

# Foraging and provisioning in Antarctic fur seals: interannual variability in time-energy budgets

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This study examined three competing hypotheses to explain how lactating Antarctic fur seals (*Arctocephalus gazella*) respond to changes in the level of resource availability. Antarctic fur seals have episodic bouts of suckling (1–3 days), alternating with foraging trips (3–10 days). Foraging time budgets varied significantly ( $p < .001$ ) among 8 consecutive years at Bird Island, South Georgia. Foraging trip duration increased during periods of relative food shortage. Time spent ashore was more consistent among years than foraging trip duration but declined during a year of particularly low food availability. In 4 of the 8 years, there was a significant positive correlation between time spent ashore and foraging trip duration. In the other years, the relationship was close to statistical significance. Energy delivery to pups during suckling bouts followed an asymptotic power function. Energy gain during foraging trips was estimated from diving behavior, which suggested that the energy gain function was linear. Distance traveled during foraging trips was correlated with foraging trip duration, and long foraging trips were associated with reduced foraging intensity. There was support for the hypothesis that lactating Antarctic fur seals compensate for reduced resources by increasing the foraging trip duration rather than working harder and increasing their energy expenditure. However, there was most support for the hypothesis that lactating Antarctic fur seals adjust time spent ashore as well as foraging trip duration, possibly to maximize the delivery of food to their offspring. Lactation appears to impose constraints on provisioning of offspring that differ from those of seabirds foraging in the same environment and often on the same prey. *Key words:* *Arctocephalus gazella*, Antarctic fur seals, lactation, optimization, provisioning, time budgets. [*Behav Ecol* 10:198–208 (1999)]

Provisioning of young is a central component of parental care in many birds and mammals (Clutton-Brock, 1991), but there appear to be few generalizations about how parents adjust their foraging under different natural levels of resource availability (Wright et al., 1998). In the specific case of marine predators, parental foraging time budgets appear to vary in relation to the resources available (Burger and Piatt, 1990; Cairns, 1987; Croxall et al., 1988; Gentry, 1998; Gentry and Kooyman, 1986; Monaghan, 1996; Monaghan et al., 1994; Montevecchi, 1993; Trillmich et al., 1991; Wanless and Harris, 1992). Consequently, parental time foraging budgets have been used as indicators of variability in marine resources (Agnew, 1997; Montevecchi, 1993).

There are at least three ways for foragers to respond to varying conditions of resource availability. They may (1) increase their energy expenditure by working harder under conditions of low food availability to provide a constant level of resources to young (e.g., Costa and Gentry, 1986; Harris and Wanless, 1990; Monaghan, 1996; Trillmich, 1990), (2) increase the time they spend foraging (e.g., Croxall et al., 1988; Montevecchi, 1993), or (3) they may optimize their foraging time budget, including the time allocated to different activities, to maximize the rate of food delivery to young under all conditions (Houston et al., 1996). These hypotheses are developed more formally in the appendix. In the case of a lactating mammal, the first hypothesis would result in a constant time spent with the offspring delivering a consistent load of milk up to the point at which parental foraging effort reached a maximum (Hammond and Diamond, 1997). After the maximum effort has been reached, time spent delivering the load

will decline as the load declines. Offspring growth rate would also then decline. The second hypothesis would produce gradually declining offspring growth rates because, although the load size delivered to the offspring may be constant, the average rate of delivery will decline across the whole of the period of offspring dependency. The response, if the third hypothesis holds, is more difficult to predict but will most probably lead to adjustments of the time spent delivering the load and the load size in relation to the foraging conditions. These predators may be maximizing their efficiency or rate of energy delivery to the offspring (Houston, 1995; Schmid-Hempel et al., 1985) rather than their effort.

The present study tested these hypotheses in lactating Antarctic fur seals (*Arctocephalus gazella*) by examining foraging time budgets together with estimates of rates of energy delivery to the pup and energy gain during foraging trips. Past studies have shown that foraging trip duration increases as food availability declines, and this is matched by declines in pup growth rate (Croxall et al., 1988; Lunn et al., 1993), which supports the hypothesis that female fur seals simply increase the proportion of time devoted to foraging in response to reduced food availability. Energetics studies of the northern fur seal (*Callorhinus ursinus*), a species with close behavioral and ecological similarities to Antarctic fur seals, suggested that foraging effort increased in response to reduced food availability, whereas it did not increase in Antarctic fur seals because they normally operate close to the metabolic maximum (Costa et al., 1989). The explanation for this difference has been that northern fur seals spend more time resting than Antarctic fur seals, and they have a greater capacity to increase their foraging effort (Costa et al., 1989; Trillmich, 1990). However, Antarctic fur seals also rest at the surface for long periods when at sea (Boyd et al., 1997), and the energetic costs during foraging trips are negatively related to the intensity of foraging as measured by diving behavior (Arnould et al., 1996c).

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In addition, foraging trip duration and the time spent ashore between foraging trips are positively correlated (Boyd et al., 1991), which suggests that Antarctic fur seals may be adjusting the whole of their time budget to maximize delivery of food to their pups under all conditions. Time spent ashore between foraging trips is highly consistent in northern fur seals but was extended when females were prevented from reuniting with their pups (Gentry, 1998). This shows that the duration of time ashore depends on the rate of energy transfer to the pup so that time ashore is not constant. Moreover, foraging trip duration in this species is related to the distance to the edge of the continental shelf where these animals feed, suggesting that distance to the foraging ground is an important component of trip duration (Gentry, 1998). Therefore, overall it appears that foraging trip duration depends on food availability (amount, distance, and accessibility) but that the time ashore depends on the load of milk delivered.

The present study examined evidence for the competing hypotheses in Antarctic fur seals provisioning. A simple energy balance model (appendix) for a central-place forager (Orians and Pearson, 1979; Wetterer, 1989) was used to develop the expected patterns of behavior if fur seals are optimizing their time budgets to maximize delivery to their pups. The study was carried out over 8 consecutive years at Bird Island, South Georgia. In addition, I used extensive previously published data about the energy expenditures of lactating fur seals at this site (Butler et al., 1995; Arnould et al., 1996c; Costa and Trillmich, 1998; Costa et al., 1989), milk production and pup growth (Arnould and Boyd, 1995a,b; Arnould et al., 1996a), body composition (Arnould et al., 1996b), and foraging range (Boyd et al., 1998).

Among mammals, fur seals and sea lions are unusual in having episodic lactation normally involving 1–2 days of milk production and suckling alternating with periods of 3–10 days without suckling while the mother forages at sea (Bonner, 1984; Oftedal et al., 1987). Although the underlying physiology of this process is not understood, it appears that mothers reduce or stop milk production while foraging and that energy gained is mainly stored as adipose reserves which are subsequently incorporated into milk on return to the pup (Arnould and Boyd, 1995a). Therefore, these mammals have developed a lactation strategy similar to the provisioning of nestlings in many oceanic seabirds (Croxall and Briggs, 1991; Pennyquick et al., 1984) because of the necessity to forage at long distances (>100 km) from the offspring.

It was assumed that, within years, resource levels available are more similar than they are among years. The Antarctic fur seal has the advantage of simplicity in that a single parent provisions a single offspring and, in the case of animals in the present study, they mainly eat a single type of prey, Antarctic krill (*Euphausia superba*; Croxall and Pilcher, 1984; Reid and Arnould, 1996). The delivery phase of the time budget can also be measured accurately, as can the total energy delivered as milk. In addition, lactating Antarctic fur seals and their pups at South Georgia have few, if any, significant predators during pup rearing, although there are additional survival costs accrued to adults due to reproduction (Boyd et al., 1995). Antarctic fur seals have the disadvantage that it is difficult to divide foraging into its components of time spent traveling and time spent foraging, and it is not yet possible to measure the energy gained during individual foraging events. Nevertheless, indices of these, using remote recording of diving behavior (e.g., Boyd, 1996), are available for Antarctic fur seals.

This study examined variability in foraging time budgets (1) among individuals within years, when foraging conditions were likely to be broadly similar for all individuals, and (2) among groups of individuals from the same population in dif-

**Table 1**

**Number of female Antarctic fur seals in which the foraging cycle was measured during a minimum of six consecutive foraging cycles for each year from 1988–1989 to 1995–1996**

| Year      | Number of females | Mean foraging trip duration (days) | Mean time ashore (days) |
|-----------|-------------------|------------------------------------|-------------------------|
| 1988–1989 | 19                | 4.97 ± 1.23                        | 2.37 ± 0.62             |
| 1989–1990 | 103               | 4.37 ± 0.95                        | 2.02 ± 0.52             |
| 1990–1991 | 37                | 8.23 ± 1.45                        | 1.88 ± 0.47             |
| 1991–1992 | 20                | 4.62 ± 1.08                        | 2.00 ± 0.32             |
| 1992–1993 | 17                | 5.06 ± 1.38                        | 1.68 ± 0.42             |
| 1993–1994 | 9                 | 9.23 ± 4.02                        | 1.12 ± 0.44             |
| 1994–1995 | 14                | 5.89 ± 1.19                        | 2.15 ± 0.51             |
| 1995–1996 | 20                | 3.77 ± 0.89                        | 1.96 ± 0.51             |

Only in 1993–1994 were a minimum of three consecutive foraging cycles used. Also shown are the means and standard deviations for foraging trip duration and time spent ashore in each year.

ferent years, when foraging conditions were known to have varied significantly among years (Brierley et al., 1997).

## MATERIALS AND METHODS

### Foraging–lactation cycles

A foraging–lactation cycle was defined as a single period of foraging at sea (foraging trip) followed by a single period spent ashore in the company of the pup. The behavioral time budgets of lactating female Antarctic fur seals were measured during eight consecutive reproductive seasons from, 1989 to, 1996 at Bird Island, South Georgia (54° S, 38° W), each reproductive season being referred to by the year in which the austral summer ended. A total of 2305 foraging–lactation cycles from 239 individuals were measured (Table 1). Annual samples were independent because individuals were only sampled in a single year. The foraging time budgets of individuals were averaged over a minimum of six foraging–lactation cycles starting from the first time a female departed to sea after giving birth. Thus, animals were sampled at the same stage of the reproductive season in each year. Only in, 1994 were a minimum of three foraging–lactation cycles used because large numbers of pups died due to low food availability (Boyd et al., 1995), causing many study animals to be lost from the sample.

The time spent ashore (the lactation phase of the cycle) and at sea (the foraging phase of the cycle) were measured either by direct observation (accurate to the nearest 0.5 days and used to supplement observations made in, 1989–1990) or by monitoring the presence or absence of mothers from the beach using an automated data logger in all years. The data logger detected signals from radio transmitters attached to the fur of the mothers (accurate to 30 min; Boyd et al., 1991). Other studies at this site have shown that these females only come ashore at the breeding site where monitoring took place (Boyd et al., 1998).

### Energy delivery

The rate of energy delivery and the form of the energy delivery function,  $D(t_a)$  (see appendix), was investigated by serially weighing pups in, 1996 after they were reunited with their mothers. Six mother–pup pairs were captured when the mother arrived back from a foraging trip (in all cases the first or second trip after birth) and placed in an enclosure (3 m × 4

m) to ensure that pups could be recaptured and weighed at predetermined intervals (4–24 h) and that mothers could be kept with the pups for a set period (72 h). I assumed that the digestive efficiency of the pups when feeding on milk was close to 100% and that the pups remained in water balance, as shown by analyses of total body water (Arnould et al., 1996a). Although the relative proportion of fat and protein in milk changes through lactation bouts (Arnould and Boyd, 1995b), the magnitude of this change is not large enough to have a significant effect on the use of mass gain as a measure of energy transferred to the pup. Thus, mass gained by the pup during the period when mothers and pups were kept together was representative of the milk consumption by the pup minus the mass loss due to the maintenance metabolic costs of the pup. Pup mass was measured to the nearest 50 g ( $\sim 0.7\%$  of total mass). There was also no evidence that the disturbance caused by serial weighings of pups influenced the rate of growth because the growth rates obtained in this study were similar in magnitude to those in the study of Arnould et al. (1996a), in which weighing was carried out before the return of the mother and then again after her departure.

Mothers returned to sea voluntarily when released and were then observed to continue normal foraging–lactation cycles. The mass change of pups continued to be measured for a further 24–48 h after separation from the mother. The rate of mass loss during this time was added to the mass gained while pups were accompanied by their mothers. This compensated for the costs, in terms of pup mass lost, of maintenance metabolism during the time that mothers were with their pups.

An asymptotic growth model (appendix) was fitted to the measurements of mass gained by each of the six pups during the period they spent with their mothers. This used the Marquardt-Levenberg algorithm to find the minimum sum of squares between the observed and expected value (SAS Institute, 1990).

### Energy gain

Arnould and Boyd (1995a) provided information about the absolute amount of energy gained by lactating female fur seals during foraging. However, the form of the energy gain function (i.e., the rate of gain through the foraging trip) has not been estimated previously. Time-depth recorders (TDRs; TDR Mk V, Wildlife Computers, Redmond, Washington, USA) were used during January to March 1996 to examine the distribution of time spent foraging during foraging trips. Here, I assume that foraging mainly occurs when diving is detected and that the amount of time spent diving is proportional to energy gain, as shown by Arnould et al. (1996a; but see Francis et al., 1998). The time-depth recorders are small enough (7 cm  $\times$  5 cm  $\times$  2 cm, 50 g,  $<0.2\%$  of body mass) that they probably have no significant effect on diving and swimming behavior. TDRs sampled depth every 5 s (for TDR) or 10 s (for satellite-linked TDR). Data were recovered from both types of TDRs when females returned to the pup. In some cases, the memory of the TDR was filled before a female returned to the pup. Only data from records of complete foraging trips were used.

The rate of energy gain was assumed to be proportional to the time spent feeding. Although it is not yet possible to measure food intake directly in fur seals, because fur seals feed by diving, the pattern of diving has been used to indicate feeding (Boyd, 1996; Croxall et al., 1985). It was not possible to test this assumption directly but, as lactating female Antarctic fur seals at South Georgia are mainly monophagous on Antarctic krill (*Euphausia superba*) that occur in dense swarms, I have assumed that female fur seals will only feed on prey patches when the patches satisfy some minimum threshold of net en-

ergetic gain. Thus the gain function with foraging trip duration,  $g(t_f)$ , was assumed to be directly proportional to  $t_{sub}$ , the time spent submerged, or to  $t_{bout}$ , the time spent in bouts of diving. Bouts were defined by the method given by Boyd et al. (1994). This used a sequential search of the diving record to define surface intervals that increased significantly compared with the set of past surface intervals that had occurred since the previous significant increase. These significant changes in surface interval were designated as defining the end of bouts of diving. The slopes of the functions,  $t_{sub}/t_f$  or  $t_{bout}/t_f$  were assumed to be proportional to the rate of energy gain.

### Foraging range at sea

I measured the distance that females traveled to forage from locations of females during foraging trips tracked using the Argos satellite system. During 1996 lactating females were tracked during two consecutive foraging trips. These were the same individuals used to examine the diving time budgets during foraging trips. Platform transmitter terminals (PTTs; Wildlife Computers, 1 W, 250–500 g, and Telonics ST-10, 0.5 W, 200 g) were attached to the hair using epoxy glue along the dorsal midline between the scapulae. Boyd et al. (1997) showed that the largest versions of these PTTs (12  $\times$  5  $\times$  4.5 cm) significantly reduce swimming speed and cause an increase in foraging trip duration. The PTTs had a minimum transmission interval of 45 s, and they only operated when a saltwater switch, located close to the base of the antenna, showed that the antenna was out of the water. The location of the transmitter was calculated to a precision of  $0.001^\circ$  of latitude and longitude ( $\sim 111$  m). The maximum error associated with locations was 8.6 km (Boyd et al., 1998).

### Time–energy budget models

A simple set of models of the time–energy budgets of lactating Antarctic fur seals was constructed to test the three hypotheses examined in the present study. The models, which are detailed in the appendix, combine all the relevant information about time and energy in this species within a single theoretical framework. In this case, the time budget was treated as the dependent variable and the rates of energy gain, delivery, and energy expenditures during different activities were the independent variables in the model. All the model parameters are described in the appendix. The optimization model (model 3) has a similar construct to energy balance models proposed by Houston and Carbone (1992) and Wetterer (1989).

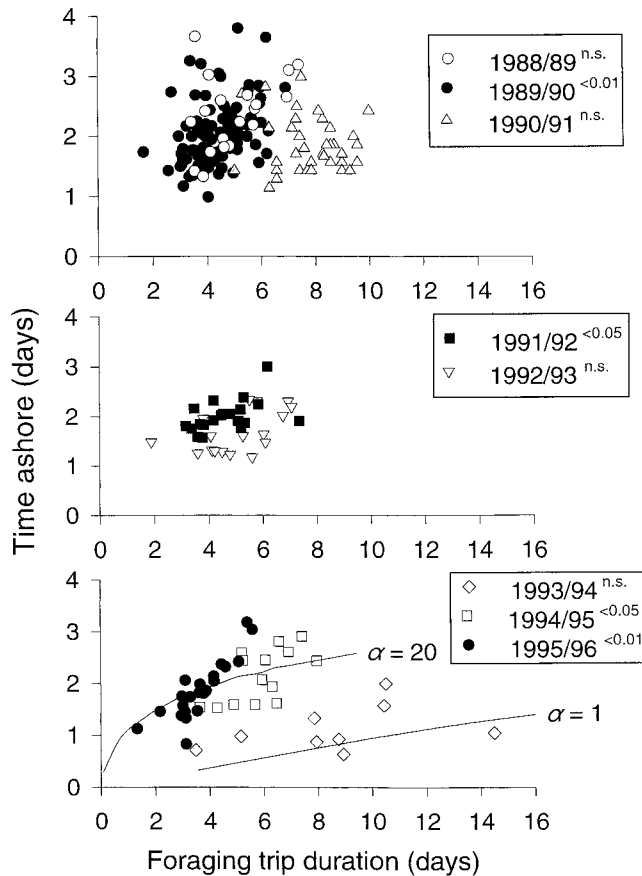
### Statistics

Many of the variables used in the analysis were not normally distributed. Consequently, I used appropriate nonparametric statistical tests for hypothesis testing.

## RESULTS

### Foraging–lactation cycles

Foraging trip duration and the time spent ashore varied significantly among years (Table 1; Kruskal-Wallis test, ashore  $\chi^2 = 34.85$ ,  $df = 7$ ,  $p < .001$ ; at sea  $\chi^2 = 104.38$ ,  $df = 7$ ,  $p < .001$ ). The variability in foraging trip duration was mainly caused by particularly long foraging trips in, 1990–1991 and 1993–1994. However, there was no correlation among years in the foraging trip duration and the time spent ashore (Spearman rank correlation coefficient,  $r = .536$ ,  $p = .181$ ), suggesting that the factors influencing variability in foraging trip

**Figure 1**

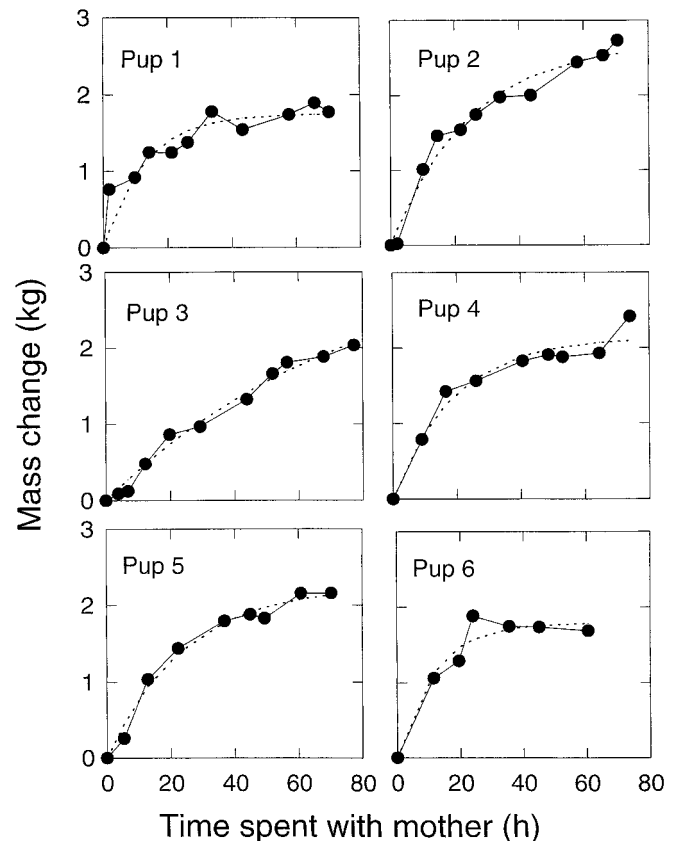
The relationship between time spent ashore and foraging trip duration by lactating Antarctic fur seals during 8 consecutive years. Each point is the mean for an individual fur seal (see Table 1 for sample sizes). These relationships are split between three diagrams to improve the clarity of the illustration, and there is no significance to the groupings of years in each diagram. The expected relationship for two values of  $\alpha$ , the rate of energy gain while foraging, is shown in the bottom diagram, and these are based on model 3 (appendix), which uses the rates of energy gain, expenditure, and delivery to the pup to predict the relationship between time spent ashore and foraging trip duration. Note that these model data are not fitted to the empirical relationships in the bottom diagram but are overlain to illustrate the qualitative congruence of the relationship.

duration were independent of the factors affecting variability in the time spent ashore.

There was a significant positive relationship among individuals between time spent ashore and foraging trip duration in 4 of 8 years (Spearman rank correlation coefficient,  $p < .05$ ); the relationship was nearly significant in the other years ( $p < .1$ ). Although it is likely that foraging trip duration and time spent ashore are not related in a linear manner, possibly accounting for the nonsignificant relationship in some years, this relationship suggests that individuals making long foraging trips also spent longer ashore (Figure 1).

#### Energy delivery

The mass gained by pups when with their mothers followed an asymptotic power function (appendix; Figure 2, Table 2). In all cases the model explained  $>89\%$  of the variation in the data, and in four of the six individuals  $>95\%$  of the variation was explained by the model. Therefore, pups gained mass

**Figure 2**

Mass gained by pups after being reunited with their mothers after a foraging trip. The asymptotic growth model fitted to these data is described in the appendix, and the parameter values are given in Table 2. Compensation for mass lost due to maintenance metabolism of the pups was carried out by adding the rate of mass decline in the absence of the mother to the growth rate in the presence of the mother.

and, by implication, energy at a faster rate over the first 12 h after being reunited with their mothers than during the subsequent time spent together; it appeared that the decline in delivery rates to pups occurred gradually during the time spent ashore by mothers. Based on the milk composition estimates of Arnould and Boyd (1995b), the average asymptotic energy delivered was  $50.2 \pm 5.2$  MJ (Table 2), which is in the middle of the range of measured values given by Arnould et al. (1996a).

#### Energy gain

During foraging trips, energy gain, as indicated by diving activity, occurred intermittently (Figure 3). When averaged over a whole foraging trip, however, there was no indication of a systematic change in the average rate of energy gain between different stages of the foraging trip. This is illustrated in Figure 3 by the diving records of six representative individuals. These records show significant variation among individuals in the slopes of both diving indices (see Figure 3).

The foraging trip duration was inversely related to the proportion of time spent diving (i.e., time submerged) (Figure 4). This relationship is unlikely to be linear because the proportion of time spent diving cannot be zero in individuals that are balancing their energy budgets, and the foraging trip duration cannot be zero at the same time as there is a positive rate of energy gain. The most intuitive relationship between



**Table 2**  
Parameter values ( $\pm$ SE) obtained from the least-squares fit of the asymptotic growth model (see Appendix) to the change in mass of pups when reunited with their mothers after the mother had returned from a foraging trip

| Pup number | $\beta$           | $k$               |                 | $n$ | Coefficient  |          | $r^2$ |
|------------|-------------------|-------------------|-----------------|-----|--------------|----------|-------|
|            |                   | kg                | MJ <sup>a</sup> |     | % of $\beta$ | % of $k$ |       |
| 1          | $0.079 \pm 0.020$ | $1.748 \pm 0.116$ | 37.67           | 10  | 25.1         | 6.6      | .898  |
| 2          | $0.041 \pm 0.006$ | $2.709 \pm 0.149$ | 58.37           | 10  | 14.0         | 5.5      | .976  |
| 3          | $0.013 \pm 0.003$ | $3.301 \pm 0.580$ | 71.14           | 11  | 26.0         | 17.6     | .988  |
| 4          | $0.053 \pm 0.009$ | $2.137 \pm 0.118$ | 46.05           | 8   | 18.6         | 5.5      | .957  |
| 5          | $0.042 \pm 0.006$ | $2.251 \pm 0.113$ | 48.51           | 8   | 13.9         | 5.0      | .985  |
| 6          | $0.087 \pm 0.025$ | $1.792 \pm 0.123$ | 38.62           | 7   | 25.8         | 6.9      | .945  |

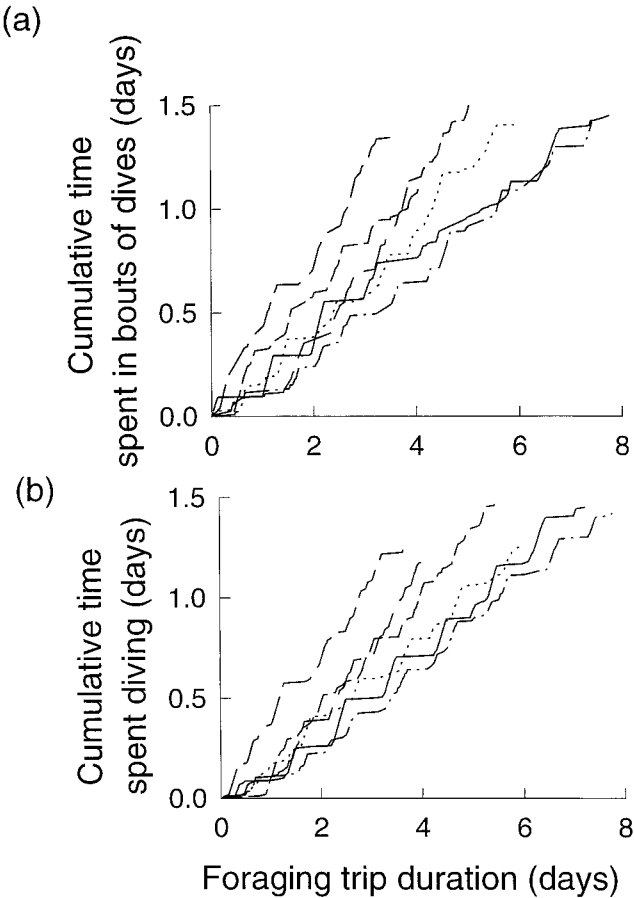
Mass change was adjusted for mass used for maintenance metabolism while pups were with their mothers. The parameter  $\beta$  is the slope parameter,  $k$  is the asymptotic mass change, which is also given in units of energy, and  $n$  is the number of data points.

<sup>a</sup> This assumes that the pup mass gain is 50% fat, 10% protein, and 40% water (Arnould and Boyd, 1995a). Using the energy equivalence of 39.5 MJ/kg for fat and 18 MJ/kg for protein (Schmidt-Nielsen, 1975), mass gain was assumed to have an energy density of 21.55 MJ/kg. The metabolic rate for pups was 2 W/kg (equivalent to 1.4 MJ/day for an 8-kg pup), based on standard allometry (Lavigne et al., 1986).

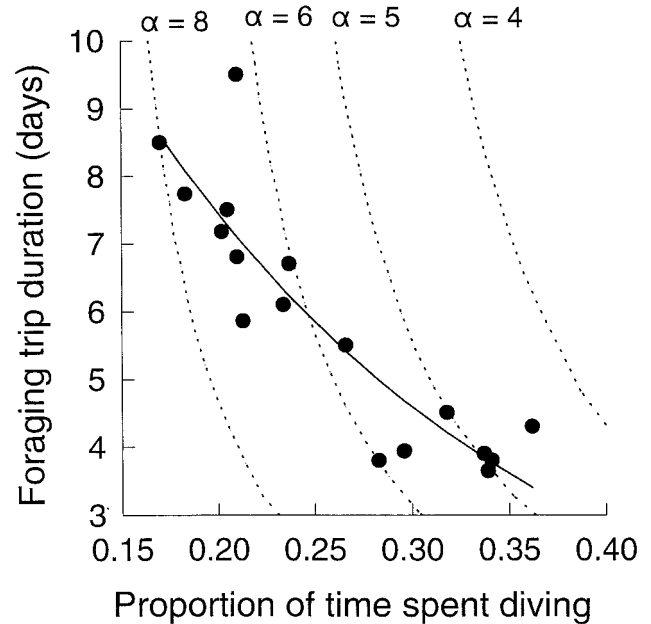
these parameters is a form of negative exponential, which is the line illustrated in Figure 4. This model explained slightly more of the variation in the foraging trip duration than a linear model (least-squares regression; exponential model  $r^2 = .809$ ; linear model  $r^2 = .784$ ).

**Foraging range**

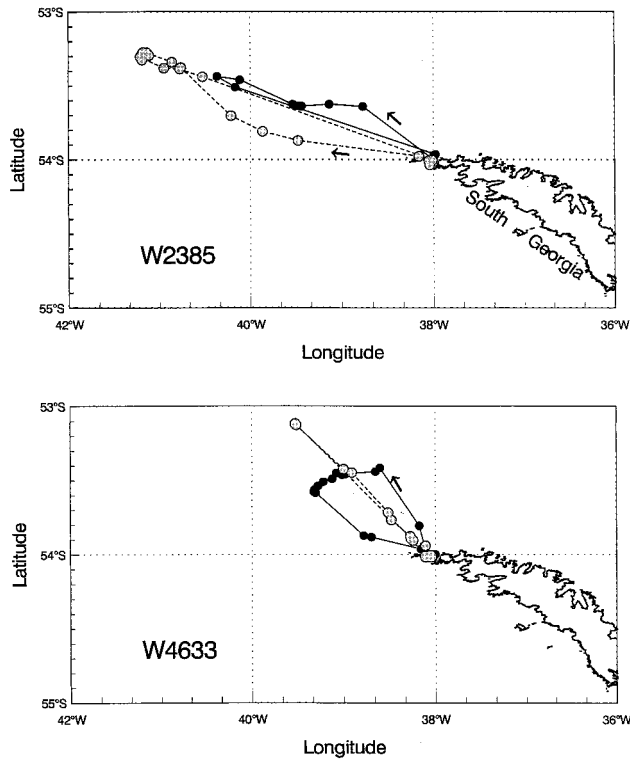
Tracks of female fur seals at sea showed that individuals tended to travel away from the location of the pup along a roughly constant bearing and then return along a bearing within 0–30° of the reciprocal of the outgoing bearing. Representative examples of these tracks are illustrated for two individuals in Figure 5. The maximum distance traveled during a foraging



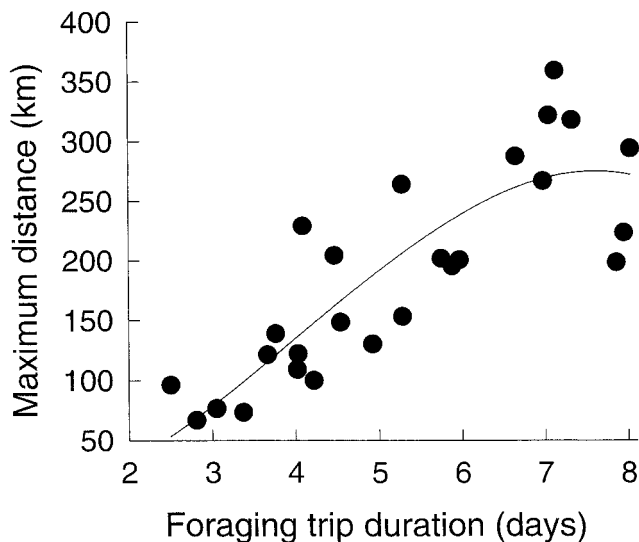
**Figure 3**  
Cumulative time spent in bouts of dives (a) and spent submerged (b) in relation to cumulative time spent at sea by six lactating Antarctic fur seals during January–March 1996. There was significant variation in the slopes of these relationships (panel a:  $F_{5,532} = 2.75$ ,  $p < .018$ ; panel b:  $F_{5,1125} = 22.06$ ,  $p < .001$ ).



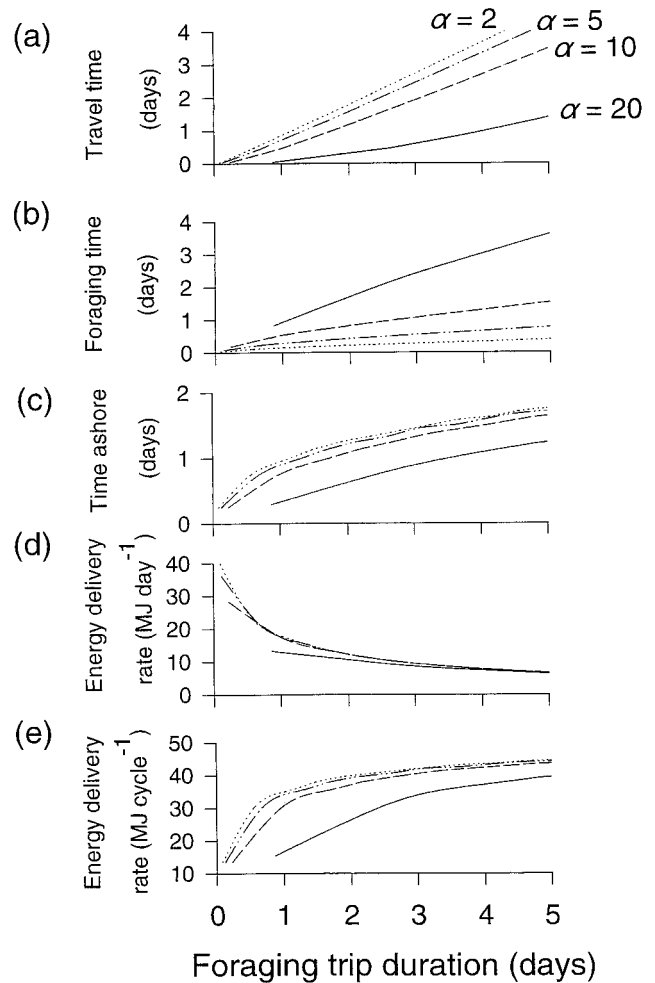
**Figure 4**  
The relationship between foraging trip duration by 17 lactating Antarctic fur seals and the proportion of time spent diving, which is assumed to be proportional to energy gained while foraging. Data were from female fur seals tracked during January–March 1996, and only data from foraging trips in which all dives were recorded are included. The regression model (shown by the solid line) was fitted by least squares regression and is given by  $t_s = c \exp(-\gamma r_s)$ , where  $c$  is the intercept,  $r_s$  is the nominal rate of energy gain (defined as  $t_{sub}/t_s$ ), and  $\gamma$  is the slope of the regression. The fitted values of  $c$  and  $\gamma$  were  $19.59 \pm 3.03$  and  $4.83 \pm 0.66$ , respectively, and  $r^2 = .809$ . The dotted lines show the predicted relationship, based on the model given in the appendix (model 3), between foraging trip duration and the proportion of time spent feeding for two values of  $\alpha$ , the rate of energy gain during foraging.



**Figure 5**  
Examples of tracks of two lactating Antarctic fur seals foraging to provision their pups located on Bird Island, at the west end of South Georgia during January–March 1996. In each case two foraging trips are illustrated (trip 1, solid dot; trip 2, shaded dot), and the direction of movement is indicated by the arrows.



**Figure 6**  
The relationship between the maximum distance traveled during a foraging trip made by lactating Antarctic fur seals and the duration of the foraging trip. Data were from female fur seals tracked during January–March 1996. The model fitted to the data is a third-order polynomial that was forced through the origin (maximum distance =  $17.94x^2 - 1.49x^3 - 14.20x$ , where  $x$  is the foraging trip duration;  $r^2 = .738$ ).



**Figure 7**  
The predicted relationships between foraging time (a), time ashore (b), energy delivery per day (c), and energy delivery per cycle (d) and the foraging trip duration based on the model 3 described in the appendix. Each line within individual diagrams is the relationship for different values of  $\alpha$ , the rate of energy gain during foraging.

trip was positively related to foraging trip duration (Figure 6), showing that the distance traveled during a foraging trip was an important component of trip duration.

#### Time–energy budget model

The predicted time budget was estimated for model 3 (appendix) to examine the pattern expected if mothers were optimizing their trip duration and time ashore in relation to rates of energy gain and delivery. Travel time, foraging time, and time ashore were varied in the model to maximize the gross rate of energy delivery to the pup at different levels of energy gain (appendix, model 3). This process was independent of the measurements made of time ashore and foraging trip duration. The main predictions produced by the model are shown in Figure 7, which illustrates relationships for animals maximizing the net rate of energy delivery to the pup. The relationships for gross rate of energy delivery and efficiency were qualitatively similar to those shown. In quantitative terms, a currency involving the net rate of delivery was always inferior to maximization of efficiency or gross rate of delivery, but the differences between the effects of maximiz-

Table 3

Predicted rate of energy delivery to pups (MJ/day) by lactating female Antarctic fur seals with energy intake rates of 2, 4, 8, and 16 MJ/h while foraging

| $t_i$ | Gross        | Net   | Efficiency | Gross         | Net   | Efficiency |
|-------|--------------|-------|------------|---------------|-------|------------|
|       | $\alpha = 2$ |       |            | $\alpha = 4$  |       |            |
| 0.25  | 9.41         | 9.51  | 9.49       | 16.16         | 16.30 | 16.23      |
| 1.0   | 6.41         | 6.57  | 6.55       | 10.39         | 10.62 | 10.53      |
| 2.0   | 4.73         | 4.92  | 4.90       | 7.44          | 7.71  | 7.66       |
| 4.0   | 3.16         | 3.38  | 3.37       | 4.86          | 5.17  | 5.14       |
|       | $\alpha = 8$ |       |            | $\alpha = 16$ |       |            |
| 0.25  | 20.45        | 20.61 | 20.48      | 22.91         | 23.08 | 22.90      |
| 1.0   | 12.70        | 12.95 | 12.81      | 13.95         | 14.21 | 14.04      |
| 1.5   | 8.95         | 9.25  | 9.16       | 9.74          | 10.06 | 9.95       |
| 4.0   | 5.77         | 6.12  | 6.07       | 6.24          | 6.61  | 6.55       |

Values are given for individuals maximizing the gross rate of delivery, net rates of delivery, and the efficiency of delivery (Appendix, model 3,) over different travel times ( $t_i$ ), expressed in days.

ing these currencies were small (Table 3). The model predicted that time spent traveling or foraging, time ashore, and the energy delivered per foraging cycle increased in relation to foraging trip duration, whereas the energy delivered per day declined with increasing foraging trip duration (Figure 7). Foraging time, time ashore, and energy delivered per foraging cycle were sensitive to the rate of energy gain (Figure 7). The time spent ashore and the energy delivered per foraging cycle both declined as the rate of energy gain declined, whereas the time spent foraging increased. The model also predicted that the foraging trip duration should be a declining curvilinear function of the proportion of time spent foraging (Figure 4). Therefore, the empirical relationship illustrated in Figure 4 may represent the optimal time budgets for individuals foraging over a wide range of rates of energy gain.

## DISCUSSION

This study has shown a relationship between time spent ashore and foraging trip duration together with differences in the foraging time budgets of lactating Antarctic fur seals among years (Figure 1), which are likely to be related to variations in food availability. For example, during 1993–1994, when the slope of the relationship between foraging trip duration and time spent ashore was particularly low (Figure 1) and when large numbers of fur seal pups died (Boyd et al., 1995), independent measures from ship-based surveys showed that krill abundance was lower than normal (Brierley and Watkins, 1996). Similarly, in 1990–1991, which was another year of long foraging trips (Table 1), measures of body condition in fish that predate krill also suggested that krill abundance was reduced (Kock et al., 1994). Conversely, in 1995–1996, when foraging trips were short in relation to time spent ashore, independent measures of krill abundance showed that krill was particularly abundant in that year, with an estimated krill biomass some 20 times that observed in 1993–1994 (Brierley et al., 1997).

## Competing hypotheses

The study was constructed to test several competing hypotheses of how foraging behavior is likely to vary with changes in food availability. Because foraging trip duration appeared to

increase as food availability declined, the hypothesis that foraging effort is increased to compensate for reduced food availability (appendix, model 1) is not supported by the data. This is perhaps not surprising since most studies of Antarctic fur seal energetics (Arnould et al., 1996c; Butler et al., 1995; Costa et al., 1989) suggest that these animals operate close to the maximum sustained metabolic rate while foraging (Hammond and Diamond, 1997).

Apart from 1993–1994 (Table 1, Figure 1), there was a narrow range of variation in time spent ashore, suggesting that in most circumstances the amount of milk delivered at each visit was independent of foraging trip duration. Moreover, Boyd et al. (1997) simulated increased foraging costs in female fur seals by adding drag and found that this increased foraging trip duration but had no effect on either the amount of energy delivered to the pups or the time spent ashore between trips. These results tend to support the hypothesis that mothers adjust the length of foraging trips to deliver a constant load of milk to the pup at each visit (appendix, model 2). However, variation in time spent ashore was as great within years as it was among years, so there is some doubt if the statistical power existed to detect differences between time spent ashore among years, except in the case of, 1993–1994 which was clearly an extreme.

During half of the years examined, there was a positive relationship between time spent ashore and foraging trip duration. This accords with the observations of Boyd et al. (1991) and would support the hypothesis that, within years, female Antarctic fur seals may be optimizing their time budgets by adjusting the time spent ashore and the amount of food delivered at each visit in order to maximize the average rate of energy delivery to offspring (appendix, model 3). The two scenarios from the optimization model illustrated in Figure 1 also support the optimization of the time budget as an explanation for differences among years. The results of different levels of energy gain ( $\alpha = 1$  and  $\alpha = 20$ ) are illustrated. The curves in Figure 1 are not an explicit fit of the model to data because of uncertainties about the form of the energy gain function. However, they illustrate the expected pattern of behavior under different conditions of food availability when using the empirical observations of energy expenditures and delivery rates from this species. They also illustrate the different patterns of behavior expected if the energy gain varied directly with the magnitude of the measured difference in krill biomass between 1995–1996 and 1993–1994 (Brierley et al., 1997), and they suggest a high degree of congruence between the behavior expected from the optimization model and the observed differences among these two years. In general, these observations provide support for the hypothesis that Antarctic fur seals optimize their time budgets (appendix, model 3).

A further complication with these interpretations is that mothers can increase the energy content of their milk after longer foraging trips (Arnould and Boyd, 1995b). This could be interpreted as a maternal strategy to maintain a constant rate of delivery of milk, even when foraging trip duration increases because increased milk energy density would most likely increase the slope of the milk energy delivery function and tend to reduce the time spent ashore by mothers. This effect was incorporated explicitly into model 3 (appendix) and may be part of a time-energy budget optimization process.

Any increase in foraging effort should have survival costs in addition to energetic costs. In starlings (*Sturnus vulgaris*) the pattern of food allocation to chicks gave a better fit to a model that maximized lifetime reproductive success than to the maximization of delivery to the offspring (Kacelnik and Cuthill, 1990) and, as in Antarctic fur seals (Boyd et al., 1995), most of the detrimental effects of food shortage are passed to the

offspring (Wright et al., 1998). Food allocation to maternal growth was included in the metabolic costs of the mother (appendix) because metabolic rate and energy gain were net of these costs, but it is likely that this quantity varied between individuals, possibly in relation to their reproductive value. However, if Antarctic fur seals are operating close to their metabolic maximum under normal conditions of food availability, then this may explain the large proportion of maternal mortality (40–50%) due to reproduction in this species (Boyd et al., 1995). The apparently high survival cost of reproduction may mean that Antarctic fur seals are more likely to risk their own survival to maintain investment in offspring than is the case with other closely related species (Trillmich, 1990).

Foraging trip duration declined with an increasing proportion of time spent foraging. The optimization model of foraging time budgets suggesting that part of the reason for the form of this relationship was because of variable rates of energy gain between individuals. Based on the predicted relationships for different values of  $\alpha$  (Figure 4), animals that had lower rates of energy gain would have spent a greater proportion of time foraging than those with high rates of energy gain. The difference between proportion of time spent diving (which is what was measured) and proportion of time spent foraging (which is what was modeled) makes quantitative comparisons between the observed and predicted relationships unrealistic. However, the presence of this relationship in the data supports the assumption that foraging trip duration is a function of the rate of energy gain, at least to the extent that this is represented by diving activity (Figure 4).

Overall, it appears that there is greater support for the time-energy optimization hypothesis (appendix, model 3) than for the other two alternatives, but with two important caveats. First, the assumption that energy gain is broadly linear across the whole of a foraging trip was only testable using an index (time spent diving). Introducing nonlinearities into the energy gain function could result in different and more complex relationships than currently predicted (Stephens and Krebs, 1986; Wetterer, 1989). Second, although optimization models often explain patterns of behavior, they may not provide important insights into the mechanism used by animals like female Antarctic fur seals to actually achieve, or approach, an optimal time-energy budget (Stephens and Krebs, 1986). There is a distinction, apparently missed by Pierce and Ollason (1987), between using an optimization model to examine the type of strategy possibly being used by an animal and concluding that, because an optimization model explains a greater proportion of the variance in the data than alternatives, the animals concerned are foraging optimally.

### Sources of variability in time budgets

The distance traveled to a foraging site has been suggested as one of the major limiting factors in the evolution of foraging patterns of guilds of some marine predators (Houston et al., 1996). The distance to foraging sites and the richness of prey patches are the two main extrinsic variables that affect foraging time budgets. In a diving predator such as a fur seal, the depth of the prey patch is also a factor determining its richness (Houston and Carbone, 1992; Kramer, 1988). For many species, especially birds and flying insects, the intrinsic limitation on the delivery of food to offspring is the load that can be carried (e.g., Schmid-Hempel et al., 1985; Wetterer, 1989). For fur seals, the major intrinsic limiting factor is likely to be the time taken to transfer energy from mother to offspring rather than load size. This is because there is an upper limit to the rate at which milk can be synthesized and delivered, and fat storage capacity is potentially large compared with the total energy delivered during a visit to the pup. For

example, Arnould et al. (1996b) showed that lactating Antarctic fur seals can have 6 kg of fat stores, which compares with an average delivery during a visit ashore of approximately 1.5 kg (Arnould et al., 1996a).

Variability between individuals in their time and energy budgets will be caused by a combination of extrinsic and intrinsic factors. Intrinsic variability will result partly from variability in the milk delivery function but also because of differing individual quality relating to, for example, parasite load, health, or age. Variation in the values of  $\beta$  (rate of delivery) and  $k$  (asymptotic amount of energy delivered) involving the way in which milk was delivered to the pup could account for much of the intra-annual variation illustrated in Figure 1. Extrinsic factors causing variability between individuals are likely to be those causing different rates of energy gain. Temporal variability in marine resources will mean that prey patches encountered during one foraging trip will probably not be present during subsequent trips because of potentially high rates of krill flux through the region (Murphy, 1995). It appears that females may adopt a simple strategy of swimming away from the colony along a constant bearing (Figure 5), and the rate at which prey are encountered determines the time spent diving and, by implication, the energy gain (Figure 4). Those that encounter high prey densities have high rates of energy gain and make short trips in terms of both distance and time (Figure 6). It is also possible that individuals follow foraging strategies that are more successful than others.

### Lactation as a method of energy delivery

The energy delivered per foraging cycle was predicted to increase with the length of foraging trip (Figure 7d). Arnould and Boyd (1995a) showed that total energy delivery per foraging trip increased with foraging trip duration. They also showed that mothers stored energy ultimately destined for milk as adipose tissue, even though it would probably be simpler and energetically more efficient for them to have made milk directly from the food eaten when at sea. This study has suggested that mothers are flexible in the proportion of energy they pass to their pups during a visit ashore and that maintaining their energy stores as adipose tissue, rather than milk, which cannot be used for purposes other than feeding the pup, allows mothers to have this flexibility.

Few mammals appear to be as restricted as fur seals in the time they have available to feed their young. In general, mammals tend not to uncouple foraging from provisioning in such a clear-cut way. Although bats feed milk to their offspring, in their case the limiting factor is likely to be time available for foraging and the optimum load carried, rather than the time they spend with their offspring (e.g., Swift, 1980). Lagomorphs have a lactation strategy close to that of fur seals because offspring are fed for only a few minutes each day (Zarrow et al., 1965), but in this case foraging location is not uncoupled from the region in which the pups are located, as it is in fur seals. The spotted hyena (*Crocuta crocuta*) is probably the only other mammal in which there is a strong parallel with otariid seals in that nursing occurs periodically between long foraging trips by the mother (Hofer and East, 1993). As found in this study, trip duration in hyenas is related to food availability (Hofer and East, 1993).

### Comparison with seabirds

Some of the principles applied to analyzing the foraging time budgets of birds feeding nestlings (Houston, 1987; Houston et al., 1996; Kacelnik and Cuthill, 1990) can be applied to a mammal following a similar strategy, but with two main dif-



ferences. First, the time spent with the offspring becomes a more significant part of the time budget. Unlike a bird that can deliver a load of food to a chick as a bolus produced from its crop, a seal delivers food as milk that must be synthesized and secreted. Thus, a seal may have to spend a few days feeding its pup, whereas seabirds may spend only a few minutes feeding their chicks at each visit to the nest. Second, this apparent disadvantage to seals is offset by the advantage that the amount of food delivered to the offspring is not limited by crop size or the mass that can be carried during flight; i.e., the load capacity is large and transport costs are negligible.

Houston et al. (1996) suggested that, among murre, the most important factor limiting chick growth rate was the distance that parents had to travel on a foraging trip because of the high transport costs of flight. It is likely that this conclusion applies generally to flighted seabirds. Penguins would appear to be less constrained than either flying seabirds or fur seals because they have neither the costs of flight to contend with nor the limitations imposed by lactation on the time taken to deliver food to the offspring (Prince and Harris, 1988). However, owing to physical limitations on gut capacity, they are probably more constrained than fur seals in terms of the amount of energy they can deliver at each foraging trip, and this will restrict the time and the distance to which penguins can forage. Among fur seals, there will also be an upper limit to the distance at which mothers can forage from the colony (Boyd et al., 1998), mainly because of the time constraint due to the potential starvation duration of the pup (Boness and Bowen, 1996; Boyd, in press). This intrinsic limit to the degree to which fur seals can compensate for changing prey distribution by adjusting their time-energy budgets probably explains the observation that pup growth rate declines with increased foraging trip duration when trip duration is >5 days (Lunn et al., 1993).

## Conclusions

These results suggest that female Antarctic fur seals are limited in their rate of energy delivery to the pup by a combination of factors, including the milk delivery function and the availability of prey. Differences in foraging time budgets across years are most probably caused by changes in the level of prey availability between years. Although there may be other explanations for the observed behavior, the results of the present study are generally consistent with the hypothesis that mothers adjust their behavior to maximize energy delivery to the pup. These results provide potential insight into the causes of variability in foraging performance, and therefore fitness, between individuals and within populations across years. However, they also illustrate some of the difficulties that exist with matching theoretical predictions to empirical data. Ideally, all the model parameters should be measured in each individual, but the technical difficulties of measuring field metabolic rates, energy delivery functions, and behavioral time budgets in the same individual make this impractical. As a result, it is only possible to examine the fit of models to data averaged across individuals.

These results also provide an insight into the major factors that are likely to limit the provisioning rate of pups by female fur seals in comparison with other predators that operate in a similar way, especially in the marine environment. This study suggests that the evolution of strategies for provisioning offspring in pinnipeds has been driven, at least in part, by the constraints imposed by the limitations on the rate of energy transfer during lactation. The production of concentrated milk by pinnipeds (Oftedal et al., 1987), including fur seals (Arnould and Boyd, 1985a; Trillmich and Lechner, 1986), is

likely to be an adaptation to increasing the value of  $\beta$ , the rate of energy delivery to the pup.

## APPENDIX

The time budget of a foraging, lactating fur seal was divided into four types of activities:  $t_a$ , time spent ashore;  $t_s$ , foraging trip duration;  $t_r$ , time spent traveling (and inclusive of time spent at rest), and  $t_f$ , time spent feeding. In practice  $t_i$  and  $t_j$  were assumed to be accumulated across whole foraging trips and were considered as the total amount of time allocated to each of those activities during a foraging trip. Energy was used as the most important currency, even though it is probable that other constituents of milk are important. The rate of energy expenditure while ashore was described as  $m_a$ , which was set at three times the basal metabolic rate ( $BMR = 0.293 \times \text{mass}^{0.75}$  where the units are MJ/day; Costa and Trillmich, 1988; Lavigne et al., 1986) and while at sea it was  $m_s$ , which was set at  $BMR \times 5$  (Arnould, 1995; Butler et al., 1995; Costa et al., 1989). The rate of energy expenditure while animals were at sea was assumed to be the same whether the seals were swimming or at rest (Butler et al., 1995). Therefore,

$$t_s = t_i + t_j \quad (1)$$

and the total maternal metabolic costs will be  $m_a t_a + m_s(t_i + t_j)$ . The energy delivered to the pup in milk,  $D(t_a)$ , will be

$$D(t_a) = k[1 - \exp(-\beta t_a)], \quad (2)$$

where  $k$  is a constant representing the asymptotic energy delivery to the pup that also minimizes the cost to the mother in terms of her own survival and  $\beta$  is the parameter representing the rate of delivery of energy to the pup. Conversely, the net energy gained when at sea will be

$$G(t_s) = \alpha t_f - m_s t_f - m_s t_r, \quad (3)$$

where  $\alpha$  is the rate of energy gain during foraging. If, on average, energy is balanced over foraging cycles, then

$$D(t_a) = G(t_s) - m_a t_a. \quad (4)$$

The assumption that energy is balanced over foraging cycles is generally upheld by observation. Arnould (1995) weighed females at regular intervals throughout lactation and, although there was a slow increase in mass, the cost of this involved a <13% addition to daily energy intake. Therefore, for simplicity, this was assumed to be contained within the value of  $m_s$ .

### Model 1: Adjustment of foraging effort to compensate for reduced food availability

Mothers may increase their foraging effort to compensate for reduced food availability. If the rate of gain declines from  $\alpha_1$  to  $\alpha_2$  then the rate of energy gain must increase by  $\alpha_1 - \alpha_2 = \delta$  in order to compensate for the change. From Equation 3, this can be represented as

$$G(t_s) = (\alpha_2 + \delta + j) t_f - (m_s + j) t_f - m_s t_r, \quad (5)$$

where  $j$  is the additional rate of energy expended in order to achieve the additional rate of energy gain  $\delta$ . The net result will be that  $D(t_a)$  remains constant up to the maximum sustainable metabolic rate (Hammond and Diamond, 1997), after which  $D(t_a)$  will decline. The way in which  $\alpha$  varies with  $m_s$  is likely to depend on circumstances but this relationship is likely to be asymptotic because the potential value of  $\alpha$  is limited by the absolute prey abundance. However, if the time spent ashore depends on the load of milk delivered, this model predicts that time spent ashore should remain constant up to the point at which the maximum sustained metabolic rate

is reached and it should then begin to decline. It also predicts that foraging trip duration should remain constant.

### Model 2: Adjustment of foraging trip duration to compensate for reduced food availability

Mothers may increase the time they spend foraging to compensate for a reduced rate of energy gain. In terms of Equation 3, this represents an increase in  $t_f$  and, by implication, also of  $t_s$ , the total time spent at sea. Therefore, although the total energy gained during a foraging trip may be the same as when the value of  $\alpha$  was greater, the total trip duration is increased. Overall, mothers will deliver less energy to their pups because they are able to make fewer trips during lactation. Consequently, we would expect foraging trip duration to increase as  $\alpha$  declines but that the time spent ashore should be insensitive to  $\alpha$  because mothers will deliver the same amount of energy at each visit.

### Model 3: Optimization of time spent ashore and trip duration

An alternative hypothesis is that mothers adjust both the time spent ashore and the foraging trip duration to maximize the amount of energy delivered to the pup under any circumstances. The optimal time spent ashore ( $t_a^*$ ) is given by the marginal value theorem (Charnov, 1976) such that

$$D'(t_a^*) = \frac{D(t_a^*)}{t_a^* + t_s}; \quad (6)$$

i.e., when the rate at which energy is being delivered to the pup falls to the average rate of expenditure when the animal is not foraging. Therefore, if

$$D'(t_a) = k\beta \exp(-\beta t_a), \quad (7)$$

then, because energy is assumed to be balanced over foraging cycles, it also follows that

$$D'(t_a) = \frac{G(t_s) - m_a t_a}{t_a + t_s}. \quad (8)$$

Optimal conditions will occur to maximize the rate of energy delivery to the pup when

$$k\beta \exp(-\beta t_a^*) - \frac{G(t_s) - m_a t_a^*}{t_a^* + t_s} = 0. \quad (9)$$

Hence, from Equations 2, 3, and 4 we can derive the time spent foraging

$$t_f = \frac{k[1 - \exp(-\beta t_s)] + m_a t_a + m_s t_s}{\alpha - m_s}. \quad (10)$$

Arnould and Boyd (1995b) showed that milk energy content increased with increasing foraging trip duration. I therefore made  $\beta$  vary with foraging trip duration such that  $\beta = t_s^r$  where  $r$  was set to 0.015 and  $0.015 < \beta < 0.090$  based on the lower and upper limits of  $\beta$  in Table 2. Assuming that values of  $k$  and  $\beta$  are known, it is possible to derive  $t_f$  from Equation 9 by iterating  $t_i$  and  $t_a$  for different values of  $\alpha$  that maximize the gross rate of energy gain by the mother given by

$$\frac{\alpha t_f}{t_a + t_s}. \quad (11)$$

Alternatively, it is also possible that net rate of delivery of energy to the pup or the maternal energetic efficiency may be maximized. These are given as the values of

$$\frac{\alpha t_f - m_a t_a - m_s t_s}{t_a + t_s} \quad (12)$$

and

$$\frac{\alpha t_f}{m_s t_s + m_a t_a} \quad (13)$$

that maximize  $D(t_a)$ , respectively.

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### REFERENCES

- Agnew D, 1997. The CCAMLR Ecosystem Monitoring Programme. *Antarct Sci* 9:235–242.
- Arnould JPY, 1995. The energetics of lactation in Antarctic fur seals (*Arctocephalus gazella*) (PhD dissertation). Aberdeen: University of Aberdeen.
- Arnould JPY, Boyd IL, 1995a. Inter- and Intra-annual variation in milk composition in Antarctic fur seals (*Arctocephalus gazella*). *Physiol Zool* 68:1164–1180.
- Arnould JPY, Boyd IL, 1995b. Temporal patterns of milk production in Antarctic fur seals (*Arctocephalus gazella*). *J Zool* 237:1–12.
- Arnould JPY, Boyd IL, Socha DG, 1996a. Milk consumption and growth efficiency in Antarctic fur seal (*Arctocephalus gazella*) pups. *Can J Zool* 74:254–266.
- Arnould JPY, Boyd IL, Speakman JR, 1996b. Measuring the body composition of Antarctic fur seals (*Arctocephalus gazella*): validation of hydrogen isotope dilution. *Physiol Zool* 69:93–116.
- Arnould JPY, Boyd IL, Speakman JR, 1996c. The relationship between foraging behaviour and energy expenditure in Antarctic fur seals. *J Zool* 239:769–782.
- Bonner WN, 1984. Lactation strategies in pinnipeds: problems for a marine mammal group. *Symp Zool Soc Lond* 51:253–272.
- Bonnes DJ, Bowen WD, 1996. The evolution of maternal care in pinnipeds. *Bioscience* 46:645–654.
- Boyd IL, 1996. Temporal scales of foraging in a marine predator. *Ecology* 77:426–434.
- Boyd IL, 1998. Time and energy constraints in pinniped lactation. *Am Nat* 152:717–728.
- Boyd IL, Arnould JPY, Barton T, Croxall JP, 1994. Foraging behaviour of the Antarctic fur seal during periods of contrasting prey abundance. *J Anim Ecol* 63:703–713.
- Boyd IL, Croxall JP, Lunn NJ, Reid K, 1995. Population demography of Antarctic fur seals: the costs of reproduction and implications for life-histories. *J Anim Ecol* 64:505–518.
- Boyd IL, Lunn NJ, Barton T, 1991. Time budgets and foraging characteristics of lactating Antarctic fur seals. *J Anim Ecol* 60:577–592.
- Boyd IL, McCafferty DJ, Reid K, Taylor R, Walker TR, 1998. Dispersal of male and female Antarctic fur seals. *Can J Fish Aquat Sci* 55: 845–852.
- Boyd IL, McCafferty DJ, Walker TR, 1997. Variation in foraging effort by lactating Antarctic fur seals: response to simulated increased foraging costs. *Behav Ecol Sociobiol* 40:135–144.
- Brierley AS, Watkins JL, 1996. Acoustic targets at South Georgia and the South Orkney Islands during a season of krill scarcity. *Mar Ecol Prog Ser* 138:51–61.
- Brierley AS, Watkins JL, Murray AWA, 1997. Krill abundance at South Georgia: acoustic evidence of large interannual variability. *Mar Ecol Prog Ser* 150:87–98.
- Burger AE, Piatt JF, 1990. Flexible time budgets in breeding common murre: buffers against variable prey abundance. *Stud Avian Biol* 14:71–83.
- Butler PJ, Bevan RM, Woakes AJ, Croxall JP, Boyd IL, 1995. The use of data loggers to determine the energetics and physiology of aquatic birds and mammals. *Brazil J Med Biol Res* 28:1307–1317.

- Cairns DK, 1987. Seabirds as indicator of marine food supplies. *Biol Oceanogr* 5:261–271.
- Charnov EL, 1976. Optimal foraging: marginal value theorem. *Theor Popul Biol* 9:129–136.
- Clutton-Brock, TH, 1991. The evolution of parental care. Princeton, New Jersey: Princeton University Press.
- Costa DP, Croxall JP, Duck CD, 1989. Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology* 70:596–606.
- Costa DP, Gentry RL, 1986. Free-ranging energetics of northern fur seals. In: *Fur seals: maternal foraging strategies on land and at sea* (Gentry RL, Kooyman GL, eds). Princeton, New Jersey: Princeton University Press; 79–101.
- Costa DP, Trillmich F, 1988. Mass change and metabolism during the perinatal fast: a comparison between Antarctic (*Arctocephalus gazella*) and Galapagos fur seals (*A. galapagoensis*). *Physiol Zool* 61:160–169.
- Croxall JP, Briggs DR, 1991. Foraging economics and performance of polar and subpolar Atlantic seabirds. *Polar Res* 10:561–578.
- Croxall JP, Everson I, Kooyman GL, Ricketts C, Davis RW, 1985. Fur seal diving behaviour in relation to vertical distribution of krill. *J Anim Ecol* 54:1–8.
- Croxall JP, McCann TS, Prince PA, Rothery P, 1988. Reproductive performance of seabirds and seals at South Georgia and Signy Island, South Orkney Islands, 1976–1987: implication for Southern Ocean monitoring studies. In: *Antarctic ocean and resource variability* (Sahrhage D, ed). Berlin: Springer-Verlag; 261–285.
- Croxall JP, Pilcher MN, 1984. Characteristics of krill *Euphausia superba* eaten by Antarctic fur seals *Arctocephalus gazella* at South Georgia. *Br Ant Surv Bull* 6:117–125.
- Francis J, Boness D, Ochoa-Acuña, 1998. A protracted foraging and attendance cycle in female Juan Fernández fur seals. *Mar Mamm Sci* 14:552–574.
- Gentry RL, 1998. The behavior and ecology of the northern fur seal. Princeton, New Jersey: Princeton University Press.
- Gentry RL, Kooyman G (eds), 1986. *Fur seals: maternal strategies on land and at sea*. Princeton, New Jersey: Princeton University Press.
- Hammond KA, Diamond J, 1997. Maximum sustained energy budgets in humans and animals. *Nature* 386:457–462.
- Harris MP, Wanless S, 1990. Breeding success of British kittiwakes *Rissa tridactyla* in 1986–88: evidence for changing conditions in the northern North Sea. *J Appl Ecol* 27:189–214.
- Hofer H, East ML, 1993. The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. III. Attendance and maternal care. *Anim Behav* 46:575–589.
- Houston AI, 1987. Optimal foraging by parent birds feeding dependent young. *J Theor Biol* 124:251–274.
- Houston AI, 1995. Energetic constraints and foraging efficiency. *Behav Ecol* 6:393–396.
- Houston AI, Carbone C, 1992. The optimal allocation of time during the diving cycle. *Behav Ecol* 3:255–265.
- Houston AI, Thompson WA, Gaston AJ, 1996. The use of a time and energy budget model of a parent bird to investigate limits to fledging mass in the thick-billed murre. *Funct Ecol* 10:432–439.
- Kacelnik A, Cuthill I, 1990. Central place foraging in starlings (*Sturnus vulgaris*): II. Food allocation to chicks. *J Anim Ecol* 59:655–674.
- Kock K-H, Wilhelms S, Everson I, Gröger J, 1994. Variations in the diet composition and feeding intensity of mackerel icefish *Chamsocephalus gunnari* at South Georgia (Antarctic). *Mar Ecol Prog Ser* 108:43–57.
- Kramer DL, 1988. The behavioural ecology of air breathing by aquatic animals. *Can J Zool* 66:89–94.
- Lavigne DM, Innes S, Worthy GAJ, Kovacs KM, Schmitz OJ, Hickie JP, 1986. Metabolic rates of seals and whales. *Can J Zool* 64:279–284.
- Lunn NJ, Boyd IL, Barton T, Croxall JP, 1993. Factors affecting the growth rate and mass at weaning of Antarctic fur seals at Bird Island, South Georgia. *J Mammal* 74:908–919.
- Monaghan P, 1996. Relevance of the behaviour of seabirds to the conservation of marine environments. *Oikos* 77:227–237.
- Monaghan P, Walton P, Wanless S, Uttley JD, Burns MD, 1994. Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding guillemots *Uria aalge*. *Ibis* 136:214–222.
- Montevecchi WA, 1993. Birds as indicators of change in marine prey stocks. In: *Birds as monitors of environmental change* (Furness RW, Greenwood JJD, eds). London, Chapman and Hall; 217–266.
- Murphy EJ, 1995. Spatial structure of the Southern Ocean ecosystem: predator-prey linkages in Southern Ocean food webs. *J Anim Ecol* 64:33–347.
- Oftedal OT, Boness DJ, Tedman RA, 1987. The behavior, physiology, and anatomy of lactation in the pinnipedia. *Curr Mammal* 1:175–245.
- Orians GH, Pearson NE, 1979. On the theory of central-place foraging. In: *Analysis of ecological systems* (Horn DJ, Mitchell RD, Stairs CR, eds). Columbia: Ohio State University Press; 154–177.
- Pennycuik CJ, Croxall JP, Prince PA, 1984. Scaling of foraging radius and growth rate in petrels and albatrosses (Procellariiformes). *Orn Scand* 15:145–154.
- Pierce GJ, Ollason JG, 1987. Eight reasons why optimal foraging theory is a complete waste of time. *Oikos* 49:111–118.
- Prince PA, Harris MP, 1988. Food and feeding ecology of alcid and penguins. *Proc XIX Intl Ornithol Congr* 1195–1204.
- Reid K, Arnould JPY, 1996. The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. *Polar Biol* 16:105–114.
- SAS Institute, 1990. SAS/STAT user's guide, version 6.1, 4th ed. Cary, North Carolina: SAS Institute.
- Schmid-Hempel P, Kacelnik A, Houston AI, 1985. Honeybees maximize efficiency by not filling their crop. *Behav Ecol Sociobiol* 17: 61–66.
- Schmidt-Nielsen K, 1975. *Animal physiology, adaptation and environment*. Cambridge: Cambridge University Press.
- Stephens DW, Krebs JR, 1986. *Foraging theory*. Princeton, New Jersey: Princeton University Press.
- Swift SM, 1980. Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. *J Zool* 190:285–295.
- Trillmich F, 1990. The behavioral ecology of maternal effort in fur seals and sea lions. *Behaviour* 114:3–20.
- Trillmich F, Lechner E, 1986. Milk of the Galapagos fur seal and sea lion, with a comparison of the milk of eared seals. *J Zool* 209:271–277.
- Trillmich F, Ono KA, Costa DP, DeLong RL, Feldkamp SD, Francis JM, Gentry RL, Heath CB, Le Boeuf BJ, Majluf P, York AE, 1991. The effects of El Niño on pinniped populations in the Eastern Pacific. In: *Pinnipeds and El Niño* (Trillmich F, Ono KA, eds). Berlin: Springer-Verlag; 247–270.
- Wanless S, Harris MP, 1992. Activity budgets, diets and breeding success of kittiwakes *Rissa tridactyla* on the Isle of May. *Bird Study* 39: 145–154.
- Wetterer JK, 1989. Central place foraging theory: when load size affects travel time. *Theor Popul Biol* 36:267–280.
- Wright J, Both C, Cotton PA, Bryant D, 1998. Quality versus quantity: energetic and nutritional trade-offs in parental provisioning strategies. *J Anim Ecol* 67:620–634.
- Zarrow MX, Denenberg VM, Anderson CO, 1965. Rabbit: frequency of suckling the pup. *Science* 150:1835–1836.