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## Variation in maternal provisioning by lactating Antarctic fur seals (*Arctocephalus gazella*): response to experimental manipulation in pup demand

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**Abstract** An experiment involving the supplementary feeding of pups was conducted on Antarctic fur seals to investigate the factors influencing maternal foraging-attendance cycles and the differential use of nutritional resources for growth, maintenance and storage by pups. For 40% of the lactation period, male pups were given a supplement mimicking the chemical composition of Antarctic fur seal milk at a dose equivalent to 35% of the normal mass-specific milk energy intake for the species. Milk consumption, body composition and growth rates were monitored during and after the supplementary feeding period and maternal foraging-attendance cycles were monitored throughout lactation. During the supplementary feeding period, treatment pups ( $n=8$ ) grew 32% faster and deposited greater adipose tissue stores than controls ( $n=8$ ) but consumed the same amount of maternal-delivered milk. When supplementary feeding was stopped (timed to coincide with peak maternal milk yield in this species), treatment pups lost mass whereas control group pups continued to grow. Treatment pups weaned at a younger age (109 days) than control pups (116 days) but at the same mass (13 kg). Maternal attendance durations did not differ between the treatment and control groups throughout lactation. However, mothers of treatment pups had significantly shorter foraging trip durations (3.74 days) than mothers of control pups (4.74 days) during the period of supplementary feeding (there were no

significant differences throughout the rest of lactation). These findings are in accordance with predictions of a marginal-value model of fur seal lactation behaviour.

**Keywords** Antarctic fur seal · Maternal investment · Feeding · Growth · Lactation

### Introduction

Animals that provision their offspring from a remote food source are faced with making decisions about how long to spend searching for food before returning to their offspring, how much food to provide the offspring and how long to stay with them (Houston et al. 1996). Parental fitness may be maximised at a level of food delivery to offspring that provides sufficient food for both parental survival and for offspring survival, and there will be an optimum set of decisions that will maximise fitness depending upon circumstances (Schmid-Hempel et al. 1985).

From experiments, we know that parents of some species will vary the decisions they make in relation to variation in food availability (Welham and Ydenberg 1993). This appears to provide parents with the capacity to adjust their time budgets to cope with varying conditions and, up to a point, this behavioural plasticity can buffer reproductive investment against environmental variability. In the Antarctic fur seal (*Arctocephalus gazella*), these types of behavioural adjustment appear to manifest in changes in the relative time spent foraging and subsequently delivering milk to the offspring (Boyd 1999). During periods of relatively low food availability, animals maintain the growth rate of offspring by foraging longer and spending proportionately less time ashore delivering milk to their offspring. Added time spent foraging is offset by reduced time spent with the offspring but the latter represents the period of the maximum potential rate of milk delivery. Female fur seals appear to exploit the non-linearities in the milk delivery curve to maintain offspring growth during periods of low food availability.

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Experimental manipulation of the foraging performance of Antarctic fur seals showed that individuals were able to adapt their foraging behaviour to minimise the impact of higher foraging costs (Boyd et al. 1997). Nevertheless, a potential inability of pups to absorb all the energy mothers are capable of delivering may preclude a greater rate of energy transfer between mother and offspring. Our aim in this study was to change the food delivery function to pups by providing them with additional food when the mother was absent. If the offspring's capacity to absorb food is the factor that limits parental fitness, we expected the provision of additional food to reduce the mothers' need to forage but that it would not affect the growth rate of the offspring, assuming that controls were being fed by mothers with access to normal levels of food. In addition, based upon a marginal-value model of fur seal provisioning behaviour (Boyd 1999), we predicted that additional feeding might alter the rate at which mothers could deliver food during visits to their pups and that this would affect the foraging-time budgets of mothers. In particular, for a given rate of food intake while foraging, we predicted that mothers of pups that were given additional food would likely have shorter foraging trips and that times spent ashore with offspring may also decline, although this second result would depend upon the shape of the energy delivery function while fur seals were ashore.

Therefore, the objectives were to: (1) examine the possibility that an upper limit to offspring growth may be a factor determining the investment patterns of parents and (2) determine if changes in the appetite of pups (which will affect the rate of milk delivery by mothers) can alter maternal foraging time budgets in a predictable way.

## Methods

### Study site and instrumentation

The study was conducted on Bird Island (54°00' S, 38°02' W), South Georgia, during the 1998/1999 austral summer. As sex-based differences in growth patterns have been recorded in Antarctic fur seal pups (Arnould et al. 1996a), with females appearing to maximise energy storage and males growing more lean tissue, we predicted that the effects of supplementary feeding on growth and body composition would be most detectable in male pups. Consequently, to reduce sources of variability, this study was limited to male pups.

During the peak pupping period (1–6 December), 20 mothers with newborn male pups were selected at random. Each female was captured with a noose-pole and held in a restraint-board (Gentry and Holt 1982) while a small VHF transmitter (Sirtrack, Havelock North, New Zealand) was glued to the dorsal fur using quick-setting epoxy (RS Components, Corby, UK). Individual numbered plastic tags (Dalton Jumbo Rototags; Dalton Supplies, Henley-on-Thames, UK) were also inserted into the trailing edge of the fore-flippers.

While the mother was restrained, each pup was numbered on the dorsal fur with commercial hair bleach (Clairol Born Blonde; Bristol-Myers, Ickenham, UK). The mother-pup pair was then released and left to suckle normally. The subsequent foraging trip and attendance durations of the females were monitored for the remainder of the lactation period using an automatic scanning re-

ceiver and data-logger (RX-900E; Televilt Int. AB, Lindesberg, Sweden) located next to the colony. The receiver was programmed to continually scan each frequency for 30 s every 15 min. In addition, throughout the entire study, the presence or absence of a transmitter signal was manually monitored daily and the nursing sites of mother-pup pairs were located visually. Towards the end of the lactation period, several females moulted their transmitter. The presence or absence of these females from the colony was, thereafter, monitored by visual inspection of the colony and the hinterland. Because of the lack of temporal resolution in the visual inspection of the colony (in comparison to radio-telemetry), these females were excluded from the analyses of foraging trip and attendance patterns during the postsupplementation period (see below).

### Experimental protocol

Four pups died (one from starvation and three from trauma injuries) prior to the experimental period and their mothers were removed from the study. At approximately 30 days postpartum, mother-pup pairs were randomly assigned to either the control ( $n=8$ ) or treatment ( $n=8$ ) group. During the next maternal foraging trip, each pup was captured 2 days after the female had departed to sea and weighed on a spring scale ( $\pm 0.1$  kg). After being processed for determination of body composition and milk consumption (see below), treatment group pups were fed a mixture of water, herring oil, casein, whey, and mineral and vitamin additives in proportions mimicking the lipid, protein and mineral contents of Antarctic fur seal milk (40% lipid, 10% protein, 0.7% minerals, 45% water; Arnould and Boyd 1995; Arnould et al. 1996a). The supplement was given by stomach tube in two pulse-doses over consecutive days at a rate corresponding to 35% of the mean normal milk energy intake (i.e. 35% of 7 MJ·kg<sup>-1</sup>·bout<sup>-1</sup>; Arnould et al. 1996a) before the pup was released and allowed to resume normal behavioural activity. The supplement was given during each subsequent maternal absence, 2–3 days after she had departed to sea, for the next 50 days (ca 40% of lactation period). The end of the supplementary feeding period was timed to coincide with the period of peak maternal milk yield for Antarctic fur seals at this colony (Arnould et al. 1996a).

The control group pups were captured, weighed and handled during each maternal absence in the same manner as the treatment pups but no supplement was passed through the stomach tube. After the supplementary feeding period (30–40 days), all pups were weighed during each maternal absence until weaning. The date of weaning was defined as the last day mother and pup were seen together. This method of determining the weaning date is accurate because mothers return and remain ashore for periods of up to 7 days after their pups have left the colony (Lunn et al. 1993). Weaning mass is defined as the last mass recorded prior to the defined weaning date. Individual growth rates both during and after the supplementary feeding period were determined by least-squares regression of mass on age for each pup.

### Body composition and milk consumption

The body composition and milk consumption of both the treatment and control pups were determined using hydrogen isotope dilution techniques (Costa 1987). Immediately prior to the beginning of the supplementary feeding period, each pup was weighed and given an intra-muscular injection (ca 1 ml) of a weighed dose ( $\pm 0.01$  g) of tritiated water (HTO; 200  $\mu$ Ci·ml<sup>-1</sup>). They were kept in an enclosure for 3–4 h before an equilibration blood sample was collected, to determine the total body water pool (TBW) size, and then released. Thereafter, upon each capture and prior to supplementary feeding, each pup was weighed and blood sampled. Approximately 20–25 days after the first injection, having taken the usual blood sample, each pup was given a second injection (ca 1 ml) of weighed HTO (200  $\mu$ Ci·ml<sup>-1</sup>) in order to maintain sufficient circulating levels of isotope and determine changes in TBW. The pups were again kept in an enclosure for the 3- to 4-h equilibration period before blood was sampled and they were re-

leased. Following the last supplementary feed (or sham manipulation for the control group), a final blood sample was collected after the subsequent maternal attendance. A final intra-muscular injection (ca 1 ml) of weighed HTO ( $50 \mu\text{Ci}\cdot\text{ml}^{-1}$ ) was given and a blood sample collected 3–4 h later to again determine changes in TBW.

Blood samples (9 ml) were collected into heparinised syringes by venipuncture of an inter-digital vein in the hind-flipper. All blood samples were kept at  $4^\circ\text{C}$  for several hours before being centrifuged and the plasma fraction separated. Aliquots (2–5 ml) of plasma were stored frozen ( $-20^\circ\text{C}$ ) in plastic vials until analysis. Upon thawing, subsample aliquots of plasma (0.2 ml) were distilled into preweighed scintillation vials following the procedures of Ortiz et al. (1978). The vials were then reweighed, to obtain the mass of the sample water, accurate to 0.1 mg. Scintillant (10 ml Ultima Gold; Canberra Packard, Mt Waverly, Australia) was added to the vials which were then counted for 5 min in a Packard Tri-carb 2100TR liquid scintillation analyser with correction for quenching by means of the sample channels ratio and an external standard to set the counting window for each vial. Samples were analysed in duplicate and each vial was counted twice, with the results averaged in both cases. Subsamples (0.2 g) of the injectant were counted in the same way, and at the same time, as the water from the plasma samples to determine the specific activity of the tritium injected.

TBW was calculated from HTO dilution space, and total body lipid (TBL) was calculated from its relationship with TBW, using equations determined empirically in Antarctic fur seal pups (Arnould et al. 1996b). For each pup, TBW measurements were made only at the beginning, middle and end of the supplementary feeding period. Therefore, the published relationship between TBW and mass (Arnould et al. 1996a) was used to estimate the TBW of pups at times during the supplementary feeding period when it was not measured directly by isotope dilution.

Milk water intake (MWI) was calculated as:

$$\text{MWI}=\text{TWI}-\text{MWP}$$

and

$$\text{MWI}=\text{TWI}-(\text{MWP}+\text{SFW})$$

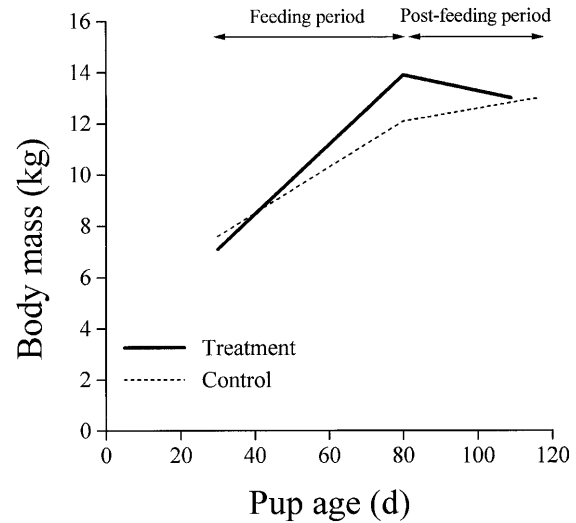
in control and treatment pups, respectively, where TWI is total water influx, MWP is metabolic water production and SFW is supplementary fed water. Metabolic water production was estimated from the published relationships between MWP and age for Antarctic fur seal pups at this colony (Arnould et al. 1996a). Total water influx was calculated from the decrease in specific activity of body water using Nagy and Costa's (1980) Eq. 5 (TBW changing linearly with time) during feeding periods. Milk consumption was calculated as MWI divided by the water content of the milk determined using the regression equations in Arnould and Boyd (1995) for the relationships between milk composition and days postpartum in Antarctic fur seals.

Statistical analyses were performed using the Systat statistical software (Version 7.0.1, SPSS Inc.). The Kolmogorov-Smirnov test was used to determine whether the data were normally distributed and an *F*-test was applied to confirm homogeneity of variances. Differences between linear regressions were tested by ANCOVA after testing for homogeneity of slopes. Unless otherwise stated, data are presented as means $\pm$ 1 SE and results were considered significant at the  $P<0.05$  level (two-tailed).

## Results

### Pup growth rates and weaning

The growth rate of pups during the supplementary feeding period (Fig. 1) was 32% greater in the treatment group ( $113\pm 8 \text{ g}\cdot\text{day}^{-1}$ ) than in the control group



**Fig. 1** Average growth curves for treatment ( $n=8$ ) and control ( $n=8$ ) group pups during and after the supplementary feeding period

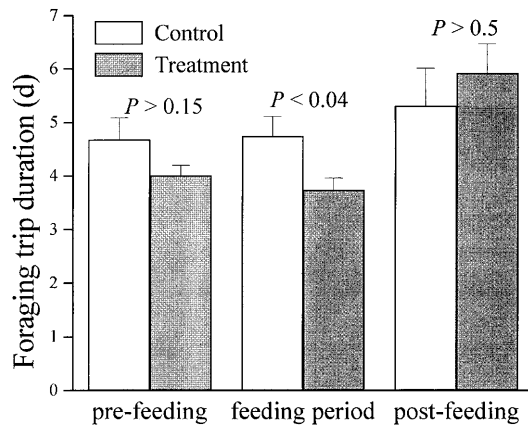
**Table 1** Growth rate, body composition, milk consumption, weaning age and weaning mass of Antarctic fur seal treatment (supplementary fed) and control pups

	Treatment pups	Control pups	$t_{14}$	$P$
Growth rate ( $\text{g}\cdot\text{day}^{-1}$ ), feeding period	$113\pm 8$	$85\pm 8$	2.51	$<0.03$
Growth rate ( $\text{g}\cdot\text{day}^{-1}$ ), postfeeding period	$-18\pm 11$	$52\pm 22$	2.82	$<0.02$
Milk consumption ( $\text{g}\cdot\text{day}^{-1}$ )	$427\pm 85$	$352\pm 85$	0.62	$>0.5$
Mass-specific milk consumption ( $\text{g}\cdot\text{day}^{-1}\cdot\text{kg}^{-1}$ )	$18.0\pm 1.2$	$23.2\pm 1.1$	3.23	$<0.01$
Per bout milk consumption ( $\text{g}\cdot\text{bout}^{-1}$ )	$2,694\pm 287$	$3,650\pm 361$	2.07	$<0.06$
Total body lipid (%), start of feeding period	$11.6\pm 1.3$	$13.4\pm 1.6$	0.80	$>0.4$
Total body lipid (%), end of feeding period	$21.6\pm 1.2$	$17.6\pm 0.7$	2.80	$<0.02$
Weaning age (days)	$109\pm 1.8$	$116\pm 2.4$	2.17	$<0.05$
Weaning mass (kg)	$13.7\pm 1.0$	$12.3\pm 0.4$	1.22	$>0.2$

( $85\pm 8 \text{ g}\cdot\text{day}^{-1}$ ;  $t_{14}=2.51$ ,  $P<0.03$ ) indicating the level of supplementary nutrition (35%) had a proportional effect on growth. Following the supplementary feeding period, most treatment pups lost mass ( $-18\pm 11 \text{ g}\cdot\text{day}^{-1}$ ) whereas control pups either continued to gain or maintained their mass ( $52\pm 22 \text{ g}\cdot\text{day}^{-1}$ ;  $t_{14}=2.82$ ,  $P<0.02$ ). Treatment pups weaned at a significantly younger age ( $109\pm 1.8$  days) than control pups ( $116\pm 2.4$  days;  $t_{14}=2.17$ ,  $P<0.05$ ; Table 1). Weaning mass, however, did not differ significantly between the two groups (combined:  $13.0\pm 0.7 \text{ kg}$ ;  $t_{14}=1.23$ ,  $P>0.2$ ).

### Milk consumption and body composition

Milk consumption was measured for an average of  $6.9\pm 0.3$  (range 5–9) maternal attendance visits for each



**Fig. 2** Foraging trip durations of mothers of treatment ( $n=8$ ) and control ( $n=8$ ) group pups before, during and after the supplementary feeding period

pup during the supplementary feeding period. Mean daily milk consumption ranged between 166–859 g·day<sup>-1</sup>, and there was no significant difference between the treatment and control groups (combined: 390±59 g·day<sup>-1</sup>;  $t_{14}=0.62$ ,  $P>0.5$ ). Due to their larger size, however, mean daily mass-specific milk consumption was significantly lower in the treatment group (18.0±1.2 g·day<sup>-1</sup>·kg<sup>-1</sup>) than in the control group (23.2±1.1 g·day<sup>-1</sup>·kg<sup>-1</sup>;  $t_{14}=3.23$ ,  $P<0.01$ ). There were no significant relationships between maternal foraging trip duration and per bout or daily milk consumption in either the treatment or control groups ( $P>0.2$  in all cases). The difference in per bout milk consumption between treatment (2,694±287 g·bout<sup>-1</sup>) and control (3,650±361 g·bout<sup>-1</sup>) pups, however, approached significance ( $t_{14}=2.07$ ,  $P<0.06$ ).

Total body lipid reserves (%) did not differ significantly between the groups at the beginning of the supplementary feeding period (combined: 12.5±1.4%;  $t_{14}=0.80$ ,  $P>0.4$ ). By the end of the period, however, the treatment pups, in addition to experiencing greater increases in lean body mass (3.97±0.33 kg) than control group pups (2.93±0.35 kg;  $t_{14}=2.14$ ,  $P<0.05$ ), had acquired significantly greater body lipid reserves (21.6±1.2%) than control group pups (17.6±0.7%;  $t_{14}=2.80$ ,  $P<0.02$ ).

#### Maternal foraging trip and attendance durations

Maternal foraging trip durations (Fig. 2) prior to the supplementary feeding period did not differ significantly between the two groups (combined: 4.34±0.30 days;  $t_{14}=1.49$ ,  $P>0.15$ ). During the period of supplementation, however, the mothers of treatment pups made significantly shorter foraging trips (3.74±0.22 days) than the mothers of controls (4.74±0.38 days;  $t_{14}=2.28$ ,  $P<0.04$ ). Following the feeding period, there was again no significant difference in foraging trip durations between the two groups (combined: 5.63±0.65 days;  $t_9=0.70$ ,  $P>0.5$ ).

Maternal attendance durations did not differ between the two groups during the prefeeding period (combined:

1.60±0.18 days;  $t_{14}=2.10$ ,  $P>0.05$ ), feeding period (combined: 2.16±0.09 days;  $t_{14}=0.94$ ,  $P>0.3$ ) or postfeeding period (combined: 2.06±0.12,  $t_9=1.01$ ,  $P>0.3$ ).

## Discussion

### Response of pups to supplementary feeding

During the supplementary feeding period, the treatment pups consumed milk at the same daily rate as the control group and grew faster in proportion to the level of supplementation. This indicates that Antarctic fur seal pups are able to assimilate nutrients in excess of what is provided by the mother during mid-lactation (i.e. the period of increasing milk yield). However, the fact that the per bout milk consumption in treatment pups was lower (approaching significance) than in the control group suggests that the supplementary feeding may have reduced pup appetite to some degree.

We had expected that a potential response to supplementary feeding by pups might have been to use the additional nutrition for metabolic energy during increased levels of activity, leading to faster behavioural development. While no activity data were collected, the increase in growth rate in proportion to the level of supplementation suggests that the treatment group pups did not expend significantly greater amounts of energy than the control group. It would be of interest, however, for future studies to investigate in detail the behaviour of supplementary-fed pups to assess the effect of additional nutrition on the development of their swimming and diving capabilities and, thus, their ability to cope with nutritional independence.

Sex-based differences in pup body composition have been recorded in Antarctic fur seals (Arnould et al. 1996a) and northern fur seals (*Callorhinus ursinus*; Donohue 1998, M.J. Donohue, unpublished data), with female pups depositing greater adipose stores than males. Arnould et al. (1996a) suggested that, in highly sexually dimorphic polygynous species such as fur seals, selection might favour rapid structural growth in young male infants, as large size confers an advantage in male-male interactions during the breeding season and, hence, an increase in reproductive success (McCann 1980). In contrast, female reproductive success is less determined by size (Lunn and Boyd 1993a, 1993b) and selection would not necessarily favour rapid structural growth. Supplementary-fed male pups, therefore, might be expected to direct the extra nutrition into lean body mass growth to maximise their future reproductive potential. The results of this study support this hypothesis. However, in addition to an increase in the rate of lean body mass growth, the treatment pups also deposited larger body lipid reserves than the control group, suggesting that there may be an upper limit to the rate of structural growth. Several studies of mammal and bird species have shown the maximal rate of structural growth to be restricted by genetically determined physiological constraints (Taylor 1990; Owens et al. 1993; Ricklefs et al.

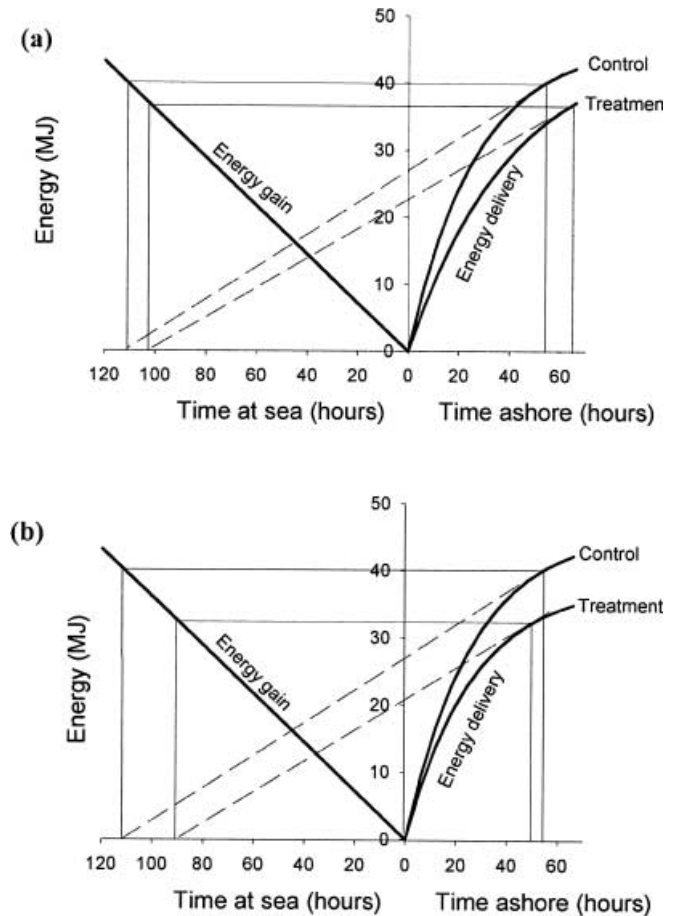
1994; Short et al. 1999; Knap and Jorgensen 2000). Thus, within the normal range of maternal provisioning, male Antarctic fur seal pups are probably close to their upper limit of structural growth rate.

The end of supplementary feeding coincided with the timing of peak maternal milk yield for the species (ca 80 days postpartum; Arnould et al. 1996a). Following the period of supplementation, all pups in the treatment group lost mass. This indicates that, during the phase of decreasing milk yield in late lactation (after the supplementary feeding period), maternal provisioning was insufficient for the larger treatment pups at a time when the control pups maintained mass or continued to grow. Consequently, in accordance with the suggestion of Martin (1984) that weaning will occur when the rate of maternal delivery ceases to meet offspring demand, the treatment pups weaned at a younger age than the control group. Alternatively, supplemental feeding of the treatment pups may indeed have led to accelerated behavioural development so that pups were able to cope with full independence earlier. Interestingly, despite weaning earlier, treatment pups did so at the same mass as control pups. While no body composition data were obtained prior to weaning, the mass lost by treatment pups following the end of the supplementation period is likely to have been largely derived from lipid reserves (Rea et al. 2000; Arnould et al., in press). This suggests there may be an optimum weaning mass and that, during the decreasing phase of the lactation period, pups make the decision to leave the natal colony based on recent provisioning history in conjunction with some intrinsic assessment of their body condition.

#### Maternal response to supplementary feeding of pups

This study was conducted in a year of normal food availability (as evidenced by pup growth rates and the reproductive success of several seabird species in comparison to other years; British Antarctic Survey, unpubl. data), so the capacity of nursing females to deliver milk was unlikely to have been limited by adverse foraging conditions. Consequently, a corollary to supplementary-fed pups having faster growth rates (and the ability to assimilate resources at levels greater than mothers provide) is that under normal conditions, Antarctic fur seal females may be provisioning pups at their maximal possible rates.

During the supplementary feeding period, mothers of treatment pups reduced their foraging trip durations in line with predictions from a marginal-value model of fur seal lactation behaviour (Boyd 1999; Fig. 3). In this model, we assumed that the rate of energy gain by females was the same for the control and treatment groups because both were foraging in the same water mass adjacent to the study site. If, on average, mothers balance their energy reserves amongst foraging cycles, which seems most probable, then we expected the rate of energy transfer to the pup to be altered by the supplementary feeding. In the case that this rate was reduced (perhaps due to a lower sucking rate as a result of a reduction in



**Fig. 3** Cartoon diagrams of the marginal-value model of female fur seal foraging behaviour during lactation. These were based upon the model proposed by Boyd (1999). Two cases of changes in the energy delivery function are illustrated. The energy delivery function in this example takes the form  $E=k(1-e^{-\beta t})$ , where  $E$  is the energy delivered,  $k$  is the asymptotic amount of energy that can be delivered,  $\beta$  is the rate of energy transfer, and  $t$  is the time in hours that the mother has been ashore with the pup. We assumed either that the supplementary feeding of the treatment group caused a reduction in  $\beta$  (a) or that it caused a reduction in  $k$  (b). The energy and time budgets illustrated here are representative of the real budgets of lactating Antarctic fur seals. Energy gain and delivery functions are shown as *bold lines*, tangents of the marginal-value model are shown as *dashed lines*, and the lines connecting equality of energy gain and energy delivery (representing a balanced energy budget) and showing the optimal times to spend ashore and at sea in order to achieve the maximum rate of energy delivery to the pup are both shown as *thin solid lines*.

the appetite of the pup), then we predicted that the optimal time budget for females would be a shorter foraging trip duration and longer period spent ashore (Fig. 3a). This would not necessarily have led to an overall reduction in the average amount of milk delivered to the offspring but it would have led to less milk being delivered after more, but shorter, individual foraging trips.

In the case that the asymptotic amount of energy delivered to pups by mothers was reduced, then the model predicted that mothers would also reduce their foraging trip durations but that the time spent ashore with the pup would decline slightly or remain the same as in the control

group (Fig. 3b). This result is closest to our observations in the present study and may suggest that the supplementary feeding affected the total potential amount of milk that the mother could have delivered to the pup, rather than the rate of milk transfer, as a result of a change in the appetite of the pups. Indeed, this scenario is supported by the tendency of treatment pups to consume less milk per maternal attendance bout compared with control pups. As with Fig. 3a, such a response would not necessarily lead to an overall reduction in the average rate of milk delivery to the offspring but, rather, to less milk being delivered after more, but shorter, individual foraging trips. The results of this study, therefore, suggest that the mother's foraging behaviour is determined by a combination of the richness of the food supply (Boyd 1999) and also by the quality and behaviour (demand) of the pup.

## Conclusions

Our study has shown that male Antarctic fur seal pups are able to assimilate nutrition in excess of what is provided by their mother but suggests that, under normal conditions, their structural growth rates are close to maximal limits and additional nutrition is directed mostly into adipose stores. This ability of pups to assimilate additional resources suggests that maternal investment patterns are not limited by offspring demand. However, the results also suggest that pup appetite may be influencing maternal foraging time budgets by limiting the total amount of milk mothers can deliver per shore visit. This is consistent with studies in other fur seal species which have found that maternal foraging trip durations increase with pup age and, thus, sucking ability and stomach capacity (Gentry and Kooyman 1986; Arnould and Hindell 2001). Importantly, in accordance with marginal-value model predictions, the results of this study show that, within normal food availability conditions, these alterations to maternal foraging time budgets do not alter the overall delivery of nutrition to the offspring.

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