L did not contribute uniquely to the regression, these variables were deleted from the analysis. The final predictive equation, based on 187 chick-nights between 15 and 60 days of age, was $SUM (g) = 1.924 (0.153 SE) + 0.072 (0.009) M + 1.026 (0.026) NET + 0.159 (0.026) NET1 + 0.145 (0.025) NET2 + 0.097 (0.028) NET3 + 0.077 (0.023) NET4$ [$F(6,180) = 287, P < 0.0001, R^2 = 0.91$]. The SD of observations about the regression was 1.96 g. The mean value of *SUM* was 6.57 g. This regression was used to estimate nightly feeding for the unmanipulated nests between the ages of 15 and 60 days.

Because the rotation experiments were continued only through 50 days, a separate relationship between *SUM* and *NET* was calculated from the sample of 146 chick-nights within this age range. In this case, the equation was $SUM (g) = 5.73 (1.24 SE) + 1.023 (0.026) NET - 0.37 (0.09) X + 0.00485 (0.00141) X^2 + 0.133 (0.014) M + 0.115 (0.028) NET1 + 0.086 (0.025) NET2$ [$F(6,139) = 285, P < 0.0001, R^2 = 0.925, SD$ about regression = 1.81 g].

Variation in feeding rate among unmanipulated nests.—The frequency distribution of estimated values of *SUM* for the entire sample revealed

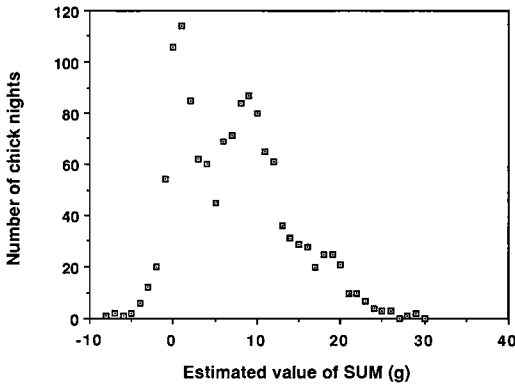


Fig. 1. Values of *SUM* estimated from initial masses and daily mass increments of Leach's Storm-Petrels on 1,343 chick-nights (ages 15–60 days) at 28 unmanipulated nests during August and early September 1985.

peaks centering on about 0 and 8 or 9 g, corresponding to zero and one feed (Fig. 1). A shoulder on the distribution at about 18 g reflects nights on which chicks received two feeds (Ricklefs et al. 1985). The intrinsic variability associated with the estimate of *SUM* is indicated by the tail of observations for which *SUM* has a large negative value.

The estimated mean nightly mass of food delivered to each chick between 15 and 60 days of age varied between 4.8 and 8.5 g for the 28 unmanipulated nests. A median test (Siegel 1956) indicated significant heterogeneity among nests in nightly values of *SUM* ($X^2 = 42.5$, $df =$

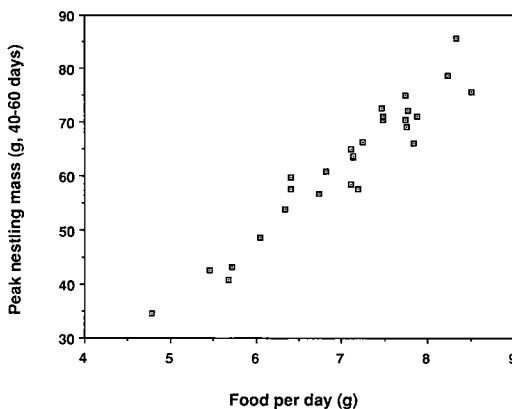


Fig. 2. Relationship between the mean mass of a chick between 40 and 60 days of age and the mean value of *SUM* between ages 15 and 60 days for 28 unmanipulated nests.

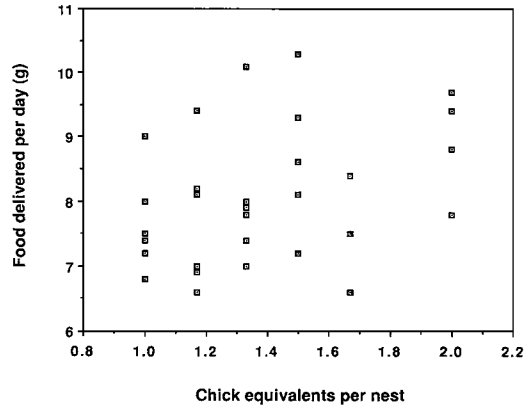


Fig. 3. Means of the estimated values of *SUM* for individual nests in each of the sets of rotations of i chicks through n nests.

27, $P = 0.03$). The overall growth performance of these chicks was estimated by the mean of masses between 40 and 60 days of age (*PEAK*), roughly corresponding to the period of reduced rate of mass increase leading up to the peak nestling mass (Ricklefs et al. 1985). Within this range, 66% of the variation in nestling mass within the population during 1985 was associated with differences between chicks ($n = 28$), only 11% was associated with age, and the remainder was "error," consisting of day-to-day variation in mass, reflecting recent feeding history plus measurement error [$F(28,559) = 64$, $P < 0.0001$, $R^2 = 0.77$, error SD = 7.3 g]. Differences in mass among chicks were significantly related to variation among nests in mean daily feeding (*SUM*) (Fig. 2). The regression of 40–60-day mass on *SUM* was described by *PEAK* (g) = -27.6 (5.3 SE) + 12.8 (0.8) *SUM* (g/night) [$F(1,26) = 294$, $P < 0.0001$, $R^2 = 0.92$]. The SD about the regression was 3.6 g.

Response of parental feeding to increased chick-equivalents.—The mean amount of food delivered per day in the rotation nests (Fig. 3) indicates that parents responded weakly, or not at all, to increased food demand. Although there was a slight, marginally significant, increasing trend in the rate of food delivery with increasing number of chick-equivalents [$F(1,29) = 4.1$, $P = 0.052$, $R^2 = 0.12$], a one-way ANOVA failed to reveal heterogeneity in values of *SUM* among rotation treatments [$F(5,25) = 1.55$, $P > 0.2$], and the trend was weak compared with the variation among nests within each treatment. One 2/1 rotation and one 5/3 rotation were termi-

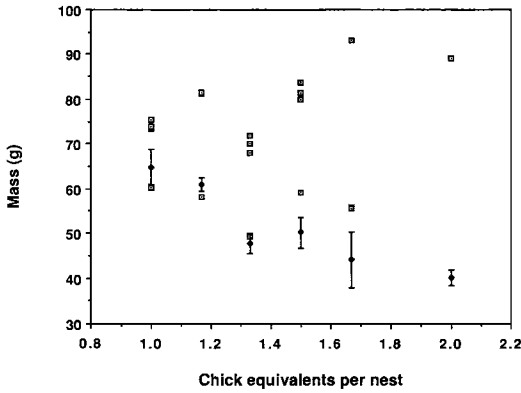


Fig. 4. Mean mass of chicks in each set of rotations between the ages of 30 and 50 days. Each solid symbol is the average of the mean 30-50-day mass of all the chicks in each set; 1 SE of this mean is indicated by the vertical line. The open symbols represent peak masses of individual chicks after the termination of the rotations and just before the period of pre fledging mass loss.

nated when one chick in each rotation wandered from its burrow and was lost (at ages 18 and 14 days, respectively). A second 2/1 rotation was terminated when one of the chicks died at an early age.

The lack of a feeding response to increased food requirement at the nest was reflected in the average masses of chicks during the last half of the rotation experiment, i.e. between 30 and 50 days (Fig. 4). Means of these average values for each treatment decreased from about 65 g for the 6/6 rotation (which does not differ significantly from unmanipulated nests) to about 50 g in the 3/2 rotations and 40 g in the 2/1 rotations (Table 1). Chicks in the 5/3 and 2/1 rotations occasionally were fed small amounts of olive oil when their masses were below 40 g, and several probably would not have survived the experiment without these supplements.

Many of the chicks taken off the rotations at an age of 50 days and replaced in their natal burrows gained mass rapidly to average or above-average peaks before undergoing the usual pre fledging mass loss exhibited by Leach's Storm-Petrel chicks, which normally begins about 60 days after hatching. Peak mass is indicated individually by the open symbols in Fig. 4. The amount regained after the end of the experiment and, to a lesser extent, the peak pre-

TABLE 1. Mean masses (days 31-50) and mean wing lengths (day 50) of chicks in different rotations.

Rotation	Chick-equivalent	n	Mean	SD	SE	DMRT ^a
Mass^b (g)						
2/1	2.00	8	40.2	5.0	1.8	B
5/3	1.67	4	44.1	12.3	6.2	B
3/2	1.50	9	50.2	10.1	3.4	B
4/3	1.33	6	47.7	5.7	2.3	B
7/6	1.17	3	61.0	2.7	1.5	A
6/6	1.00	6	64.8	9.6	3.9	A
Wing length^c (mm)						
2/1	2.00	8	75.0	14.4	5.1	C
5/3	1.67	4	86.5	26.2	13.1	BC
3/2	1.50	9	96.3	21.0	7.0	ABC
4/3	1.33	6	91.0	17.3	7.1	ABC
7/6	1.17	3	106.0	1.0	0.6	AB
6/6	1.00	6	112.2	7.3	3.0	A

^a Duncan's multiple-range test; values with the same letter do not differ significantly.

^b ANOVA with rotation as main effect: $F(5,30) = 7.5, P < 0.0001, R^2 = 0.56$.

^c ANOVA with rotation as main effect: $F(5,35) = 3.8, P = 0.0086, R^2 = 0.39$.

fledging mass attained were positively related to the average amount of food delivered per day to the nest during the rotation experiment ($r_s = 0.75, P < 0.01$ and $r_s = 0.40, P = 0.05$, respectively; $n = 18$). Most of the chicks in the rotations fledged or were healthy at the end of the field season, although the development of chicks (wing length) was slowed in direct relation to the number of chick-equivalents per nest (Table 1), and age at fledging seemed to be retarded in all of the rotations compared with chicks in unmanipulated nests. Among the latter, fledging age of chicks that left the nest before the end of our field season averaged 68.5 days (SD = 2.9, $n = 15$); among rotation nests, only 3 of 24 ages at fledging were known to be less than 70 days.

DISCUSSION

In this study the rate of food delivery to the nest varied significantly among pairs of Leach's Storm-Petrel, the peak masses of chicks were directly related to rates of food delivery, and adults did not substantially increase food delivery in response to the chronic presence of single, undernourished chicks in their nests. Additional observations revealed that adults did not increase food delivery to their natural chicks

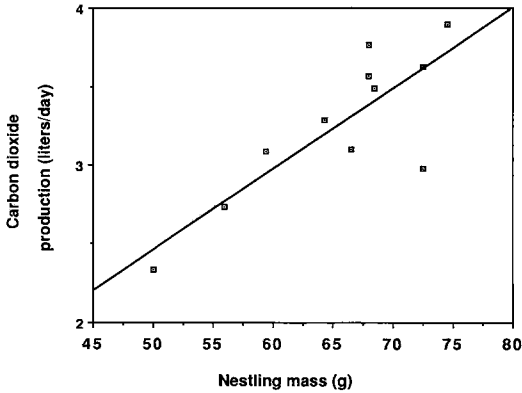


Fig. 5. Daily carbon dioxide production, determined by the doubly labeled water method, of individual chicks under natural burrow conditions. Measurements were made of 24-h periods on chicks aged between 37 and 52 days during August 1984 on Kent Island. Procedures followed Ricklefs et al. (1986).

after the end of the rotation experiments, although the mass of many undernourished chicks quickly increased to normal or above-normal levels.

Measurements of daily energy expenditure of older chicks in burrows, using the doubly labeled water method (Nagy 1980, Ricklefs et al. 1986), indicated that carbon dioxide production by the chick varied in direct proportion to body mass (Fig. 5). Therefore, underweight chicks placed in the normal feeding environment may assimilate a substantial excess of food over their maintenance requirements. For example, assuming an energetic equivalent of 26.8 kJ/l CO_2 respired, a 66-g chick metabolizes about 85 kJ/day; when its mass is reduced to two-thirds that level (44 g), it consumes only 60 kJ/day, leaving an excess of 25 kJ/day. This is enough to accumulate almost 1 g of fat per day or perhaps 2–3 g body mass per day; only one-third to one-half of differences between masses of chicks of the same age consist of fat (Ricklefs et al. 1980a, unpubl. data). These values agree reasonably well with the observed post-rotation mass increases, particularly if it can be assumed that a part of the regained mass represents undigested food and hypertrophy of tissues with low energy densities.

Body mass during the latter part of the nestling period appears to bring food requirement, which is directly proportional to mass, into balance with a fixed parental feeding rate. This is the basis for the relationship between mass and

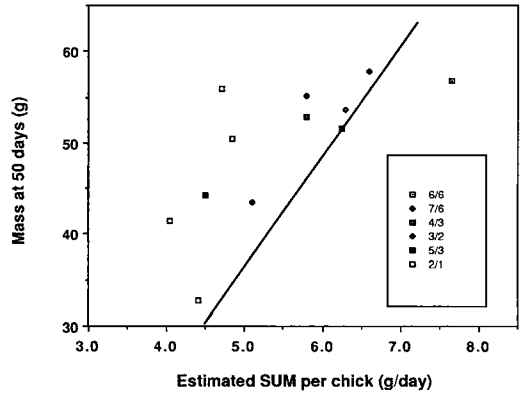


Fig. 6. Mean mass of 50-day-old chicks in each set of rotations as a function of the mean value of *SUM* between 15 and 50 days. Several of the rotation schedules are represented by more than one set of nests, i.e. there are three sets of 3/2 rotations. The solid line is the regression of mean 40–60-day mass on *SUM* for unmanipulated nests (see Fig. 2).

SUM shown in Fig. 2. According to this relationship, chronic food deprivation should have a predictable effect on mass. Dividing the average values of *SUM* in a set of rotation nests by the number of chicks in the rotation gives the average *SUM* per chick. Mass at 50 days is plotted with respect to these values of *SUM* in Fig. 6. Although the relationship between mass and *SUM* in the experimental nests was similar to that in unmanipulated nests, chicks in the 5/3 rotation and several of the 2/1 rotations were heavier than predicted. Some of the chicks in these higher chick-equivalent rotations were provided supplemental food and occasionally exhibited reduced body temperatures (cf. Boersma 1986), presumably reducing food requirement. It is also possible that adults of those chicks increased the energy density of meals by concentrating lipids. Furthermore, because the confidence limits about any regression line expand as extreme values of the independent variables are approached, the equation used to predict food intake from values of age, body mass, and *NET* may have been biased at lower body mass.

Adult storm-petrels apparently do not respond to the chronic undernourishment of chicks produced by the rotations used in this study. Harris (1966) claimed that pairs of Manx Shearwaters (*Puffinus puffinus*) provided with twins fed their broods more often (once each 1.34 days) than did parents of single chicks (once

each 1.68 days). But Harris recorded a feeding when the daily mass increment (*NET*) exceeded zero, which may have introduced an artifact into his results. This study revealed that the value of *NET* is sensitive to both the initial mass of the chick and the previous history of feeding. Undernourished chicks not recently fed tended to have higher values of *NET* per mass of food consumed (*SUM*) than did well-nourished chicks. Thus, using only *NET* overestimates feeding rate to undernourished chicks relative to healthy ones.

Within the resolution of this analysis, the average mass of food delivered each day by each pair appeared to be relatively fixed at a value that varied significantly among pairs. The apparent lack of response of feeding rate to increased food demand may be appropriate to the conditions experienced by Leach's Storm-Petrels. When undernourished rotation chicks were settled into their natal burrows, many quickly regained mass back to normal levels, indicating that the usual feeding schedule is sufficient to allow undernourished chicks to recover quickly without an increase in feeding rate. Additionally, seriously undernourished chicks are rarely found in the colony on Kent Island, there is little evidence of frequent or prolonged periods of reduced feeding in the colony as a whole (Ricklefs et al. 1985, pers. obs.), and fledging success is high (C. E. Huntington pers. comm., unpubl. data). Hence, adults rarely encounter marked undernourishment in their chicks.

It also may be pointless for adults to adjust feeding rate closely to short-term fluctuations in the nutritional status of their chicks. Each member of a pair feeds its chicks independently, once every 2-3 nights (Ricklefs et al. 1985). Between feedings by a particular parent, the chick's state of nutrition may change greatly and unpredictably depending on whether the mate has fed the chick in the interim. On the whole, it may be most reasonable for the parent to feed the chick at a more or less fixed rate. With such a strategy there would be no point in a chick's signaling its nutritional status to the parent, even though chick vocalizations appear to be an integral part of feeding. Were this scenario an accurate representation of parent-chick interaction in Leach's Storm-Petrel, experimental increase of food demand by the chicks would not elicit increased feeding by the parent regardless of its ability to gather more food. Thus,

the negative result I obtained does not shed light on whether feeding rates in storm-petrels are maximized or optimized. It does, however, raise questions concerning the regulation of feeding rates by adults and the nature of food-solicitation and parental-response behaviors in these species.

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