

Flexible effort in breeding seabirds: adjustment of provisioning according to nestling age and mass

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Abstract: We examined whether rhinoceros auklet (*Cerorhinca monocarata*) parents are able to adjust their provisioning effort in response to chick demand. A fostering experiment in which nestlings of different ages and masses were exchanged between burrows was employed to examine parental provisioning effort before and after the exchange. Daily mass increments of the nestlings were used to estimate the amount fed on the previous night, using a model based on data from captive chicks raised on a controlled diet. Our results demonstrate that rhinoceros auklet parents somehow assess and respond to the needs of their chicks by delivering more to older and larger fostered chicks and less to younger and smaller fostered chicks. Our results confirm and extend a growing body of information which shows that seabird parents can adjust provisioning effort when feeding young. We highlight how studies to date have differentially manipulated nestling age and hunger, thus complicating a comparative approach. Testing for interspecific differences in parental ability to respond to chick demands will require studies that employ comparable types of manipulations for a variety of seabird species.

Résumé : Nous avons tenté d'établir si, chez le Macareux rhinocéros (*Cerorhinca monocarata*), les parents sont capables d'ajuster leurs efforts d'approvisionnement de nourriture aux exigences de leurs oisillons. Nous avons procédé à un élevage expérimental dans lequel des oisillons de masses et d'âges divers ont été interchangeés d'un terrier à l'autre et nous avons mesuré les efforts d'approvisionnement des parents avant et après l'échange. Les augmentations quotidiennes de masse ont été utilisées pour estimer la quantité de nourriture apportée la nuit précédente d'après un modèle basé sur des données obtenues chez des oisillons en captivité soumis à un régime connu. Nos résultats indiquent que les parents réussissent à évaluer les besoins des oisillons et à y répondre en apportant plus de nourriture aux oisillons adoptifs plus âgés et plus gros et moins aux oisillons adoptifs plus jeunes et plus petits. Ces résultats confirment ceux des études antérieures qui démontrent que les couples parentaux des oiseaux marins sont capables d'ajuster leurs efforts d'approvisionnement de nourriture aux oisillons. Nous soulignons le fait que les études antérieures sont basées sur des manipulations différentielles de l'âge et de la faim des oisillons, compliquant de ce fait l'interprétation d'études comparatives. Pour évaluer les différences interspécifiques dans la capacité des parents à répondre aux besoins des oisillons, les études qui s'imposent doivent utiliser des types comparables de manipulations chez un grand nombre d'espèces d'oiseaux marins.

[Traduit par la Rédaction]

Introduction

In this study we examine whether rhinoceros auklet (*Cerorhinca monocarata*) parents are able to make adjustments in the level of provisioning in response to chick demand. Previous studies of this question have led to varied results. For example, when small (young) and large Atlantic puffin (*Fratercula arctica*) chicks were exchanged (Hudson 1979), parents fed foster chicks according to their previous feeding schedule and not according to the age of the foster chick. Hudson (1979) acknowledged, however, that his experiments monitored parents for only a brief period after the exchange and that foster parents may have adjusted provisioning effort over the long term. Moreover, Hudson (1979) did not measure the size of food loads, therefore the total amount of food delivered to chicks could not be measured.

More recent studies (Harris 1983; Johnsen et al. 1994) have shown that Atlantic puffin parents can respond to chick demand. In a study on Leach's storm-petrels (*Oceanodroma leucorhoa*), Ricklefs (1987) increased food demand by rotating chicks among a number of nests and also found that parents did not alter their level of food provisioning. Hamer and Hill (1994) obtained similar results in a study on Cory's shearwater (*Calonectris diomedea*). Ricklefs (1987, 1992) suggested that either storm-petrel chicks do not communicate their level of nutrition to the parent or parents do not (or cannot) respond to such information. Bolton (1995), however, showed that parents reduced provisioning to storm-petrel (*Hydrobates pelagicus*) chicks given supplementary food. Recently, Johnsen et al. (1994) hypothesized that the relationship between parental energy expenditure and feeding efficiency may explain interspecific differences in the ability of seabirds to respond to the chick's nutritional need.

In the experiments reported here, nestling rhinoceros auklets were exchanged (fostered) between burrows. Similar experiments with the closely related Atlantic puffin (Hudson 1979; Johnsen et al. 1994) and many other seabirds show that parents readily accept foster nestlings, in the case of the rhinoceros auklet even of different species (Vermeer and

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Table 1. Mean ages and masses of nestlings on the day of the exchange during three fostering sessions.

Year	Session	Group	n	Age (d)		Mass (g)		Mean number of delivery nights	
				Mean	SD	Mean	SD	Pre-exchange	Post-exchange
1987	Early	C	14	24.8	2.7	235.3	62.9	6.9	7.0
		S	14	17.1	1.5	165.9	33.6		
		L	14	26.3	1.1	265.6	34.6		
1986	Late	C	9 ^a	40.0	2.7	304.9	26.1	4.9	5.0
		S	7	31.6	5.1	273.6	52.8		
		L	4 ^b	43.7	3.0	335.4	36.0		
1987	Late	C	9 ^c	35.1	7.0	317.8	67.3	6.9	6.1
		S	12 ^c	28.3	3.8	262.0	36.7		
		L	13 ^c	42.8	2.0	347.4	36.5		

Note: Nestlings in the control group (C; foster and natal nestlings of the same size) were exchanged with each other. Other nestlings were exchanged so that parents received a foster nestling either smaller (S) or larger (L) than their natal nestling. Also shown is the mean number of nights on which deliveries were estimated before and after the exchange.

^aThere were 12 chicks (six pairs) on the day of the exchange, but 3 chicks were subsequently lost.

^bThere were seven chicks on the day of the exchange.

^cThere were 14 chicks on the day of the exchange.

Cullen 1979). We predict that if offspring somehow communicate their need for food to their parents, and if parents are capable of adjusting the amount they provision, parents should increase the amount provisioned when the foster nestling is larger than the natal nestling and vice versa. We discuss our results in relation to those of other studies which have examined parental provisioning in seabirds and distinguish between those that have manipulated nestling age and those that have manipulated nestling hunger.

Methods

The study was conducted in 1986 and 1987 on the Lucy Islands (54°18'N, 130°37'W), an archipelago located west of Prince Rupert, British Columbia, Canada. Details of the breeding biology of rhinoceros auklets can be found in Wilson and Manuwal (1986) and Bertram et al. (1991). Parents provision nocturnally, usually about midnight, and between them make one or two visits to the nesting burrow (range 0–3 visits). On each visit during the 45–70 d of the nestling period a load of small fish totaling approximately 30 g (wet mass) is delivered to the single offspring. The amount provisioned each night varies greatly, ranging from 5 to 116 g (Bertram et al. 1991), and generally increases with the age of the nestling (Harfenist 1995), though the pattern is highly variable (see Bertram et al. 1991).

Fostering experiments

We fostered a total of 110 nestlings in three separate sessions, one during the 1986 breeding season and two in 1987. Of these, 35 pairs (70 individuals) of exchanged nestlings were of unequal ages and masses, so that their parents received a foster offspring larger or smaller than their natal nestling. The age differences of exchanged pairs ranged from 7 to 19 d, while the mass differences ranged from 18 to 250 g. A further 20 pairs of “control” nestlings were more similar, with age differences of less than 4 d and mass differences that ranged from 0 to 80 g. Each chick was tethered into its foster burrow for the first night following the exchange (see Bertram et al. 1991). This procedure prevented most desertions, but a few

nestlings deserted their foster burrow after the tether was removed, leaving the sample sizes reported in Table 1.

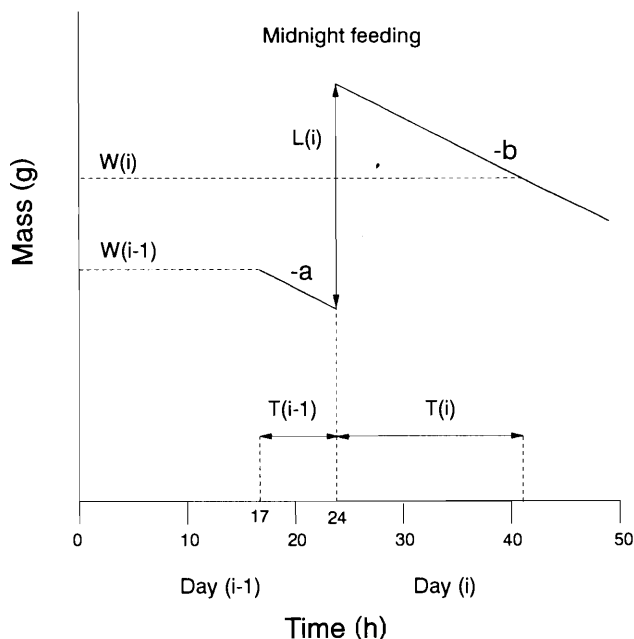
For at least 6 d prior to and following exchanges, each nestling was weighed daily to within 2 g at about the same time between 17:00 and 23:00. Deliveries on the first 2 nights following the exchange were excluded from the analysis because each parent needed time to encounter and respond to the demands of the foster chick. In addition, data were excluded if fewer than three deliveries could be estimated from either the pre- or post-exchange period.

Estimating total nightly delivery

We estimated the amount of fish provisioned by parents each night by means of a multiple regression model based on nightly weighings of the chicks and the timing of those weighings (see Fig. 1). The model requires as input two successive weighings of a chick (i.e., prior to and after a feed) and the times at which the masses were determined. Incorporating the time of weighing is necessary because rhinoceros auklet chicks lose mass continuously after a feeding (Vermeer and Cullen 1982). The model assumes that feeding occurs at midnight (which is close to the time when feeding visits at the colony reach a peak; D.F.B., personal observation), with a linear rate of decline in postfeeding mass. We used this model to predict the mass of deliveries to wild nestlings on the basis of our measurements of their daily mass increments. These estimates of delivery mass were used to compare parental provisioning between the pre- and post-exchange periods.

The model was calibrated with controlled feedings of captive nestlings. In 1986 and again in 1987 we raised 6 chicks at our camp on the Lucy Islands (Permits BC PC 86/09 and BC PC 87/12). Mean chick age was 17.5 d (SD = 2 d, range 14–20 d) at the start of the study and chicks were kept for 36 d (32 d in 1987), housed in artificial burrows. The holes measured approximately 1 m (length) × 20 cm × 20 cm and were covered with Arborite and soil. A 3 cm diameter plastic pipe provided ventilation. Each night, between 23:00 and 01:00, the “camp chicks” were fed a known quantity of fish, using an adult rhinoceros auklet puppet (for details see Welham and Bertram 1993). The following day the chicks were weighed to the nearest 2 g at 10:00, 14:00, 16:00, and 22:00. Chicks were fed fish meals that had been collected from adult auk-

Fig. 1. Graphical representation of the method used to estimate the amount of food delivered overnight. The example depicts a chick whose measured mass was $W(i-1)$ at 17:00. It lost mass at rate a until midnight, when it was fed $L(i)$ g of fish. It then lost mass at rate b until it weighed $W(i)$ at 17:00 the following day. The model estimates the size of the delivery to the chick, $L(i)$. The derivation is outlined in the Appendix. a is the rate of mass loss before feeding; b is the rate of mass loss after feeding; $T(i-1)$ is the time from weighing on day $(i-1)$ and midnight feeding; $T(i)$ is the time between midnight feeding and weighing on day (i) ; $W(i)$ is mass measured on day i ; and $W(i-1)$ is mass measured on day $i-1$.



lets returning to the colony. These meals consisted almost entirely of Pacific sand lance (*Ammodytes hexapterus*; see Bertram and Kaiser 1993).

Results

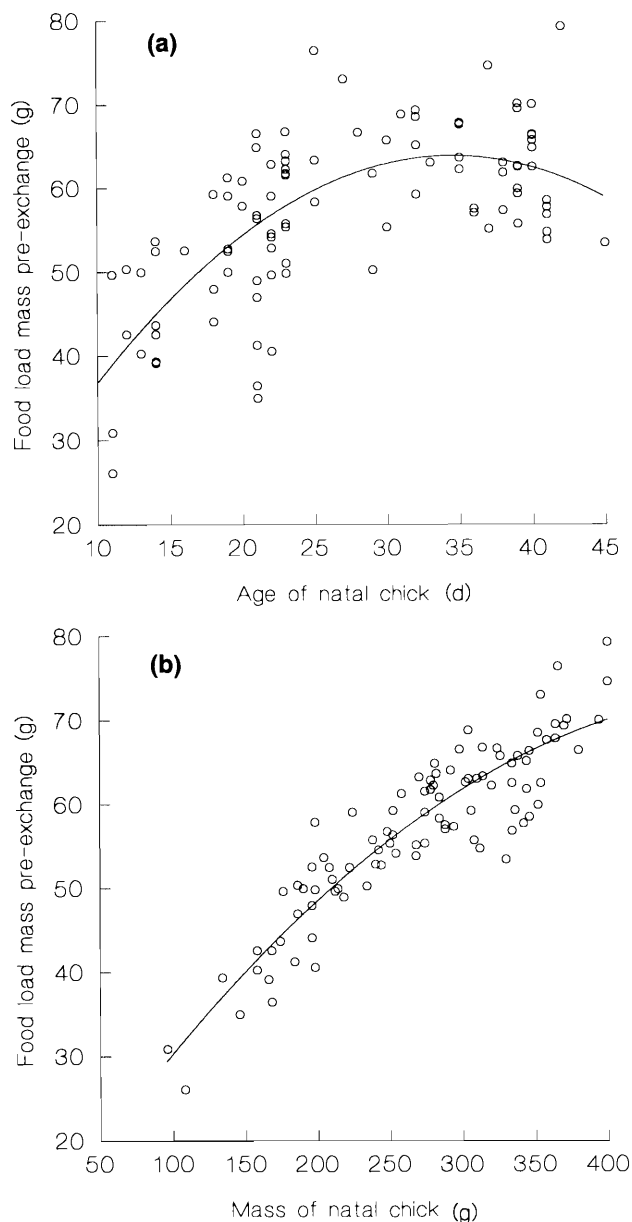
Model calibration

In 1986 the camp chicks grew from an average mass of 167 g (range 144–196 g) to 318 g (range 290–338 g) and in 1987 from an average of 130 g (range 116–148 g) to 290 g (range 272–312 g), within the range of their wild counterparts. Parameter estimates for the models based on the camp chick data are given in the Appendix. Predictions of fish delivery made from the models were highly correlated with the true delivery (i.e., the amount of fish fed) in both years ($r^2 = 0.712$ in 1986 and 0.788 in 1987; both $P < 0.0001$). The procedure therefore provides a reliable method of estimating total nightly delivery.

Provisioning prior to the exchange

We estimated the total nightly delivery for an average of 4.9–6.9 nights prior to each exchange (see Table 1). The mean total delivery in relation to nestling age (age was taken halfway through the pre-exchange period) is shown in Fig. 2a. The total nightly delivery initially increases with

Fig. 2. Relations between nestling age and the amount provisioned by parents to natal nestlings (prior to the exchange): $y = 10.3 + 3.1x - 0.045x^2$; $n = 96$, $r^2 = 0.47$ (a) and between nestling mass and the amount provisioned by parents to natal nestlings (prior to the exchange): $y = 7.12 + 0.26x - 0.00025x^2$; $n = 96$, $r^2 = 0.83$ (b).

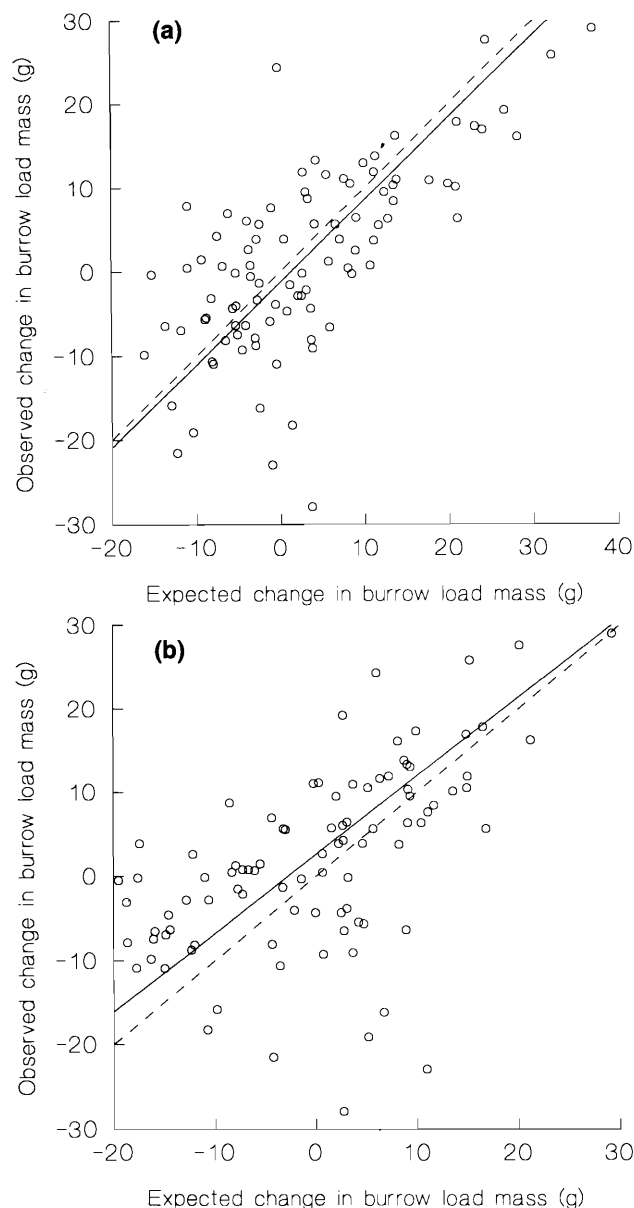


nestling age and then levels off. The mean total delivery in relation to nestling mass is shown in Fig. 2b. The total nightly delivery increases steadily but at a diminishing rate with increases in nestling mass.

Effect of the exchange

Fostering may have an effect on parents independently of the size of the foster nestling. To examine this we compared the total nightly delivery to the control group prior to and following the exchange. Control parents did not alter the amount they provisioned ($t = 0.59$, $df = 31$, $P = 0.56$), showing that fostering itself had no detectable effect.

Fig. 3. Observed change in total nightly delivery (post-exchange mean minus pre-exchange mean) in relation to that expected on the basis of age (a) and mass (b). The calculation of the expectations is based on Fig. 2, and is described in the text. The broken lines indicate where observed and expected values are equal, and the solid lines are the equations of the major axis: $y = -1.23 + 0.98x$; $n = 96$ (a); $y = 2.61 + 0.94x$; $n = 96$ (b). The upper and lower 95% confidence limits to the slopes are 0.79 and 1.22 (a) and 0.67 and 1.31 (b), respectively. In both cases the upper limits exceed 1, indicating that the slope is not significantly different from unity. The intercept does not differ from zero for the equation based on age ($t_2 = 1.01$, $df = 94$, $P < 0.5$ (a)), but is slightly higher than zero for the equation based on mass ($t_2 = 2.3$, $df = 94$, $P < 0.05$ (b)).



Fostering experiments

If there is parent–offspring communication of any form about the nestling's need for food, parents should provision a foster nestling with the amount they would provide to a natal nestling of the same age and mass. We can therefore use

Fig. 2 to predict how much we expect parents to provision a foster nestling. We computed for each burrow the expected *change* in provisioning level as the difference in food load, based on the ages and masses of the natal (pre-exchange) and foster (post-exchange) nestlings.

The results are portrayed in Fig. 3. Both the observed and expected values are subject to error, and because they have the same units, are best suited to major axis regression (Sokal and Rohlf 1981). There is a highly significant and positive relationship, with parents increasing the amount delivered when the foster nestling was older (Fig. 3a) and larger (Fig. 3b) than their natal nestling, and decreasing the amount delivered when the fostered chick was younger (Fig. 3a) and smaller (Fig. 3b). The intercepts of the regression equations do not differ from zero (Fig. 3a), or are very close to zero (Fig. 3b), supporting the conclusion made above that fostering by itself has no impact on the parents' provisioning behavior. For analyses based on both age and mass the observed change in parental provisioning did not differ from the expectation because the slopes are not significantly different from 1.

Discussion

Our results demonstrate that rhinoceros auklet parents reduced provisioning to small foster chicks and increased the food delivered to larger foster chicks. (It is unlikely that small foster chicks rejected food, since captive puffin chicks readily consume more than wild parents deliver (Harris 1978; Hudson 1979). Moreover, fish were very rarely found in burrows and it is unlikely that parents would consume prey intended for nestlings.) Our findings are supported by studies on the closely related Atlantic puffin. Johnsen et al. (1994) exchanged chicks aged 6 and 20 d, and could not detect a difference between the growth rates of foster chicks and control nestlings of similar age. They reasoned that, in order for the foster chicks to have achieved those growth rates, the foster parents must have adjusted their provisioning effort.

Harris (1983) found that played back recordings of a hungry, begging chick caused parents to increase the frequency of food deliveries. This study differs in an important way from that of Johnsen et al. (1994): the playback study manipulated the (apparent) hunger of the nestlings, while the fostering study manipulated the age of the nestling (and may not have altered hunger). (Note that small foster chicks will experience less hunger than large foster chicks if parents provision according to the size of their own chick.) Because of these differences, these two types of manipulations are not strictly comparable. Manipulations of hunger mean that upon returning to the burrow, parents find their nestling hungrier or less hungry than average, presumably communicating this by their behavior (e.g., begging). Fostering experiments result in the parent being faced with a nestling markedly older (larger) or younger (smaller) than it previously had. Hunger or condition (mass corrected for age, e.g., Bolton 1995) may not have been manipulated in fostering studies to date.

Parent seabirds may respond differently to different types of nestling manipulations (e.g., manipulations of hunger versus age). The basic energy requirements of nestlings are likely to be different in fostering studies (because young and

old individuals are typically compared) but not in studies that manipulate hunger in nestlings of similar ages. Moreover, begging calls may not effectively signal hunger (see also Ricklefs 1987, 1992) in some seabird species.

Studies that have attempted to manipulate provisioning effort in seabirds (other than brood enlargement and cross-fostering studies) have employed a variety of techniques, used different species, and have reached varied conclusions. Experiments that have increased hunger by depriving petrel chicks of food, either by periodically preventing feeding (Ricklefs 1987) or by removing food from the proventriculus (Ricklefs 1992), have provided some support for the view that parents do not or cannot increase provisioning. It cannot be determined if parent puffins increased the total amount of food delivered to played-back recordings of hungry chicks because food load mass was not reported in Harris' (1983) study. In fostering experiments on petrels (Ricklefs 1992) and shearwaters (Hamer and Hill 1994), researchers exchanged chicks of similar ages (differences in condition probably existed but were not reported) and found that parents did not alter their provisioning schedule. Note that any differences in the hunger of nestlings could not be gauged in the fostering studies of Ricklefs (1992) and Hamer and Hill (1994). Ricklefs (1992) and Hamer and Hill (1994) also reduced the hunger of chicks in supplementary feeding experiments and found that parents did not respond by delivering less. In contrast, Bolton (1995) demonstrated that parent storm-petrels delivered fewer, smaller loads when chick hunger was reduced by supplementary feeding. Hudson (1979) exchanged (fostered) puffin chicks of different ages and masses but could not detect a change in the number of feeding visits in the short time frame of his experiment (see above). In more extensive fostering experiments, our results and those of Johnsen et al. (1994) show that parents do adjust provisioning in accordance with the age of their chick. Johnsen et al. (1994) suggested "that the ability to respond to chick's nutritional need may vary between seabird species," and, further, hypothesized "that the relationship between parental energy expenditure and feeding efficiency may be crucial in explaining such interspecies differences" (Johnsen et al. 1994). In light of the discussion above we suggest that Johnsen et al.'s (1994) idea cannot be adequately evaluated because, to date, sufficient *comparable* types of manipulations have not been performed on different seabird species.

Our results confirm and extend a growing body of literature from single-chick manipulations (see above), brood enlargements (see Ydenberg and Bertram 1989 for a review; also Anderson 1990), and cross-fostering studies (Shea and Ricklefs 1985) showing that parents from a broad range of seabird species can adjust provisioning effort. To determine if interspecies differences in parental ability to respond to chick demands are general (cf. Johnsen et al. 1994) will require studies that employ comparable types of manipulations in a variety of species, preferably in the same colonies at the same time. Such studies should separate the effects of nestling age, hunger, and condition on parental provisioning effort and must control for variation in quality among parents. Possible interactions between prey abundance and the willingness or ability of seabird parents to alter provisioning effort (see Bertram and Kaiser 1993) are also of particular interest.

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Appendix

We estimated the amount of fish ($L(i)$; in grams) fed to the nestling as follows. The method is portrayed in Fig. 1, where all the symbols are also defined. The mass of the nestling measured on day i (following feeding) is

[1] $W(i) = [W(i - 1)e^{-aT(i-1)} + L(i)]e^{-bT(i)}$

Rearranging and solving for $L(i)$ we find

[2] $L(i) = W(i)e^{bT(i)} - W(i - 1)e^{-aT(i-1)}$

The variables $W(i)$, $W(i - 1)$, $T(i)$, and $T(i - 1)$ are known, but parameters a and b must be estimated from the data. To enable us to use multiple regression, we approximate the rate of mass loss over the intervals $T(i)$ and $T(i - 1)$ as linear. Then

[3] $L(i) = W(i)(c_1 + c_2T(i)) + W(i - 1)(c_3 + c_4T(i - 1))$

where c_1 , c_2 , c_3 , and c_4 are constants. Rearranging yields

[4] $L(i) = c_1W(i) + c_2W(i)T(i) + c_3W(i - 1) + c_4W(i - 1)T(i - 1)$

Multiple regression yields the following parameter estimates (numbers in parentheses are standard deviations).

	1986	1987
Intercept	23.1 (4.6)	13.8 (2.7)
c_1	1.37 (0.11)	1.25 (0.08)
c_2	0.0286 (0.0044)	0.0238 (0.0046)
c_3	-1.95 (0.07)	-1.69 (0.06)
c_4	0.0294 (0.0045)	0.0232 (0.0047)
F	192	431
df	4,310	4,463
P	<0.0001	<0.0001
r^2	0.712	0.788