The relationship between foraging behaviour and energy expenditure in Antarctic fur seals

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By using time-depth recorders to measure diving activity and the doubly-labelled water method to determine energy expenditure, the relationship between foraging behaviour and energy expenditure was investigated in nine Antarctic fur seal females rearing pups. At-sea metabolic rate (MR) (mean of 6.34 ± 0.4 W·kg⁻¹; 4.6 times predicted BMR) was positively correlated to foraging trip duration (mean of 4.21 ± 0.54 days; r² = 0.5, P < 0.04). There were no relationships between MR and the total number of dives, the total time spent diving or the total vertical distance travelled during the foraging trip. There was, however, a close negative sigmoidal relationship (r² = 0.93) between at-sea MR and the proportion of time at sea spent diving. This measure of diving behaviour may provide a useful, inexpensive means of estimating foraging energy expenditure in this species and possibly in other otariids. The rate of diving (m·h⁻¹) was also negatively related to at-sea MR (r² = 0.69, P < 0.005). Body mass gain during a foraging trip had a positive relationship to the time spent at sea (r² = 0.58, P < 0.02) and the total amount of energy expended while at sea (r² = 0.72, P < 0.004) such that, while females undertaking long trips have higher metabolic rates, the energetic efficiency with which females gain mass is independent of the time spent at sea. Therefore, within the range of conditions observed, there is no apparent energetic advantage for females in undertaking foraging trips of any particular duration.

Introduction

To satisfy the energetic cost of milk production, maternal food consumption must be increased prior to, and/or during, lactation (Sadleir, 1984). During lactation, however, maternal foraging activities may be hindered by the offspring: when foraging in the company of their offspring, females have to spend more time being vigilant, and/or consume food of lower quality, in areas of reduced danger from predators (Sadleir, 1969; Carl & Robbins, 1988); when foraging alone, females are restricted in their foraging range by the fasting ability of the offspring and/or the amount of resources they can carry (Broekhuizen & Maaskamp, 1980; Sadleir, 1984; Gittleman, 1988; Gittleman & Thompson, 1988). Maternal foraging efficiency (amount of energy consumed per unit of energy expended while acquiring it) will therefore influence the rate at which the mother can deliver resources to her offspring (Sadleir, 1984). This, in turn, will affect the growth rates of the dependent offspring and the overall cost to the mother of successfully rearing them (Gittleman & Thompson, 1988). Foraging activity in relation to provisioning rates is therefore of
major interest and has been the focus of numerous studies (e.g. Sadleir, 1982; Gittleman, 1988; Allaye Chan-McLeod, White & Holleman, 1994).

Obtaining accurate measurements of energy expenditure under field conditions is complicated, involving the use of labelled isotope techniques (Lifson & McClintock, 1966; Nagy, 1980; Speakman & Racey, 1988) or the recording of heart rates (e.g. Butler et al., 1992; Boyd et al., 1995b; Woakes, Butler & Bevan, 1995). Consequently, many studies have relied instead on measurements of behaviour and activity-specific energy expenditure (time–energy budgets) to obtain estimates of free-ranging energy expenditure (Weathers et al., 1984; Bennett, 1986; Nagy, 1989). In the study of seals (Pinnipedia), diving behaviour has been examined with the use of time-depth recorders (TDRs; Gentry & Kooyman, 1986; Boyd & Croxall, 1992) to provide indices of foraging effort (e.g. Croxall et al., 1985; Feldkamp, De Long & Antonelis, 1989; Testa, Hill & Siniff, 1989; Boyd et al., 1994). Whereas energy expenditure has been measured in several seal species (Costa & Gentry, 1986; Costa et al., 1989, 1991; Reilly, 1991; Lydersen & Hammill, 1993), the relationship between diving behaviour and energy expenditure has received little attention (Butler et al., 1995). The ability to estimate foraging energy expenditure in seals from behavioural information is therefore limited.

During lactation, fur seals and sea lions (Pinnipedia: Otariidae) alternate between short nursing periods ashore and regular foraging trips to sea (Bonner, 1984). Studies of Antarctic fur seal (Arctocephalus gazella) maternal attendance patterns have shown that some females consistently undertake long trips (6–8 days), whereas others regularly make short trips (2–4 days) (Boyd, Lunn & Barton, 1991; Lunn et al., 1993). Boyd et al. (1991) found that females making short foraging trips had a higher dive rate (metres dived per unit time) than those making longer trips and suggested that as a result their rate of energy expenditure might be higher than that of long-trip females. Therefore, it might be predicted that females regularly undertaking long foraging trips would expend less energy throughout lactation than those making short trips. Such differences might have important implications for the overall cost of pup-rearing and inter-individual variation in reproductive success (Clutton-Brock, Guinness & Albon, 1983; Clutton-Brock, 1988). The foraging energy expenditure of Antarctic fur seals has previously been examined in years of contrasting prey availability by Costa et al. (1989) but no data are available on how it varies in relation to the range of foraging behaviours observed between individuals in years of normal food abundance.

The aims of this study were: (1) to investigate the relationships between diving behaviour and energy expenditure in Antarctic fur seals and (2) to assess whether there are differences in the energetic costs, and efficiency, between the various foraging strategies they employ.

Methods

Study site and animals

The study was conducted at Bird Island (54°00′S, 38°02′W), South Georgia, during two consecutive lactation periods (austral summers of 1991/92 and 1992/93). Hereafter, the year of sampling refers to the year in which the summer began (i.e. year 1991 equals summer 1991/92). All study animals were mothers of known-age pups selected at random throughout the lactation period from a group of 300 animals that had been observed to give birth between 1 and 6 December. One of the study animals had previously been used in Costa et al.’s (1989) study of Antarctic fur seal field metabolic rates in 1983 and 1984.
Foraging behaviour and trip duration

All seals were captured by standard noose-pole and restraint board techniques (Gentry & Holt, 1982). Upon initial capture, females were weighed with a spring scale (100 ± 0.5 kg) and straight-line length was measured to the nearest centimetre with a tape measure. Each animal was fitted with a small (40 g, 2 × 2 × 7 cm) 165 MHz radio-transmitter (Advanced Telemetry Systems Inc., Minnesota, USA) and a Wildlife Computers MKIII time-depth recorder (TDR) (Wildlife Computers, Woodinville, WA, USA) on the dorsal surface. The transmitter was glued directly to the fur while the TDR was clasped by nylon cables to a strip of nylon webbing (width 2 cm) which was in turn glued to the dorsal fur by quick-setting epoxy glue. Foraging trip duration and attendance were monitored by automatic receiving stations at the colony linked to computer data-loggers (Boyd et al., 1991). Each animal was recaptured and weighed at the end of one foraging trip and the instruments were removed.

The TDRs were programmed to sample at 10 s intervals when the animals were at sea. Diving behaviour was analysed with the Wildlife Computers Dive-analysis software and only dives > 2 m were considered. The total number of dives, number of divers per hour at sea, the total time spent diving (time submerged to a depth > 2 m), the proportion of time at sea spent diving, the total vertical distance travelled whilst diving and the vertical distance travelled per hour at sea were recorded for each individual.

Energy expenditure

Energy expenditure was measured by the doubly labelled water (DLW) method (Lifson & McClintock, 1966; Nagy, 1980; Speakman, 1993). Upon capture, an initial blood sample (5 ml) was collected into a heparinized syringe in order to determine the background levels of the injected isotopes. All blood samples were collected by venipuncture of an interdigital vein in a hind flipper. Each animal was then given an oral dose, by stomach tube, of 60–70 ml H_2^{18}O 10% AP (Isotec Inc., Miamisburg, OH, USA) and a 2 ml intramuscular injection of a weighed dose (± 0.0 g) of tritiated water (HTO; 200 μCi. ml⁻¹). Each animal was kept in an enclosure for 6 h, during which it was fitted with the TDR and transmitter. A second blood sample (5 ml) was then collected before the animal was released. The time required for isotope equilibration had previously been determined, by serial blood sampling of individuals, to be less than 2 and 4 h for intramuscular (Costa, 1987; Arnould, Boyd & Speakman, 1996) and oral dosing (Fig. 1), respectively.

Females were recaptured when they next returned from a foraging trip and weighed, and a third blood sample (5 ml) was collected. All blood samples were stored at 4 °C for several hours before being centrifuged and the plasma fraction separated. For HTO analysis, sub-samples (1–2 ml) of plasma were stored frozen (−20 °C) in plastic vials until analysed in November 1993. For H_2^{18}O analysis, aliquots (25–50 μl) of plasma were stored in flame-sealed capillary tubes until analysis in January 1995.

To measure the specific activity of tritium in plasma, samples were thawed and 0.2 ml sub-samples were distilled into pre-weighed scintillation vials following the procedures of Ortiz, Costa & Le Boeuf (1978). The vials were then re-weighed to obtain the mass of the water sample, accurate to 0.1 mg. Scintillant (10 ml Ultima Gold; Canberra Packard, Brook House, Pangbourne, Berkshire, UK) was added to the vials which were then counted for 10 min in a Beckman LA1701 scintillation counter 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. Sub-samples (0.2 ml) of the injectant were counted in the same way, and at the same time, as the water from the plasma samples, in order to determine the specific activity of the tritium injected.

For ^18 oxygen analysis, a modified version of the pasteur pipette method of Nagy (1983) was used to vacuum-distil water from 100 μl plasma samples. This differed from the original protocol only in that the sample was frozen under liquid nitrogen whilst the pipette was evacuated. The ^18 oxygen content of the derived water samples was evaluated by using a small sample equilibration technique. Briefly, approximately 20 μl of the water sample was pipetted into the base of a pre-weighed (±0.0001 g) 5 ml vacutainer which had
its rubber cap removed. The vacutainer was re-weighed to obtain the mass of the water sample and then recapped. The water samples in the vacutainer was frozen under liquid nitrogen and the air above it removed with a small-gauge needle attached to a vacuum pump. The vacutainer was then allowed to return to room temperature before 4ml of pure, previously isotopically characterized, carbon dioxide was drawn from a tank of gas and introduced into the vacutainer with a gas-tight Hamilton syringe. Two vacutainers were prepared in this way from each water sample.

Each vacutainer was incubated at 60°C for 24 h to allow the oxygen in the water to come to isotopic exchange equilibrium with the CO₂ in the vacutainers. Thereafter the vacutainers were frozen, using an acetone-dry ice trap, to retain the water and the CO₂ was drawn off under vacuum and subdivided between two separate breakseals. Each plasma sample thus generated 4 separate breakseal samples. The samples were admitted directly to the inlet of a gas source isotope ratio mass spectrometer (Optima, VG Instruments) and run in comparison to a known working standard. Delta values were normalized to the SMOW/SLAP scale and were converted to ppm units using the absolute ratio of 0.0020052 for SMOW. This gas preparation and analysis procedure has been previously validated in comparison to other methods and found to provide accurate and precise results over a wide range of isotope enrichments (Speakman et al., 1990; Roberts et al., 1995).

Because the H₂¹⁸O was administered orally, we were not confident that the animals would receive an accurately measured dose and, hence, oxygen dilution space could not be determined. Total body water (TBW) was, therefore, calculated from the relationship between TBW and tritium dilution space by using the equation:

\[
\text{TBW(kg)} = 0.11 + 0.97 \cdot \text{HTO space(kg)}
\]

determined empirically by Arnould et al. (1996) in Antarctic fur seals. Total body water at the end of the study period was calculated by multiplying the fractional water content at the beginning of the study by body mass upon recapture.
Carbon dioxide production can be calculated from DLW measurements by means of several different standard equations available in the literature (Lifson & McClintock, 1966; Coward & Prentice, 1985; Schoeller et al., 1986; Speakman, 1993; Speakman, Nair & Goran, 1993). In a study comparing estimates of California sea lion (Zalophus californianus) CO₂ production determined through various equations, Boyd et al. (1995b) found that Speakman et al.'s (1993) equation (R1) provided the estimate closest to that measured by respirometry. Hence, CO₂ production rates calculated by using this equation, accounting for any changes in TBW, are presented for the animals in the present study.

A constant of 25.2 J · ml⁻¹ was used to convert CO₂ production to energy expenditure (Costa, 1987). This was calculated from the average Antarctic fur seal diet and the calorific value of its chemical components (Clarke, 1980; Croxall & Pilcher, 1984; Reid & Arnould, 1996). Time ashore was calculated as the difference between the duration of the energy expenditure measurement and the time at sea (determined by radiotelemetry). At-sea metabolic rate (MR, W · kg⁻¹) was then calculated for each animal by solving the equation given by Costa et al. (1989):

\[
\text{Measured } MR = [(\text{Ashore MR}) \cdot (\text{Proportion of time ashore})] + [(\text{At-sea MR}) \cdot (\text{Proportion of time at sea})],
\]

assuming the metabolic rate while ashore to be 4.96 W · kg⁻¹, the rate reported for Antarctic fur seal females ashore during the perinatal fast (Costa & Trillmich, 1988).

Statistical analyses followed methods outlined in Sokal & Rohlf (1981) and Zar (1984) using Unistat® Statistical Package (Version 4.5, Unistat Limited, London, UK). The Kolmogorov-Smirnov test was used to determine whether data were normally distributed and an F-test was used to confirm homogeneity of variances. Unless otherwise stated, data are presented as means ±1 S.E. and results were considered to be significant at the \( P < 0.05 \) level.

Results

In total, 14 animals were instrumented and dosed with DLW (six in 1991 and eight in 1992) but upon recapture isotope levels were too close to background to determine CO₂ production in five of the seals (four in 1991 and one in 1992). These animals were excluded from further analyses. The body mass, TBW, isotope clearance and CO₂ production rates for the remaining individuals are presented in Table I. Body mass change, metabolic rate, and diving behaviour are presented in Table II.

The mean at-sea MR was 6.34 ± 0.5 W · kg⁻¹ \((n = 9)\) recorded for a mean foraging trip duration of 4.21 ± 0.54 days. At-sea MR, however, was positively correlated with foraging trip duration \((r^2 = 0.5, P < 0.04; \text{Fig. 2a})\). There was a positive relationship approaching significance \((r^2 = 0.36, P = 0.09)\) between at-sea MR and the total number of dives \((1222 ± 103)\) made during the foraging trip. The total time spent diving \((18.8 ± 1.3 \text{ h})\) and the total vertical distance travelled \((46.1 ± 0.51 \text{ km})\) during the foraging trip were not related to at-sea MR \((P > 0.5 \text{ in both cases})\). The proportion of time at sea spent diving \((20.4 ± 1.9\%)\) was negatively correlated to at-sea MR \((r^2 = 0.76, P < 0.001)\). This relationship was found to approximate a sigmoid curve with the equation:

\[
\text{MR}_s = \frac{3.23}{(1 + e^{0.75 \cdot (x-16.71)})} + 5.26 \quad r^2 = 0.93
\]

(Fig. 2b) where \(x\) is the proportion of time at sea spent diving (%) and \(\text{MR}_s = \text{At-sea MR} \ (\text{W} \cdot \text{kg}^{-1})\). At-sea MR was also negatively related to the rate of diving \((469.4 ± 34.5 \text{ m} \cdot \text{h}^{-1})\) during the foraging trip \((r^2 = 0.69, P < 0.005, \text{Fig. 2c})\). There was also a negative relationship between the number of dives made per hour at sea \((13.0 ± 1.0 \text{ dives} \cdot \text{h}^{-1})\) and at-sea MR, which approached significance \((r^2 = 0.41, P = 0.061)\).
<table>
<thead>
<tr>
<th>Seal</th>
<th>TBW (%)</th>
<th>Body mass (kg)</th>
<th>Study interval (days)</th>
<th>Time at sea (%)</th>
<th>k_i (h⁻¹)</th>
<th>k_o (h⁻¹)</th>
<th>k_o/k_i</th>
<th>CO₂ production (ml·min⁻¹·kg⁻¹)</th>
<th>Metabolic rate (W·kg⁻¹)</th>
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TABLE 1
Percentage TBW, body mass, measurement interval, percentage time at sea, tritium and 18O clearance rates (k_i and k_o, respectively), CO₂ production rates and metabolic rate of Antarctic fur seal females fitted with TDRs.
Table II

Foraging trip duration, body mass change, at-sea metabolic rate (MR) and diving behaviour of Antarctic fur seal females

<table>
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<tr>
<th>Seal</th>
<th>Mass change (kg)</th>
<th>Time at sea (days)</th>
<th>At-sea MR (W·kg⁻¹)</th>
<th>Multiples of predicted BMR</th>
<th>Number of dives</th>
<th>Diving time (h)</th>
<th>Depth travelled (m)</th>
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<td></td>
<td></td>
<td></td>
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*BMR = 3.39·M⁰.75 W, where M is body mass in kg (Kleiber, 1975); 'a' seal number 434 of Costa et al.'s (1989) study.
Fig. 2. The relationships between at-sea metabolic rate and (a) time spent at sea, (b) proportion of time at sea spent diving (with fitted sigmoid curve, see text for equation) and (c) the rate of diving (m·h⁻¹) in lactating Antarctic fur seal females.
The amount of mass gained while at sea (1.39 ± 0.51 kg) was positively correlated to the duration of the foraging trip ($r^2 = 0.58$, $P < 0.02$, Fig. 3a). Body mass gain was also positively related ($r^2 = 0.72$, $P < 0.004$) to the total amount of energy expended while at sea (89.7 ± 17.6 MJ, Fig. 3b). In order to compare foraging efficiency between individual seals, therefore, a mass gain efficiency index (g · MJ$^{-1}$) was calculated by dividing the total mass gained during a foraging trip with the total amount of energy expended during the trip. This index varied substantially between individuals (12.1 ± 4.5 g · MJ$^{-1}$, CV = 110%) but was not related to body mass ($P > 0.5$) or the amount of time spent at sea ($P > 0.4$), the latter indicating that there is no apparent advantage for females in following any particular pattern of foraging trip duration.

Discussion

Sources of error

When using TDRs to study the diving behaviour of marine vertebrates, selecting an appropriate sampling frequency can have important effects on the results. Boyd (1993) showed, in one Antarctic fur seal, that the proportion of actual dives recorded decreased in a sigmoid fashion with increasing sampling interval. In comparison to a 5-s sampling interval, sampling of every 10 s underestimated the total number of dives by 14% and overestimated dive duration by 16% (Boyd, 1993). In the present study, to be certain that there would be sufficient TDR memory to collect diving behaviour data for the entire foraging trip, a sampling interval of 10 s was used. It is possible, therefore, that the total number of dives recorded for each individual in the present study is an underestimate. However, as this error would apply to all individuals, it should not affect the shape of the observed relationships between diving behaviour and energy expenditure, only their elevations.

The attachment of instruments (radio transmitters, time-depth recorders, etc.) to the body surface of marine animals increases drag while swimming and, hence, potentially also the total
energy that must be expended during travelling and foraging (Feldkamp, 1987). Several studies have shown that devices representing 2–8% of the body cross-sectional surface area can increase foraging trip durations in free-ranging animals (Wilson, Grant & Duffy, 1986; B. G. Walker & P. L. Boveng, pers. comm.). However, in the present study, the attached devices represented only <1% of the body cross-sectional surface area of Antarctic fur seal females. Using similar devices, Boyd et al. (1991) found no difference in foraging trip duration between instrumented and non-instrumented animals. Furthermore, Costa & Gentry (1986), also using similar-sized devices, found no difference in metabolic rate between northern fur seals (Callorhinus ursinus) that were carrying instruments and those that were not. None the less, it is expected that the devices used in the present study would have had some minor cumulative effect and, while possibly not influencing metabolic rate, may have increased the total amount of energy expended during the foraging trip by increasing the time spent at sea (B. G. Walker & P. L. Boveng, pers. comm.).

The use of the DLW method for measuring energy expenditure is widespread and the errors involved in this technique have been discussed in great detail by several authors (Lifson & McClintock, 1966; Nagy, 1980; Schoeller et al., 1986; Speakman, 1993; Speakman et al., 1993). Most studies validating the technique have been conducted on small animals (<5 kg) and have found that DLW estimates of mean energy expenditure were within ±5% of that measured by direct calorimetry or respirometry. Costa (1987) measured the energy expenditure of a single subadult male northern fur seal by both DLW and material balance methods and found a difference of only 3.3% between the results of each method. Similarly, Boyd et al. (1995b) recently found no significant difference between DLW and respirometry estimates of energy expenditure in six captive, exercising California sea lions of similar size to the animals in the present study. However, Boyd et al. (1995b) found considerable individual variation in the difference between the two methods and cautioned that DLW may in some circumstances overestimate energy expenditure in pinnipeds. None the less, if DLW overestimated the metabolic rates of Antarctic fur seals in the present study, the shape of the observed relationships between energy expenditure and diving behaviour would not be altered unless the overestimation was also a function of behaviour.

Comparison with previous studies

Mean foraging trip duration was similar to that previously reported for Antarctic fur seals in years of normal food availability (Doidge, McCann & Croxall, 1986; Boyd et al., 1991). Likewise, diving behaviour (number of dives, proportion of time spent diving, metres dived, and rate of diving) was similar to that previously reported for the species (Croxall et al., 1985; Boyd et al., 1991).

At-sea MR (6.34 W·kg⁻¹) was 4.66 times the predicted basal metabolic rate (BMR; estimated from Kleiber, 1975). This is considerably lower (by 35%) than the 9.8 W·kg⁻¹ (6.7 times predicted BMR) observed in the same species by Costa et al. (1989). Some of this discrepancy may be accounted for by the fact that Costa et al. (1989) used the Lifson & McClintock (1966) equations (modified by Nagy, 1980) for calculating CO₂ production, which Boyd et al. (1995b) found to overestimate by 7% the result obtained by using the equation employed in the present study. Indeed, recalculation of the CO₂ production of the animals in the present study using the Lifson & McClintock (1966) equation gave results 9–13% greater than those obtained by using the Speakman et al. (1993) equation. Most measurements obtained by using the Speakman et al. (1993) equation were, however, within the considerable range reported by Costa et al. (1989). It is
possible that the large range observed by Costa et al. (1989) may, as was found in the present study, have been attributable to differences in behaviour.

In their study of the energetics of exercising California sea lions, Boyd et al. (1995b) were unable to raise metabolic rate to levels greater than six times predicted BMR for substantial bouts of swimming. They suggested, therefore, that previous DLW measurements of average field metabolic rates as high as 6.7 and 8.8 times predicted BMR in otariids (Costa et al., 1989, 1991) were overestimates. The current estimates support this view. Moreover, using the relationship between heart rate and oxygen consumption, Butler et al. (1995) recently measured a mean at-sea metabolic rate in free-living lactating Antarctic fur seals of 7.2 ± 0.3 W·kg⁻¹ (5.2 times predicted BMR), a value similar to that found in the present study.

Foraging behaviour, energy expenditure, and mass gain efficiency

The negative relationships observed between the proportion of time spent diving (%), the rate of diving (m·h⁻¹) and at-sea MR were unexpected and might appear to be counter-intuitive. We had expected a priori that diving would be the most energetically expensive activity during foraging, thus resulting in positive relationships between diving behaviour and at-sea MR. Likewise, making similar assumptions, Boyd et al. (1991) observed a negative relationship between dive rate (m·h⁻¹) and foraging trip duration and suggested that females undertaking short trips would therefore have a higher rate of energy expenditure.

These interpretations of the energetic cost of diving behaviour were based, however, on the assumption that time spent at the surface is mostly spent resting. Consequently, animals with a higher dive rate would spend less time resting and, therefore, have a higher rate of energy expenditure (Boyd et al., 1991). However, recent analyses of Antarctic fur seal swimming speeds (Boyd, 1996; Boyd, Reid & Bevan, 1995a) indicate that the majority of time at the surface is spent swimming between food patches. Butler et al. (1995) found that the metabolic rate during diving in Antarctic fur seals is only 20% greater than that when swimming, the greatest elevation in MR occurring after a bout of diving when the animal is at the surface. Hence, it may be that animals with a higher dive rate spend a greater proportion of their time at the surface resting so that their overall at-sea MR is lower than that of animals with a lower dive rate. Analysis of how females allocate the time at the surface to swimming and resting in relation to diving behaviour over the entire foraging trip is needed to clarify this question.

The close sigmoidal relationship observed between the proportion of time at sea spent diving and metabolic rate may provide a useful, inexpensive means of estimating foraging energy expenditure in this species, and possibly in other otariids. Boyd et al. (1994), however, observed that in years of low prey availability both the average proportion of time spent diving and the average rate of diving increase. It seems unlikely that, as one would predict from the negative relationships between diving activity and metabolic rate observed in the present study, animals expend less energy in search of food at times when it is more difficult to find. Therefore, extrapolation of this relationship to estimate energy expenditure under different conditions should be made with caution.

Females that undertake short foraging trips spend a greater proportion of the time at sea diving and have a higher dive rate (Boyd et al., 1991; this study). The results of this study indicate that they not only have low rates of energy expenditure but gain less mass during the foraging trip. In contrast, animals staying at sea longer not only have higher metabolic rates, and spend
greater total amounts of energy, but gain more mass per trip while spending a lower proportion of time diving. This suggests that, while animals making long trips may have to spend more time and expend more energy in search of food patches, they are better at exploiting the patches, or the patches are of higher quality than those encountered by females making short trips.

All the nutrition delivered to pups during attendance periods comprises milk carried ashore and milk produced from body reserves while on land (Arnould & Boyd, 1995). Hence, the amount of mass gained during a foraging trip should provide an index of the amount of milk to be delivered to the pup. The findings of the present study, that mass gain is positively related to foraging trip duration, therefore accords with previous observations that the amount of milk females deliver to their pups during attendance periods is positively related to the duration of the preceding foraging trip (Arnould & Boyd, 1995; Arnould, Boyd & Socha, In press).

Whereas the amount of milk delivered per attendance period is positively related to the duration of the preceding foraging trip, Arnould & Boyd (1995) have shown that the overall rate of milk delivery is independent of trip duration. Consequently, as indicated by the lack of relationship (in years of normal food abundance) between maternal foraging trip duration and pup growth rates (Boyd et al., 1991; Lunn, 1993), within the range of durations observed there is no advantage to pups in mothers undertaking foraging trips of any particular duration (Arnould & Boyd, 1995). In the present study, there was no relationship between the efficiency with which females gained mass and the duration of foraging trips; thus, within the range of durations observed, there is no apparent energetic advantage to females in following any particular foraging trip duration strategy. It must be stressed, however, that these observations were made in a year of normal food abundance and it is possible that particular foraging trip duration strategies may confer energetic advantages in years of exceptionally low or high food availability. This may explain how a range of individual foraging strategies can be maintained in the population.

In summary, the results of the present study indicate that at-sea metabolic rate in Antarctic fur seal females is negatively related to the proportion of time spent diving and the rate of diving (m · h⁻¹). Consequently, as diving intensity is negatively related to foraging trip duration (Boyd et al., 1991), at-sea metabolic rate is positively related to time spent at sea. Animals that stay longer at sea spend greater amounts of energy but also gain more mass, so that the efficiency with which mass is gained is not related to foraging trip duration.

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REFERENCES


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