

# Patterns of energy acquisition by a central place forager: benefits of alternating short and long foraging trips

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In some seabirds, foraging trips have been defined as either long or short, with the length of time spent traveling to the foraging area apparently a critical feature in determining foraging trip length. Using logger technology, together with complimentary data from published studies, we investigated traveling and foraging times in 18 free-living Adélie Penguins *Pygoscelis adeliae*, which were foraging for chicks. Most deep, foraging dives were distributed around the center of the foraging trip. This central tendency was particularly apparent if the cumulative amount of undulations in the depth profile (indicative of prey capture) was considered during deep dives; values started to increase before 20.9% and ceased after 67.2% of the dives had occurred. This concentration of the feeding activity in the middle of the foraging trip indicates that birds traveled to and from a prey patch whose location varied little over the birds' trips. These data form the basis for a simple model that uses traveling and foraging times together with projected rates of prey ingestion and chick and adult gastric emptying to determine that there are occasions when, to optimize rates of prey ingestion while at sea for both adults and chicks, birds should conduct foraging trips of bimodal lengths. *Key words*: gastric emptying, seabirds, self-feeding, Spheniscidae, provisioning. [*Behav Ecol* 15:824–830 (2004)]

Breeding seabirds are central place foragers (sensu Orians and Pearson, 1979) executing foraging trips to remote locations but consistently returning to a central place, the colony, to deliver food to the brood. Recently, it has been reported that a number of seabird species, e.g., thick-billed Murres *Uria lomvia* (Benvenuti et al., 1998), thin-billed prions *Pachyptilla belcheri*, yellow-nosed albatrosses *Diomedea chlororhynchus*, wandering albatrosses *D. exulans* (Weimerskirch et al., 1994), sooty shearwaters *Puffinus griseus* (Weimerskirch, 1998), little shearwaters *P. assimilis* (Booth et al., 2000), Cory's shearwaters *Calonectris diomedea* (Granadeiro et al., 1998), and blue petrels *Halobaena caerulea* (Chaurand and Weimerskirch, 1994), execute foraging trips of bimodal lengths. Explanations for this propose that the longer trips serve to enhance body condition of the adult at the expense of the brood, whereas short trips enable the parents to provision the brood at a maximal rate (Weimerskirch, 1998), at the expense of the adult. Implicit in the explanation is that the two different modalities occur because of foraging at two different sites, one close to the breeding ground, to which the trips are short, and one distant from the breeding ground, to which the trips are long (Weimerskirch et al., 1994). The length of time traveling to the foraging area is thus, apparently, a critical feature in determining foraging trip length and whether or not bimodal foraging trip lengths might be adopted. Clarification of this matter is made difficult by the foraging habits of seabirds, which often range far out at sea where they cannot easily be observed.

Fortunately, the last decade has seen some remarkable developments in logging and telemetry, in which devices are attached to free-living seabirds so as to determine activity of birds at sea. Parameters such as undulations in the

depth profile (Kirkwood and Robertson, 1997; Wilson, 1995), stomach temperature (Pütz and Bost, 1994; Wilson et al., 1992), oesophageal temperature (Ancel et al., 1997; Charrassin et al., 2001; Ropert-Coudert et al., 2000a), and even beak angle (Wilson et al., 2002) are increasingly used to determine the times during foraging trips when seabirds ingest prey.

We used logger technology together with complimentary data from published studies to try to determine time partitioning between traveling and foraging in a free-living seabird, the Adélie Penguin *Pygoscelis adeliae*, foraging for chicks. These data form the basis for a simple model that attempts to examine the conditions under which foraging trips might be expected to have bimodal lengths according to maximized rates of energy gain by both the adults and the chicks.

## MATERIALS AND METHODS

The study was conducted on Adélie penguins from a colony located at Ile des Petrels, Adélie Land, Antarctica (66.7° S, 140.0° E) during the breeding season 1998–1999, from hatching to the beginning of the crèche phase (19 December 1998 to 9 January 1999). The study period lasted 21 days and covered only the guarding phase of penguin chick-rearing period. This ensured that the variability in the foraging behavior resulting from changes in the chick age (Wienecke et al., 2000) would be minimized.

Twenty birds were equipped with 12-bit resolution, 16 Mbyte memory, three channel UWE-PDT loggers (Little Leonardo, Tokyo, Japan) that measured depth and swim speed every second. These loggers (102 × Ø20 mm, 50 g in air, absolute accuracy for depth and speed: 0.5 m and 0.05 m/s, respectively) had an anteriorly-mounted propeller recording water flow that was subsequently transformed into speed data. As speed data have been presented elsewhere (Ropert-Coudert et al., 2001, 2002a), the present study focuses on analysis of the depth data.

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Birds were caught on the shore or directly at the nest prior to their departure to sea and were equipped with loggers. The UWE-PDT loggers were attached in the middle of birds' backs close to the tail, to minimize the drag induced by externally attached loggers (Bannasch et al., 1994), with glue (Araldite) and two cable-ties. On return of birds to the colony after one foraging trip, loggers were removed and data were downloaded to a computer. Each individual bird provided one replicate for the statistical analysis. The beginning and end of the foraging trips were determined using the first and last dive > 2 m, respectively.

Dives with maximum depth  $\leq 2$  m were excluded from analysis. This meant that information on porpoising and sub-surface traveling activities may be lost (Wilson, 1995; Yoda et al., 1999). Dives were divided into descent, bottom, and ascent phases. The beginning and end of the bottom times are defined as the first and last times a bird ascend and descend, respectively, following the descent phase from the surface. In addition, the bottom phases were further classified as with (two or more undulations > 2 m) and without an undulatory component. The frequency distribution of the maximum depth of dives was bimodal in all birds, except two individuals for which the number of dives decreased linearly with increasing maximum depth. The trough in the bimodal distribution is generally used to distinguish shallow from deep dives in Adélie and other penguin species (e.g., Ropert-Coudert et al., 2001). Traveling behavior in penguins is apparent as series of short, shallow dives (Trivelpiece et al., 1986; Wilson, 1995) and highly directional movement (Wilson, 2002). Such behavior is known to occur at the beginning and end of periods at sea (Wilson, 1995) and is readily apparent in Adélie Penguins (Wilson, 2002).

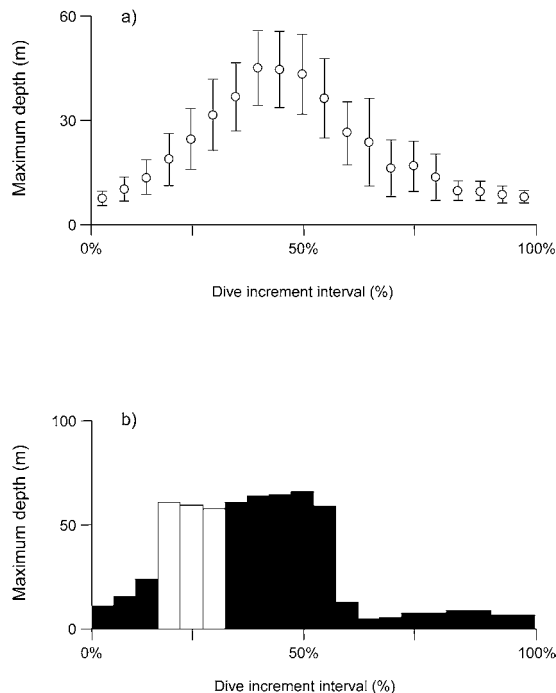
Satellite records from the National Ice center (<http://www.natice.noaa.gov/egg.htm>) indicate that the Adélie Land region (Antarctic "Wilkesland East" Ice charts, 130–150°E) was free of ice for the whole study period (December 1998–January 1999).

Finally, the relevant permission for the work to be carried out was obtained from the Commission of the Terres Australes et Antarctiques Françaises and from the scientific ethical committee of the Institut Français pour la Recherche et la Technologie Polaires. All birds were equipped following strict protocol procedures based on recommendations made to minimise stress to birds.

### Parameters and statistical analysis

Instead of plotting variables as a function of time spent foraging, foraging activity variables were plotted as a function of an x-axis where numerical increments of one corresponded to individual dives over time. In order to compare the evolution of foraging variables between birds, the x-axis was transformed into a percentage. Finally, assessed foraging variables were averaged over every 5% interval of the x-axis (these categories referred hereafter as the 'dive increment interval'). The maximum depth of dive and cumulative number of undulations per deep dive were plotted as a function of the dive increment interval.

We used Generalized Linear Models (GLM) with poisson errors and log link function corrected for overdispersion (Crawley, 1983) to examine the effect of trip duration on number of dives and number of deep dives. When acquired data did not follow a normal distribution, even after arcsine transformation, nonparametric tests were used following the procedures recommended by Sokal and Rohlf (1969). Trends were highlighted with Spearman rank correlation tests. The data were statistically treated using Statview (version 4.57, Abacus concepts Inc., USA) software. Values were presented



**Figure 1**  
Maximum depth of dive as a function of the dive increment interval (a) averaged for all birds and (b) detailed on one bird (SIWB). White bars in (b) indicate night times.

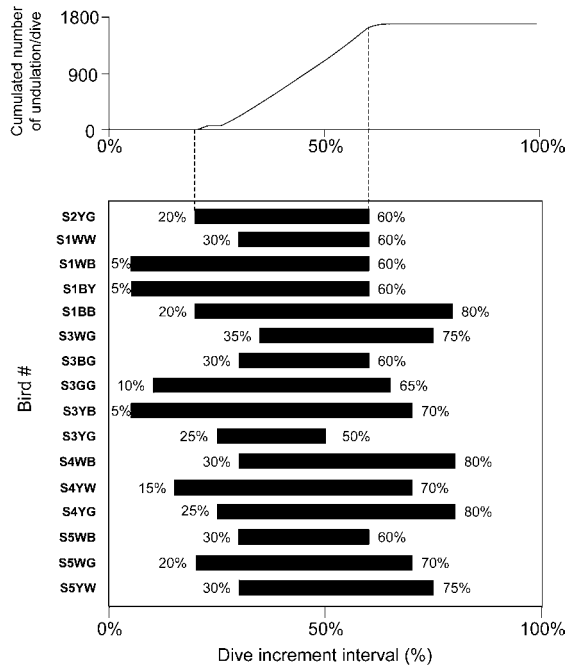
as mean  $\pm$  SD. For all statistical tests, the threshold was taken to be 5%.

### RESULTS

Depth data were recorded for a full foraging trip in 18 birds, accounting for 11,045 dives > 2 m. Foraging trips lasted on average  $23.8 \pm 9.1$  h, but there was substantial inter-individual variation. The number of dives per trip was on average  $613.6 \pm 265.1$  and was significantly related to the duration of the foraging trip ( $F_{1,16} = 28.59$ ,  $p < .001$ ), a longer foraging trip corresponding to a greater number of dives. Similarly, the number of deep dives was significantly greater when the duration of the foraging trip increased ( $F_{1,14} = 14.74$ ,  $p < .005$ ). Foraging trip duration was not determined by the departure time ( $\rho = 0.21$ ,  $Z = 0.85$ ,  $p = .40$ ) or the departure date ( $\rho = 0.21$ ,  $Z = 0.88$ ,  $p = .38$ ). The median of the maximum depth of dives was on average  $9.4 \pm 3.5$  m.

Deep diving activity was performed mainly around the middle of the foraging trip in all birds, (Figure 1a) with a clear interruption in deep diving towards the end of the trip, as illustrated on one individual (Figure 1b). In thirteen birds (67%), there was a clear interruption of the deep diving activity after  $65 \pm 7.4\%$  of dives had been performed. The position of this apparently substantial depth change was independent of foraging trip duration ( $\rho = 0.04$ ,  $Z = 0.13$ ,  $p = .90$ ) as well as of the foraging dates ( $\rho = 0.04$ ,  $Z = 0.14$ ,  $p = .89$ ). Finally, in the last six birds to be studied, either no clear interruption of deep diving activity could be determined or there was no deep diving activity at all.

The cumulative number of undulations during deep dives followed a roughly sigmoidal curve (Figure 2) in 16 birds (89%; penguins S2Z and S4BY were excluded from the analysis because no deep dives were observed for these two birds). The period during which the number of undulations increased was



**Figure 2**  
(top) Cumulative number of undulations during deep dives as a function of the dive increment interval. (bottom) Proportion of the foraging trip during which the cumulated number of undulations during deep dives increases per bird.

concentrated in the middle of the trip, starting at  $20.9 \pm 10.2\%$  and stopping at  $67.2 \pm 9.1\%$  of the dive increment interval. Thus, the period when the number of undulations increased represented on average  $46.3 \pm 12.3\%$  of the foraging trip.

The clear pattern in maximum dive depth from our data—i.e., deep diving activity concentrated in the middle of the foraging trip—coupled with undulations in the depth profile augers for foraging activity occurring at this time (Figures 1 and 2). Using the individual trip duration data and the start-end points of the foraging sequence (percentage values in Figure 2), we calculated the mean time dedicated to traveling and foraging by these 16 individuals as  $12.18 \pm 5.94$  h and  $13.27 \pm 4.07$  h, respectively (Table 1). Consideration of the time spent actually foraging indicates that, despite a relatively small sample size, there is bimodality (Figure 3).

## DISCUSSION

### Logger effect

Externally attached loggers have been shown to affect the swim speed and energy expenditure of captive birds swimming in a water canal (Kooyman, 1989; Wilson and Culik, 1992). In our study, the cross-sectional area of the logger accounted for 1.6% of the bird's cross-sectional area and would probably have caused an increase in energy expenditure of  $< 2.2\%$ , this value being derived from experiments in a water canal using a logger with a cross-sectional area 1.8% that of the Adélie penguin (Culik and Wilson, 1991), although the loggers used by Culik and Wilson (1991) were streamlined. However, externally attached loggers have been shown to modify slightly the diving behavior of King penguins (Ropert-Coudert et al., 2000b), the effect becoming more pronounced as the deployment duration increases. In our study, loggers were attached on birds for a single foraging trip. All birds equipped continued to raise

**Table 1**  
**Traveling and foraging times per individual, listed by increasing foraging dates**

Bird #	Traveling time (h)	Foraging time (h)
S1WW	10.4	15.6
S1BB	17.9	7.7
S1WB	13.1	16.0
S1BY	5.6	6.9
S2YG	9.3	6.2
S3YG	6.5	4.3
S3GG	17.7	7.6
S3WG	15.8	19.3
S3BG	10.3	19.1
S3YB	16.1	5.4
S4YG	17.1	17.1
S4WB	16.0	19.5
S4YW	13.5	16.5
S5WG	12.8	5.5
S5WB	18.8	18.8
S5YW	11.7	9.6

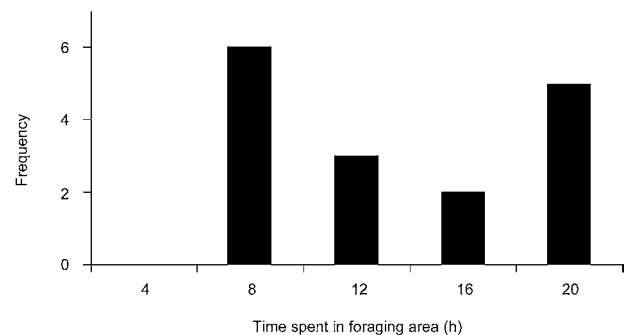
Foraging times were calculated using the trip duration and the start and end points of the foraging sequences during the trip, as determined from Figure 2.

their chicks normally and were seen during the next molting season.

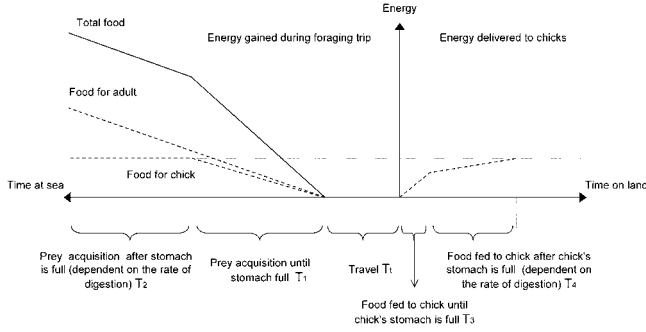
### Prey types and observed patterns

The presumed traveling time in our data ties in with the distribution of *E. superba* in Adélie Land, which is concentrated on the continental shelf at about 30 km from the colony (Wienecke et al., 2000). Apparent variability in these traveling times (see the distribution of shallow dives in Figure 1) may be accounted for by temporal changes in the local distribution of krill. For instance, fishing fleets have been suggested to modify the localization of krill patches throughout the breeding season, which may affect the krill biomass available to breeding Adélie penguins and subsequently its partitioning effort between self-feeding and chick provisioning (Mangel and Switzer, 1998).

Although Ropert-Coudert et al. (2001) observed that Adélie penguins with a bimodal distribution of the maximum dive depth feed mainly during deep dives, two individuals performed no deep dives at all with no clear central foraging activity. This may be related to dietary differences, with these



**Figure 3**  
Frequency distribution of the durations spent in the foraging areas by the Adélie Penguins equipped during the study. These values were derived by examining the depth records for deep dives with undulations in the bottom phase (see text).


**Figure 4**

Schematic diagram illustrating rates of energy gain by adults and chicks in penguins provisioning a brood. The energy gained during the time at sea (left-hand side) (after the traveling time has been discounted) increases linearly for the adult, being solely dependent on the rate of digestion. The rate of energy gain at this time is given by consideration of the actual energy gained (y-axis) in relation to the time (x-axis). The energy gained by the chick for the period at sea cannot exceed the carrying capacity of the adult, determined by maximum stomach size. The rate of acquisition of prey by the adult is also dependent on stomach fullness. The time necessarily spent on land (right-hand side) may be divided into a period where food may be passed rapidly to the chick, until the chick's stomach is full, and an extended period when food is regurgitated for the chick at a rate determined by the rate at which the chick's stomach can be emptied due to digestion.

birds probably catching different prey. A previous study reported a similarly constant shallow diving activity in one individual Adélie penguin foraging off Adélie Land. Whereas other birds usually prey on krill, this bird fed mainly on juvenile *Pleuragramma antarcticum* (Ropert-Coudert et al., 2002b). To our knowledge, such shallow foraging activity seems to be of marginal importance, having only been reported occasionally.

#### Modeling ideal solutions for travel versus foraging time

To consider the advantages in dedicating time at sea to traveling versus foraging, we need to create a simple model based on the premise that the adult's stomach may be regarded as a vessel that is filled up via ingestion of prey and emptied as digestion takes place (gastric emptying). The rates at which these two processes occur determine the amount of food found in the stomach until a certain point during the foraging trip, when digestion is fully stopped by the adult and the stomach contents thereafter remain constant until fed to the brood (Gauthier-Clerc et al., 2000; Peters, 1997). The same principles apply for the chick (for simplicity we assume that the brood may be defined by a single chick). Here, regurgitation by the adult is responsible for the filling of the stomach and the chick's own gastric emptying for its removal. In both the case of the adult and the chick the stomach cannot be filled more than a certain amount. When this stage is reached, the rate at which further food is acquired is uniquely determined by the rate of gastric emptying (Figure 4).

Let us assume that the rate at which the stomach is filled by an adult at the feeding grounds =  $dx_f/dt$  (this being linear for simplicity). By the same token, we assume, for simplicity, that the rate at which the stomach is emptied due to digestion is also linear, being  $dx_e/dt$ .

When  $dx_f/dt < dx_e/dt$ , the stomach will not fill up.

When  $dx_f/dt > dx_e/dt$ , the stomach will fill up at a rate of  $(dx_f/dt) - (dx_e/dt)$  until a maximum is reached, this point being dictated by the maximum carrying capacity of the stomach ( $V_{max}$ ). If the penguin continues to feed after  $V_{max}$  is reached, the new rate of food ingestion =  $dx_e/dt$ .

Thus, the time taken to fill the stomach is

$$T_1 = \frac{V_{max}}{(dx_f/dt) - (dx_e/dt)} \quad (1)$$

and the food gained over this time is

$$X_1 = T_1 * (dx_f/dt). \quad (2)$$

If  $T_2$  is the time spent feeding after  $V_{max}$  has been reached, then the food gained at this time is

$$X_2 = T_2 * (dx_e/dt). \quad (3)$$

The total food gained over the time spent foraging is

$$X = X_1 + X_2 = T_1 * (dx_f/dt) + T_2 * (dx_e/dt) \quad (4)$$

Substituting for  $T_1$  from Equation 1:

$$X = \frac{V_{max}}{(dx_f/dt) - (dx_e/dt)} * (dx_f/dt) + T_2 * (dx_e/dt) \quad (5)$$

Suppose, during a normal foraging trip, that the penguin spends a specific time taken to commute between the nest site and the foraging area (which includes the time for both directions), given by  $T_t$ , then the overall gain per unit time is:

$$dX_{sea}/dt = \frac{\frac{V_{max}}{(dx_f/dt) - (dx_e/dt)} * (dx_f/dt) + T_2 * (dx_e/dt)}{T_1 + T_2 + T_t} \quad (6)$$

$$= \frac{\frac{V_{max}}{(dx_f/dt) - (dx_e/dt)} * (dx_f/dt) + T_2 * (dx_e/dt)}{\frac{V_{max}}{(dx_f/dt) - (dx_e/dt)} + T_2 + T_t} \quad (7)$$

This formulation accounts for the rate of food acquisition by the adult at sea. It does not, however, account for the rate of energy removal by the brood, although this can be treated in a similar manner as that used for the adults. We assume that foraging adults manage to fill their stomachs to  $V_{max}$  and that the minute they stop foraging to return to their chicks digestion stops (Gauthier-Clerc et al., 2000).

The time taken for the brood to fill its stomach to  $V_{chickmax}$  is

$$T_3 = \frac{V_{chickmax}}{(dx_{chickf}/dt) - (dx_{chicke}/dt)} \quad (8)$$

during which time the chick will have acquired an amount of food corresponding to

$$X_{chick} = T_3 * [(dx_{chickf}/dt) + (dx_{chicke}/dt)] \quad (9)$$

Note that the  $(dx_{chicke}/dt)$  term must also be included since the chick is likely to digest food, and thus empty its own stomach, even as it is being fed.

Substituting for  $T_3$  from Equation 8:

$$X_{chick} = \frac{V_{chickmax}}{(dx_{chickf}/dt) - (dx_{chicke}/dt)} * [(dx_{chickf}/dt) + (dx_{chicke}/dt)] \quad (10)$$

However, where the adult stomach size is greater than that of the brood, or  $V_{max} > V_{chickmax}$ , then the time taken for the adult stomach contents to be emptied depends directly on the rate at which the brood removes food from the stomach due to digestion. When  $V_{chickmax}$  is reached, the time taken for the adult to give all its remaining food to the chick will be:

$$T_4 = \frac{(V_{max} - X_{chick})}{(dx_{chicke}/dt)} \quad (11)$$

Thus, taking into consideration both the time the adult spends at sea and on land, the overall rate of food acquisition by the adult for both adult and chick is defined by:

$$dx/dt = \frac{V_{\max} * (dx_f/dt) + T_2 * (dx_e/dt)}{T_1 + T_2 + T_3 + T_4 + T_t} \quad (12)$$

$$\frac{V_{\max}}{(dx_f/dt) - (dx_e/dt)} * (dx_f/dt) + T_2 * (dx_e/dt) \\ \frac{V_{\max}}{(dx_f/dt) - (dx_e/dt)} + T_2 + \frac{V_{\text{chickmax}}}{(dx_{\text{chick}f}/dt) - (dx_{\text{chick}e}/dt)} \\ + \frac{(V_{\max} - X_{\text{chick}})}{(dx_{\text{chick}e}/dt)} + T_t \quad (13)$$

This indicates that the main critical variable in determining the overall rate of food acquisition that may be manipulated by the adult is the time spent in the foraging area,  $T_2$ , since all other terms in the equation are much more likely to be dependent on standard processes such as those physiological (e.g., rates of digestion), morphological (e.g., maximum size of the stomach), or environmental (e.g., the rate of prey encounter). Note, however, that this overall rate of food acquisition applies to both the brood and to the adult. Relative benefits for the brood and the adult are different. Effective overall rates of food acquisition by the adult are given by the equation:

$$dx_{\text{adult}}/dt = \frac{(dx_e/dt) * (T_1 + T_2)}{T_1 + T_2 + T_3 + T_4 + T_t} \quad (14)$$

and those of the brood can be given by:

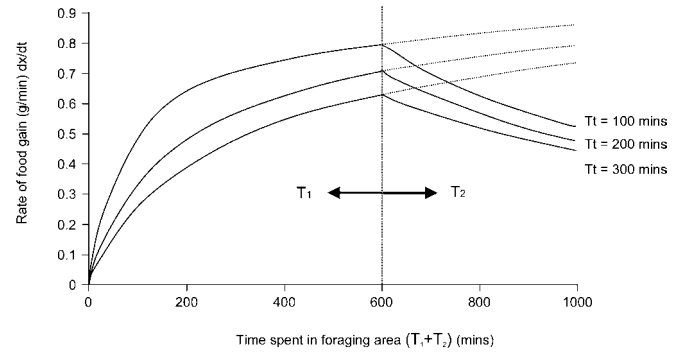
$$dx_{\text{chick}}/dt = \frac{V_{\max}}{T_1 + T_2 + T_3 + T_4 + T_t} \quad (15)$$

### Model parameter values

In attempting to provide figures which can be used for the model, we note that the lack of exact values do not preclude the model from helping understand general trends. Here, we are primarily concerned with managing a model to derive a qualitative output that will allow us to examine the extent to which variation in traveling, with respect to foraging time, may affect the rate of energy gain by adults and chicks.

Rate of prey ingestion in foraging penguins is not linear when considered over short time periods because these birds feed on patchy prey (Ropert-Coudert et al., 2001). However, overall, Wilson and Grémillet (1996) consider that during foraging African Penguins *Spheniscus demersus* may catch 1.5 g of prey per minute, King Penguins catch between 2320 g/day (Pütz and Bost, 1994) and 8.82 g/min (Kooyman et al., 1992), while Adélie Penguins are reported to catch around 7.2 g/min (Wilson et al., 1991). In this work we consider arbitrarily that penguins ingest food at an overall rate of 2 g/min, but halving or doubling this would not change the trends observed in the model except by degree. That no penguin will be able to carry on ingesting food after the stomach is full is obvious, except in tandem with gastric emptying (see earlier), and it is interesting to note that some work indicates that certain penguin species may implement a break in foraging during the trip so as to digest accumulated food (Wilson and Peters, 1999, and references therein).

Little work has been done on the rate at which penguins digest food, although Wilson et al. (1985) noted that African Penguins remove food from the stomach at rates of approx-



**Figure 5**

Rate of food gain as a function of time spent in the foraging area for Adélie Penguins foraging for chicks and traveling different distances (taking different times to do so) between nest sites and feeding areas ( $T_1$ ) (see text). Here, we have assumed that the adults ingest food at a rate of 2 g/min while in the foraging area until the stomach is full, containing a mass of 600 g. The rate of digestion by the adult is constant at 1 g/min, this being the same as that of the chicks. The rate at which food is delivered to the chicks is 10 g/min. The solid lines disappearing after  $T_1 + T_2 = 600$  are rates of food gain by the chicks, while increasing values denoted by simple dashes show rates of food gain by the adults.

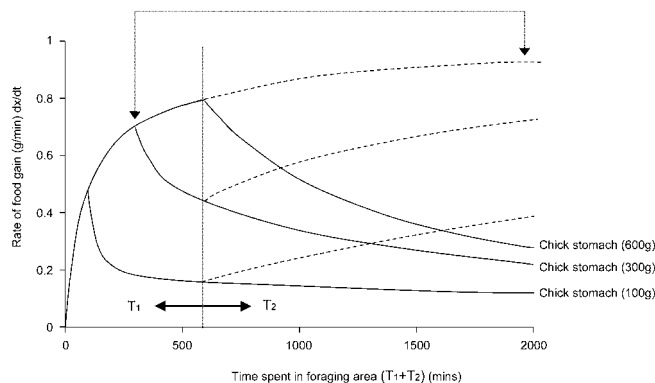
imately 0.3 g/min. Both Wilson et al. (1985) and Jackson and Ryan (1986) note, however, that the digestion rate of food is highly dependent on prey type. For our model we have assumed that adult Adélie Penguins empty food from their stomach at a rate of 1 g/min and that this rate is also applicable for chicks with a stomach size equivalent to those of adults. We also assume that the rate of digestion of the chick is directly proportional to the size of the stomach compared to that of the adult so that:

$$(dx_{\text{chick}e}/dt) \\ = (V_{\text{chickmax}}/V_{\text{max adult}}) * (dx_{\text{adult}e}/dt) \text{ (g/min)}. \quad (16)$$

The ability of adult penguins to stop digestion completely to preserve food for their brood has been demonstrated by a number of authors (Gauthier-Clerc et al., 2000; Peters, 1997; Wilson et al., 1989) for Adélie, African, Chinstrap *Pygoscelis antarctica*, Gentoo *P. papua*, and King penguins.

The use of the above equations, using approximately expected values for rates of prey ingestion, rates of digestion, traveling times, etc., shows that when the chick's stomach size equals that of the adult, increasing traveling times only decreases the rate of food gain correspondingly, without altering the general pattern (Figure 5). However, the overall rate of food gain by the chicks decreases for every minute that the adult remains in the foraging area after its stomach has been filled, whereas the rate of food gain for the adult increases (Figure 5).

This situation changes dramatically, however, when the chick's stomach is smaller than that of the adult, becoming more apparent with increasing divergence in stomach sizes. The food gain by the chick is maximized when the adult only fills its own stomach to a size that corresponds to that of the chick (Figure 6). This means that the food is delivered to the chick at a rapid rate at the nest, without being slowed down by any digestive processes. If the adult fills its own stomach beyond this point, despite the fact that the adult is acquiring food for itself as well as its chick, both adult and chick reduce their relative rate of food gain to the point where the adult's stomach has been filled (Figure 6). If the adult remains in the foraging area beyond this point, although the chick continues to have



**Figure 6**  
 Rate of food gain as a function of time spent in the foraging area for Adélie Penguins foraging for chicks of different sizes and therefore having different stomach sizes. Here, we have assumed that the traveling time between nest site and foraging location is constant at 100 min (for the return journey) and that adults ingest food at a rate of 2 g/min while in the foraging area until the stomach is full, containing a mass of 600 g. The rate of digestion by the adult is constant at 1 g/min, but that of the chicks is a fraction of that of the adult according to: rate = chick stomach size/adult maximum stomach size (g/min). Thus, chicks with stomach sizes of 600 g digest food at a rate of 1 g/min, whereas smaller chicks, with a maximum stomach mass of 100 g, digest food at a rate of 1/6 g/min. The rate at which food is delivered to the chicks is assumed to be constant, irrespective of chick size, at 10 g/min until the stomach is full, after which food delivery rate is determined by the rate of digestion. The solid lines are rates of food gain by the chicks, while those denoted by simple dashes at  $T_1 + T_2 \geq 600$  show rates of food gain by the adults. Note that for short periods spent in the foraging area ( $T \leq 600$ ) the rate of food gain is identical for both adults and chicks. Optimum rates of food gain for the chicks occur after shorter periods in the foraging area in smaller chicks. Note that optimum rates of food gain are monomodal in chicks of all sizes but are essentially bimodal for the adults (see arrows), except when chick stomach size is at least as big as that of the adult.

a reduced rate of food gain, the rate of food gain by the adult starts to increase again. Extended time in the foraging area beyond this point can ultimately lead to the adult increasing its rate of food gain to beyond the point reached in the maximum that corresponded to the chick's maximum (see arrows in Figure 6). Thus, there is apparently a discrepancy in ideal times spent in the foraging area, according to whether the situation is considered from the perspective of the chick or the adult: Food gain by the chick has a single maximum, whereas the adult has two. Although it is obviously likely to increase the likelihood of breeding success if the adult maximizes the rate of energy delivery to the chick, if the food digested by the adult during foraging does not cater for the energetic demands of this regime, the adult will have to compensate during a later foraging trip (or use body reserves). To maximize fitness, therefore, the ideal solution would be for the adult to alternate short trips with long ones because this process maximizes the rate of food gain for the adult in both instances.

Thus, the observation that many seabirds alternate long foraging trips with short ones during chick rearing (Chaurand and Weimerskirch, 1994; Clarke, 2001; Weimerskirch, 1998; Weimerskirch et al., 1994) does correspond to our model and may be explained by maximizing chick growth rates while maintaining adult fitness. However, it is not necessary to invoke the existence of different foraging areas for this strategy to be applicable (Clarke, 2001). If the extended time at sea during long foraging trips allows birds to visit more distant areas where rates of prey acquisition are particularly profitable, then such a strategy might be tenable; but if rates of gastric emptying/

rates of digestion limit the rate at which prey can be acquired, then increasing travel time in this way is disadvantageous. We note that our model does not explicitly consider cases in which either the adult or the chick effectively starves (where energy gain over the period considered is less than that used). Although this situation appears to apply to procellariiformes (Klomp and Schultz, 2000), it is less obvious in penguins because foraging trips are usually less than 2 days (see Croxall and Davis, 1999, for review) and because it is, in any event, much more difficult to ascertain genuine body weight loss because penguin body mass increases during foraging are substantial and may amount to up to 35% of their normal body mass (e.g., Wilson, 1984).

Consideration of our data from Adélie Penguins in light of the above is problematic. The time span over which birds were equipped (~21 days) could have encompassed (1) appreciable changes in travel distances between the foraging area and the colony (the variability in apparent travel time [cf. Figure 2] shows the extent of this), (2) changes in prey capture rates in the foraging areas, and (3) a systematic change in brood mass, which would result in changes to stomach size (chick masses are predicted to change from ~200 g to 2000 g (Trivelpiece et al., 1987)). Thus, although the equipment of 18 birds with devices would seem excessive, given the room for variation, it is clear that more birds need be equipped in order to determine the relevance of the various factors; they all result in changes to the timing of the peak, which determines maximum rate of gain of food for chicks and adults (Figures 5 and 6). For instance, a model by Mangel and Switzer (1998) showed that food allocation between self-feeding and chick provisioning was ultimately related to krill availability near the colony and to whether or not the krill biomass was sufficient to cover both the energy requirements of the adults and the chicks, although their model was defined at the foraging trip level and did not account for fine-scale behavioral adjustments, such as those proposed in our study. Our model also predicts that adults should return, at least periodically, with less food in their stomachs for small chicks than for large ones. Although we have no data to allow us to examine this, this trend has been noted for African penguins (Wilson et al., 1989).

**CONCLUSION**

Our model detailing the advantages of particular strategies is necessarily simplistic, but it at least provides a framework within which seabird provisioning for chicks might be examined. Further developments could be implemented. For example, we have assumed that the rate of food ingestion by birds with an empty stomach is constant irrespective of time of day. Although this might hold true for Adélie Penguins during mid-summer at high latitudes, as was the case in our study, light is known to limit the foraging capacities of penguins to the point that foraging at night might be extremely limited or precluded altogether (Cannell and Cullen, 1998; Wilson et al., 1993; Wilson and Peters, 1999). Such an enforced break would presumably allow adults to empty their stomachs, starting the next day with a correspondingly higher rate of prey ingestion. Indeed, cognizance of such things might help explain the apparent inconsistencies in departure and arrival patterns exhibited by a number of penguin species (e.g., Meyer et al., 1997). Above all, however, our model indicates that patterns of provisioning in central place foragers may be optimized by alternating strategies, even if the conditions at the foraging site do not change.

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