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The comparative energetics and growth strategies of sympatric Antarctic and subantarctic fur seal pups at Îles Crozet

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Summary

The period of maternal dependence is a time during which mammalian infants must optimise both their growth and the development of behavioural skills in order to successfully meet the demands of independent living. The rate and duration of maternal provisioning, post-weaning food availability and climatic conditions are all factors likely to influence the growth strategies of infants. While numerous studies have documented differences in growth strategies at high taxonomic levels, few have investigated those of closely related species inhabiting similar environments. The present study examined the body composition, metabolism and indices of physiological development in pups of Antarctic fur seals (*Arctocephalus gazella*) and subantarctic fur seals (*Arctocephalus tropicalis*), congeneric species with different weaning ages (4 months and 10 months, respectively), during their overlap in lactation at a sympatric breeding site in the Iles Crozet. Body lipid reserves in pre-moult pups were significantly greater (t_{28}=2.73, P<0.01) in subantarctic (26%) than Antarctic fur seals (22%). Antarctic fur seal pups, however, had significantly higher (t_{26}=3.82, P<0.001) in-air resting metabolic rates (RMR; 17.1±0.6 ml O_2 kg^{-1} min^{-1}) than subantarctic fur seal pups (14.1±0.5 ml O_2 kg^{-1} min^{-1}). While in-water standard metabolic rate (SMR; 22.9±2.5 ml O_2 kg^{-1} min^{-1}) was greater than in-air RMR for Antarctic fur seal pups (t_9=2.59, P<0.03), there were no significant differences between in-air RMR and in-water SMR for subantarctic fur seal pups (t_{12}=0.82, P>0.4), although this is unlikely to reflect a greater ability for pre-moult pups of the latter species to thermoregulate in water. Pup daily energy expenditure was also significantly greater (t_{27}=2.36, P<0.03) in Antarctic fur seals (638±33 kJ kg^{-1} day^{-1}) than in subantarctic fur seals (533±33 kJ kg^{-1} day^{-1}), which corroborates observations that pups of the former species spend considerably more time actively learning to swim and dive. Consistent with this observation is the finding that blood oxygen storage capacity was significantly greater (t_9=2.81, P<0.03) in Antarctic (11.5%) than subantarctic fur seal (8.9%) pups. These results suggest that, compared with subantarctic fur seals, Antarctic fur seal pups adopt a strategy of faster lean growth and physiological development, coupled with greater amounts of metabolically expensive behavioural activity, in order to acquire the necessary foraging skills in time for their younger weaning age.

Key words: maternal provisioning, metabolic rate, growth strategy, resource partitioning, energetics, weaning, fur seal, *Arctocephalus gazella*, *Arctocephalus tropicalis*.

Introduction

Throughout the period of maternal dependence, mammalian infants must balance the demands of lean body growth, lipid storage and energy expenditure for behavioural development from the finite nutritional resources (milk or solid food) provided by their mother (Loudon and Racey, 1987; Martin, 1984; Peaker, 1989). Trade-offs, however, exist in devoting nutritional resources to various developmental pressures. For example, rapid lean growth may confer advantages to the infant in being large at weaning (e.g. enhanced defence of food resources or against predators) but limits the amount of energy that can be devoted to physical activity due to the high maintenance metabolism costs associated with a large lean body mass (Blaxter, 1989; Innes and Millar, 1995). Conversely, high levels of energy expenditure devoted to behavioural development (usually through play) may enhance hunting ability or predator avoidance but limit the storage of body lipids that could be crucial to post-weaning survival during the early period of nutritional independence when foraging efficiency may still be low (Birgersson and Ekvall, 1997; Fisher et al., 2002). Furthermore, the ability of infants

to direct resources to various expenditures may depend on the composition (protein, lipid, carbohydrate) of the maternally provided nutrition and its rate of delivery (McAdam and Millar, 1999; Owens et al., 1993; Price and White, 1985). Therefore, as mortality in mammals is generally highest during the post-weaning stage (Clutton-Brock et al., 1987; Coulson et al., 2001; Le Boeuf et al., 1994; Van Ballenberghe and Mech, 1975), knowledge of infant growth strategies and how they differ according to environmental and maternal constraints may provide important insights into mechanisms influencing juvenile survival and life history.

Otariid seals (fur seals and sea lions) are an ideal group for investigating this topic, as females give birth to a single offspring, there is no post-weaning maternal care, and offspring are entirely dependent on milk for nutrition throughout most of lactation (Bonner, 1984). Furthermore, lactation in these species is characterised by mothers alternating between short nursing periods ashore and long foraging trips to sea during which their pup must fast (Gentry and Kooyman, 1986). Consequently, the nutritional resources delivered to the dependent pups must be allocated for growth, storage and behavioural development (e.g. learning to swim) during fasting periods as well as when the mother is ashore.

Lactation in otariid seals generally lasts 10–12 months, although in some species offspring may be suckled for up to 3 years (Bonner, 1984). Exceptions to this pattern are the Antarctic fur seal (*Arctocephalus gazella*) and the northern fur seal (*Callorhinus ursinus*), which have lactation periods lasting only 4 months. The brevity of lactation in these two species is thought to have evolved to exploit the predictably high but brief productivity of the subpolar summer and to maximise maternal transfer and offspring growth before the onset of the polar winter (Gentry and Kooyman, 1986). By contrast, the longer lactation periods of the other otariid species are thought to have evolved in response to the low seasonal variation but less predictable nature of the temperate and sub-tropical marine environments they inhabit. At three locations in the subantarctic region, however, there is the surprising situation where species representative of each strategy breed sympatrically. Macquarie Island, Marion Island and Iles Crozet are the northern and southern extents, respectively, of the Antarctic fur seal and subantarctic fur seal (*Arctocephalus tropicalis*) breeding ranges (Guinet et al., 1994; Kerley, 1984; Robinson et al., 2002). At these sites, the majority of pupping for each species occurs in December but, despite similarity in their maternal masses and pup birth masses (Goldsworthy et al., 1997; Kerley, 1985), Antarctic fur seal pups wean at the end of the Austral summer (March–April) whereas subantarctic fur seal pups wean in late winter (August–September). There are few examples worldwide of such closely related sympatric species having such divergent lactation strategies (Dempster et al., 1992; Innes and Millar, 1994).

Numerous studies have investigated the maternal characteristics (e.g. diet, foraging behaviour, foraging areas, colony attendance patterns and milk composition) and pup responses (e.g. growth rate and weaning mass) of Antarctic and subantarctic fur seals at their sympatric sites in order to understand the mechanisms driving the divergent strategies and their impacts (Goldsworthy, 1999; Goldsworthy and Crowley, 1999; Goldsworthy et al., 1997; Green et al., 1990; Kerley, 1983, 1984, 1985; Klages and Bester, 1998; Robinson et al., 2002). At Macquarie Island and Marion Island, no differences have been found in maternal diet, foraging areas or diving behaviour between the species during their summer lactational overlap (Goldsworthy and Crowley, 1999; Goldsworthy et al., 1997; Klages and Bester, 1998; Robinson et al., 2002) yet, over the same time period, growth rates of Antarctic fur seal pups are significantly greater than those of subantarctic fur seals at all sympatric sites (Goldsworthy and Crowley, 1999; Kerley, 1985; S. P. Luque et al., unpublished data). Goldsworthy and Crowley (1999) suggested that the difference in growth rates could reflect either a higher milk consumption rate in Antarctic fur seals or greater metabolic expenditure by subantarctic fur seals. However, the limited information on pup metabolic rates for the species is restricted to their allopatric sites (making comparisons difficult) and there is no information on their milk consumption rates at sympatric sites (Arnould et al., 1996a, 2001; Beauplet et al., 2003; Georges et al., 2001; Guinet et al., 1999). Furthermore, while mass gain differs between the species, it is not known whether the divergent lactation strategies influence the composition of growth and development (Owens et al., 1993; Spray and Widdowson, 1950).

The aims of this study, therefore, were to determine whether differences in body composition, metabolism and physiological development exist between sympatric Antarctic and subantarctic fur seal pups.

Materials and methods

Study site and animals

The study was conducted at La Mare aux Elephants (46°22′29″ S, 51°40′13″ E), Possession Island (Îles Crozet), during the 2001/2002 breeding season. Population growth rates for both Antarctic fur seals (*Arctocephalus gazella* Peters) and subantarctic fur seals (*Arctocephalus tropicalis* Gray) on Possession Island are currently ~18% per annum (Guinet et al., 1994). Annual pup productions at La Mare aux Elephants were 164 and 80 for Antarctic and subantarctic fur seals, respectively, in 2001/2002 and peak-pupping dates were 5 December and 25 December, respectively.

During the pupping period, 95 Antarctic and 58 subantarctic fur seal newborn pups were sexed and identified by a unique numbered piece of plastic tape glued to the fur on the top of the head (Georges and Guinet, 2000a). At about one month of age, each of these pups was tagged in the trailing-edge of both fore-flippers with an individually numbered plastic tag (Dalton Rototag, Nettlebed, UK). As part of concurrent studies, the attendance patterns of mothers of marked pups were monitored from birth until the end of March by visual inspection of the natal colony three times per day (09:00 h, 12:00 h and 17:00 h local time).

Sampling was conducted in February 2002 and was staggered by 10–15 days between the species in order to cover similar pup ages. Mean ambient and sea surface temperature during sampling were 8.0°C and 8.0°C, respectively (http//ingrid.ldgo.columbia.edu/). For all aspects of the study, selected pups were captured 1–3 days after the mother's departure to sea following a normal suckling period in order to allow sufficient time for complete voiding of ingested milk from the stomach (Arnould et al., 1996a; Donohue et al., 2002; Oftedal and Iverson, 1987). Each study pup was selected at random from the population of marked individuals and sampled for only one aspect of the study. Upon each capture, pups were weighed in a sack with an electronic suspension balance (±0.01 kg). All the study pups still had the black natal pelage and, based on close examination of the pelage, all individuals were considered to be at the pre-moult stage.

Respirometry and resting metabolic rate

Oxygen consumption, determined by an open circuit respirometry system (Butler and Woakes, 1982), was used to measure the resting metabolic rates (RMR) of pups. Pups were placed in a wooden respirometry chamber (80 cm×60 cm×50 cm; sealed with silicone and varnish) that was equipped with a small Plexiglas window and large fan that ensured complete and rapid mixing of air. Foam rubber seals ensured an air-tight junction between the door and the body of the respirometer. The chamber had a removable floor below which there was a basin 60 cm deep. The basin was filled with fresh water to within 10 cm of the rim and covered by a sheet of wire grating when a pup was placed in it.

Air was drawn through the respirometer using an air pump (B105; Charles Austen Pumps, Byfleet, Surrey, UK), and flow rate (maintained at 50 l min^{-1}) was measured using a rotameter (Fisher-Rosemount Ltd, Catham, Kent, UK). A subsample of the outlet air flow was passed through Drierite ($CaSO_4$) and CO_2 absorbent (Baralyme®) to an O_2 analyser (S103; Qubit Systems Inc., Kingston, Ontario, Canada). Sampling of ambient air was conducted every 10 min by manually switching a valve in the chamber outlet airflow line. The O_2 analyser was calibrated prior to each measurement period with atmospheric air and nitrogen (Air Products PLC, Crewe, Cheshire, UK). Ambient atmospheric pressure, temperature and humidity were measured on a digital barometer (Model BA116; Oregon Scientific Pty Ltd, Sydney, NSW, Australia) and recorded every 10 min. A humidity/temperature sensor was affixed inside the chamber.

The output signals from the O_2 analyser and the humidity/temperature sensor passed through a purpose-built interface box that amplified the signals to a range of –10 V to +10 V and then transferred them to an analogue–digital converter unit (DAQPad-1200; National Instruments Corporation, Austin, TX, USA) in a desktop computer. The computer sampled the outputs 100 times per second, took a mean of these values and saved them to a file every 1 s with a program developed using a software package for automatic instrumentation (LabView® 4.0; National Instruments Corporation). Ambient atmospheric pressure, temperature and humidity readings were manually entered into the software package as they were recorded. Water temperature was measured with a glass thermometer (±0.1°C; Hanna Instruments Ltd Pty, Keysborough, VIC, Australia) prior to, and immediately after, the pup was in the basin. For logistical reasons, the body temperature of study pups was not recorded.

The pups were introduced into the chamber and left to rest and acclimatise for 1 h. Measurements of O_2, humidity, temperature, pressure and flow were taken continuously throughout the duration of the experiment but for calculations of resting rates the values from the 10 min of minimum oxygen consumption after the hour of acclimatisation were used. Confirmation that the pup was resting but not sleeping was made by visual inspection through the Plexiglas window, which was usually kept covered. Once the measurements in air had been completed, the pup was placed in the water-filled basin and left to acclimatise for 1 h, and, thereafter, values from the 10 min of minimum oxygen consumption were used to calculate in-water standard rates. Due to equipment problems, in-air and in-water metabolic rates were not measured for all pups.

Oxygen consumption ($\dot{V}_{O_2}$) was calculated using the equation of Withers (1977):

$$\dot{V}_{O_2} = \frac{\dot{V}_{STPD} \times (F_{O_2,Amb} - F_{O_2,Exp})}{1 - F_{O_2,Amb} + RQ \times (F_{O_2,Amb} - F_{O_2,Exp})}, \quad (1)$$

where $\dot{V}_{STPD}$ is the flow rate of dry air through the respirometer (in ml min^{-1}) corrected for standard temperature and pressure, $F_{O_2,Exp}$ and $F_{O_2,Amb}$ are the fractional concentrations of O_2 in outlet and ambient air, respectively, and RQ is the respiratory quotient. Assuming a diet of milk, an RQ of 0.71 was calculated with the following metabolic constants: 2.109 l O_2 g^{-1} lipid, 0.976 l O_2 g^{-1} protein, 1.433 l CO_2 g^{-1} lipid and 0.783 l CO_2 g^{-1} protein (Costa, 1987).

Body composition, daily energy expenditure and milk consumption

The body composition and daily energy expenditure (DEE) rates of pups were measured using hydrogen isotope dilution and doubly labelled water (DLW) techniques (Costa, 1987). After weighing upon capture, a background blood sample (5 ml) was collected into a heparinised syringe from each pup by venipuncture of an inter-digital vein in a hind-flipper. They were then given an intramuscular injection of a weighed dose (±0.01 g) of tritiated water (HTO; ~1 ml, 7.4 mBq ml^{-1}). Each animal was also given an oral dose, by stomach tube, of 15–20 ml $H_2{}^{18}O$ 10% AP (Isotec Inc., Miamisburg, OH, USA). Pups were then kept in an enclosure for 3 h before an equilibration blood sample (5 ml) was collected, to determine the total body water (TBW) pool size and initial plasma ^{18}O levels, before being released at the point of capture, left undisturbed and allowed to suckle normally during the next visit ashore by their mother. Each pup was recaptured 2–3 days after the departure of the mother on her subsequent foraging

trip to sea (4–6 days after initial capture), weighed and a final blood sample (5 ml) was collected.

All blood samples were kept at 4°C for several hours before being centrifuged (3000 r.p.m., for 10 min) and the plasma fraction separated. Aliquot samples (2–5 ml) of plasma were stored frozen (–20°C) in plastic screw-cap vials (with silicon O-rings; Sarstedt Inc., Newton, NC, USA) until analysis. For tritium analysis, thawed sub-sample aliquots of plasma (0.2 ml) were distilled into pre-weighed scintillation vials following the procedures of Ortiz et al. (1978). The vials were then re-weighed to obtain the mass of the sample water (±0.1 mg). Scintillant (10 ml Ultima Gold; Canberra Packard, Mt Waverly, VIC, Australia) was added to the vials, which were then counted for 5 min in a Packard Tri-Carb 2100TR liquid scintillation analyser (Canberra Packard) 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 to determine the specific activity of the tritium injected. The ^{18}O enrichment of plasma water was determined by Metabolic Solutions (Nashua, NH, USA) using gas isotope ratio mass spectrometry.

TBW was calculated from HTO dilution space using an equation determined empirically in Antarctic fur seal pups (Arnould et al., 1996b). Lean body mass (LBM) was calculated from TBW assuming a hydration constant of 74.7% (Arnould et al., 1996b), and total body lipid (TBL) was calculated by subtracting LBM from total body mass. Total water influx (TWI) rates were calculated from the decrease in specific activity of HTO and equations 5 and 6 in Nagy and Costa (1980), assuming an exponentially changing TBW. Carbon dioxide production rates were calculated using equation 3 of Nagy (1980). DEE was calculated from CO_2 production assuming a conversion factor of 27.44 kJ l^{-1} CO_2 (Costa, 1987). Oxygen consumption was determined by dividing CO_2 production by the RQ (0.71; see above). Metabolic water production (MWP) rates were calculated from the metabolic rate determined by DLW assuming a conversion factor of 0.02629 g H_2O kJ^{-1} (Schmidt-Nielsen, 1983).

Milk consumption rates were calculated using the following equation (Ortiz, 1987):

$$\text{Milk consumption rate} = \frac{\text{TWI} - \text{MWP}}{\text{Milk water content}} . \quad (2)$$

Milk composition does not differ significantly between Antarctic and subantarctic fur seals at the study site, and mean milk water and energy contents during the study period were 41.5% and 18.9 kJ g^{-1}, respectively (S. P. Luque et al., unpublished data). Similar findings have been reported on Macquarie Island (Goldsworthy and Crowley, 1999).

Blood volume

The physiological ability of infant pinnipeds to make foraging dives has been shown to increase throughout the period of maternal dependence (Burns, 1999; Horning and Trillmich, 1997a,b). In the present study, therefore, factors affecting oxygen storage [haematocrit (Hct), haemoglobin (Hb) and total blood volume] were measured and used as indices of physiological development.

After weighing upon capture, a background blood sample (5 ml) was collected into a heparinised syringe from each pup by venipuncture of an inter-digital vein in a hind-flipper and stored cool (4°C) until all samples were centrifuged (see below). Each pup was then given an intravenous injection (~1 ml) of a weighed dose of Evans Blue dye (0.5 mg kg^{-1} body mass; Sigma-Aldrich, St Louis, MO, USA) to measure total blood volume (El-Sayed et al., 1995). After completing the injection but before removing the needle from the blood vessel, the syringe was flushed with blood 2–3 times to ensure that all dye was administered. Serial blood samples (5 ml) were collected at 10 min, 20 min and 30 min post-injection to measure the equilibration and dilution of the dye (El-Sayed et al., 1995).

Prior to centrifugation, each background blood sample was thoroughly mixed by gentle agitation. An 20 μl sample was placed in 2.5 ml of Drabkins reagent (Sigma kit 525A; Sigma-Aldrich) and later assayed for Hb concentration by colorimetric analysis. Absorbance was measured in duplicate samples on a Spectronic 1001 (Milton Roy, Ivyland, PA, USA) spectrophotometer at a wavelength of 540 nm. Hb concentration of each sample was determined by comparison with a dilution curve created from protein standards. Hct was measured in triplicate from an aliquot of the whole blood as the packed red blood cell volume in capillary tubes following centrifugation for 5 min at 11 500 r.p.m.

Total blood volume was measured by colorimetric analysis of the Evans Blue dilution. Following centrifugation at 3000 r.p.m. for 10 min, aliquots of plasma were separated and stored frozen (–20°C) in plastic vials until analysis several months later. In the laboratory, the thawed samples were agitated and centrifuged again at 3000 r.p.m. for 5 min. The absorbance of the decanted dyed plasma was determined on a Spectronic 1001 (Milton Roy) spectrophotometer at 624 nm and 740 nm following procedures outlined in Foldager and Blomqvist (1991). Dye concentrations were determined from a serial dilution curve of Evans Blue standards measured at both wavelengths. It is common practice to back-calculate the dye concentration at the time of injection by determining the intercept of a regression line between dye concentration of each serial sample and the time it was collected (Costa et al., 1998; El-Sayed et al., 1995; Foldager and Blomqvist, 1991). This method was not used because the regression between dye concentration and time post-injection for most of the seals was not statistically significant (P>0.05). Therefore, a mean dye concentration using all three samples (i.e. 10 min, 20 min and 30 min post-injection) was calculated and used for determination of blood volume. Plasma volume was calculated as follows:

$$V_p = \frac{[m_i]}{[C_e]} , \quad (3)$$

where $[m_i]$ is the initial quantity (mg) of Evans Blue dye injected, $[C_e]$ is the concentration of Evans Blue dye (mg l^{-1}) obtained from the mean of the serial samples and V_p is plasma volume (litres). Total blood volume (V_b) was then calculated as:

$$V_b = V_p\,[100\,(1 - \mathrm{Hct})] - 1\,, \qquad (4)$$

where Hct is haematocrit expressed as a fraction of whole blood.

Statistical analyses were performed using the Systat® statistical software (Version 7.0.1; SPSS Inc., Richmond, CA, USA). The Kolmogorov–Smirnov test was used to determine whether the data were normally distributed, and an *F* test was used to confirm homogeneity of variances ($P>0.2$ in all cases). Differences between linear regressions were tested by analysis of covariance (ANCOVA) after testing for homogeneity of slopes. Unless otherwise stated, data are presented as means ± 1 S.E.M. and results considered significant at the $P<0.05$ level.

Results

Resting metabolic rate

Measurements of in-air resting metabolic rate (RMR) were obtained for 14 Antarctic (six female, eight male) and 14 subantarctic (seven female, seven male) fur seal pups. Mean ambient air temperature during measurements was 10.5±0.6°C (range: 6–15°C). In-air RMR of pups was significantly positively related to body mass in Antarctic fur seals ($r^2=0.58$, $P<0.02$) but not subantarctic fur seals ($P>0.2$; Fig. 1). Mass-specific in-air RMR did not differ significantly between the sexes in either species ($P>0.1$ in both cases) so the data were combined (Table 1). Mean mass-specific in-air RMR of pups was significantly greater in Antarctic fur seals (17.1±0.6 ml O_2 kg^{-1} min^{-1}) than subantarctic fur seals (14.1±0.5 ml O_2 kg^{-1} min^{-1}; $t_{26}=3.82$, $P<0.001$).

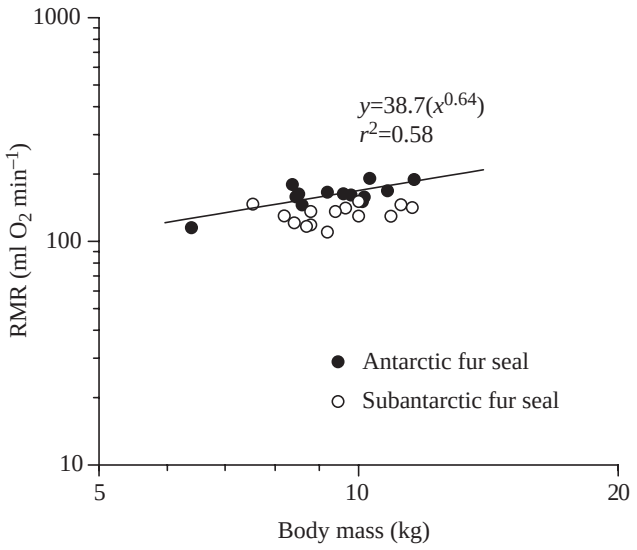

Fig. 1. The relationship between in-air resting metabolic rate (RMR) and body mass of Antarctic and subantarctic fur seal pups at Possession Island, Îles Crozet. The equation given is for Antarctic fur seal pups. No significant relationship was found for subantarctic fur seals.

Measurements of in-water standard metabolic rate (SMR) were obtained for 12 Antarctic (six female, six male) and 15 subantarctic (seven female, eight male) fur seal pups. Mean water temperature during the measurements was 10.0±0.6°C (range: 9–12°C). There was no relationship between body mass and in-water SMR in either species ($P>0.1$ in both cases). Mass-specific in-water SMR did not differ significantly between the sexes in either species ($P>0.1$ in both cases) so the data were combined (Table 1). Mean mass-specific in-water SMR of pups was significantly greater in Antarctic (22.9±2.5 ml O_2 kg^{-1} min^{-1}) than subantarctic fur seals (14.6±1.0 ml O_2 kg^{-1} min^{-1}; $t_{25}=3.41$, $P<0.003$).

Measurements of both in-air RMR and in-water SMR were made in 10 Antarctic and 13 subantarctic fur seal pups. Mean in-water SMR was significantly greater than in-air RMR for Antarctic fur seal pups (paired *t*-test, $t_9=2.59$, $P<0.03$) but not for subantarctic fur seal pups ($t_{12}=0.82$, $P>0.4$).

Body composition, daily energy expenditure and milk consumption

Body composition upon capture was determined for a total of 16 (eight male, eight female) Antarctic and 14 subantarctic (seven male, seven females) fur seal pups. No significant differences were detected between the sexes in either species ($P>0.2$ in both cases) so the data were combined. As expected, significant positive correlations were found between total body water (TBW) and body mass in both species (Fig. 2). However, the regressions differed significantly between the species (ANCOVA, $F_{1,27}=5.82$, $P<0.02$), with Antarctic fur seal pups having higher TBW per unit mass and, thus, relatively lower TBL stores (22.2±1.0%) than subantarctic fur seal pups (26.1±1.0%; $t_{28}=2.73$, $P<0.02$; Table 2).

With the exception of one female Antarctic fur seal pup (^{18}O levels were too close to background upon recapture), field metabolic rate measurements were obtained for all of the above individuals. There were no significant differences in CO_2 production between the sexes for either species ($P>0.1$ in both cases) so data were combined. Antarctic fur seal pups

Table 1. *Mass-specific metabolic rates of Antarctic and subantarctic fur seal pups on Possession Island, Îles Crozet*

	Antarctic fur seal	*N*	Subantarctic fur seal	*N*
Body mass (kg)	9.64±0.43	14	9.45±0.31	15
Age (days)	64±1	14	62±1	15
In-air RMR (ml O_2 kg^{-1} min^{-1})	17.1±0.6*	14	14.1±0.5*	14
In-water SMR (ml O_2 kg^{-1} min^{-1})	22.9±2.5†	12	14.6±1.0†	15

Values are means ± S.E.M.

* and † denote significant differences at $P<0.001$ and $P<0.003$, respectively.

RMR, resting metabolic rate; SMR, standard metabolic rate.

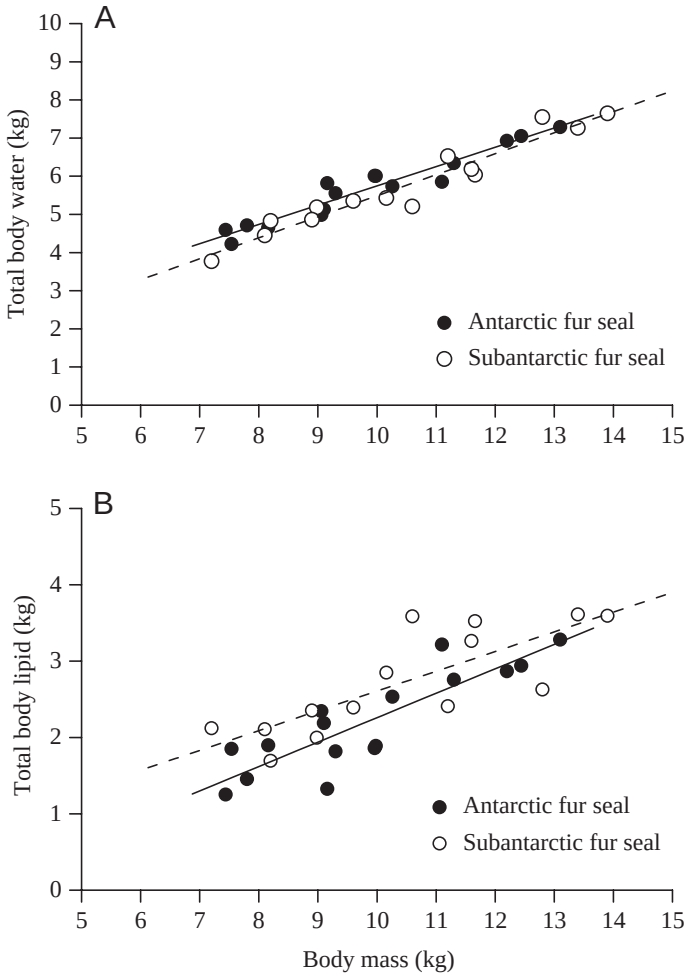

Fig. 2. The relationship between body mass and (A) total body water and (B) total body lipid in Antarctic (solid lines) and subantarctic (broken lines) fur seal pups at Possession Island, Iles Crozet. Regression statistics for both species in A: y=0.50x+0.70 (r^2=0.93, P<0.0001) and y=0.55x–0.01 (r^2=0.93, P<0.0001), respectively. Regression statistics for both species in B: y=0.32x–0.94 (r^2=0.75, P<0.0001) and y=0.26x+0.02 (r^2=0.63, P<0.0001), respectively.

had a significantly higher mean CO_2 production rate (0.97±0.05 ml g^{-1} h^{-1}) than subantarctic fur seal pups (0.81±0.05 ml g^{-1} h^{-1}; t_{27}=2.36, P<0.03). These values represent mean daily energy expenditure (DEE) and O_2 consumption rates, respectively, of 638±33 kJ kg^{-1} day^{-1} and 1.36±0.07 ml g^{-1} h^{-1} for Antarctic fur seals and 533±33 kJ kg^{-1} day^{-1} and 1.14±0.07 ml g^{-1} h^{-1} for subantarctic fur seal pups (Table 2). The higher DEE of Antarctic fur seal pups resulted in them having significantly greater metabolic water production (MWP) rates (16.8±0.8 ml kg^{-1} day^{-1}) than subantarctic fur seal pups (14.0±0.9 ml kg^{-1} day^{-1}; t_{27}=2.36, P<0.03). Mean milk water intake (MWI), however, did not differ significantly between the species (t_{27}=1.66, P>0.1; Table 2). Consequently, as milk composition did not differ between the species (S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data), there was no significant difference

Table 2. *Energy expenditure and milk consumption rates of Antarctic and subantarctic fur seal pups on Possession Island, Îles Crozet*

	Antarctic fur seal (N=15)	Subantarctic fur seal (N=14)
Body mass (kg)	10.05±0.35	10.47±0.49
Age (days)	64±1	66±2
Total body lipid (%)	22.2±1.0†,‡	26.1±1.0†
CO_2 production (ml g^{-1} h^{-1})	0.97±0.05*	0.81±0.05*
Daily energy expenditure (kJ kg^{-1} day^{-1})	638±33*	533±33*
O_2 consumption (ml g^{-1} h^{-1})	1.36±0.07*	1.14±0.07*
Total water influx (ml kg^{-1} day^{-1})	51.2±2.7†	40.7±3.5†
Metabolic water production (ml kg^{-1} day^{-1})	16.8±0.8*	14.0±0.9*
Milk water intake (ml kg^{-1} day^{-1})	34.4±3.0	26.2±3.9
Milk consumption (ml kg^{-1} day^{-1})	82.9±7.1	63.2±9.5
Milk consumption (ml $bout^{-1}$)	3879±260	3637±544

* and † denote significant differences between the species at P<0.03 and P<0.02, respectively. ‡n=16 (see text for details).

between the species in the amount of milk consumed per day by pups during the study period (t_{27}=1.70, P>0.1; Table 2). The amount of milk consumed per maternal attendance bout also did not differ significantly between the species (t_{27}=1.70, P>0.1).

Blood volume

Haematocrit (Hct) and haemoglobin (Hb) values were obtained for 10 (five male, five female) Antarctic and eight subantarctic (five male, three female) fur seal pups. There were no significant differences in either Hct or Hb between the sexes for either species (P>0.1 in all cases) so data were combined. Mean Hct did not differ significantly between Antarctic (50.2±0.9%) and subantarctic (48.1±1.0%) fur seal pups (t_{16}=1.5, P>0.1). Similarly, there was no significant difference in Hb content between Antarctic (14.5±0.3 g dl^{-1}) and subantarctic (14.6±0.4 g dl^{-1}) fur seal pups (t_{16}=0.25, P>0.8).

Blood volume estimates were obtained for five Antarctic (two male, three female) and six subantarctic (four male, two female) fur seal pups. Blood volume as a proportion of body mass was significantly greater in Antarctic (11.5±0.8%) than subantarctic (8.9±0.5%) fur seal pups (t_9=2.81, P<0.03). Assuming the same mean body composition for these pups as determined above, the difference in blood volume between the species was still significant when considered as a proportion of LBM (t_9=2.35, P<0.05).

Discussion

Body composition, resting metabolic rate and daily energy expenditure

In contrast to numerous recent studies that have documented higher mass-specific body lipid contents in female than male fur seal pups (Arnould et al., 1996a, 2001; Arnould and

Hindell, 2002; Beauplet et al., 2003; Donohue et al., 2002), no significant differences in body composition were observed between the sexes of either species in the present study. However, as with the lack of sex differences in other variables measured in the present study (e.g. mass-specific in-air RMR and in-water SMR), this is likely to be due to low statistical power because, with the small sample sizes used, only differences of >30% would have been detected (at an alpha of 0.05 and a power of 0.9). The TBL of Antarctic fur seal pups observed in the present study (22%) is within the range previously recorded for conspecific pups at South Georgia and Iles Kerguelen (Arnould et al., 1996a, 2001; Lea et al., 2002). By contrast, the TBL of subantarctic fur seal pups (26%) is substantially greater than that recorded for conspecific pups of approximately the same age at Amsterdam Island (8–12%; Beauplet et al., 2003). This difference may reflect a reduced need for subcutaneous blubber insulation in the warmer temperate climate of Amsterdam Island. Interestingly, despite similar maternal foraging trip durations during the present study (S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data), subantarctic fur seal pups had significantly greater TBL than Antarctic fur seal pups. These data are consistent with those collected from a larger sample size (N=41 and 47, respectively, for the two species) throughout the summer overlap in lactation (S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data).

The in-water SMR of Antarctic fur seal pups was significantly greater than their in-air RMR. Similar findings have been reported in comparable ambient and water temperatures for similar-aged pre-moult northern fur seals (Donohue et al., 2000). The ratio of in-water SMR to in-air mass-specific RMR, however, was substantially lower in Antarctic fur seals (1.3) than in northern fur seals (2.4), due primarily to the greater in-water mass-specific SMR (37 ml O_2 kg^{-1} min^{-1}) yet similar RMR (15 ml O_2 kg^{-1} min^{-1}) of the latter species. Baker and Donohue (2000) found that pre-moult northern fur seal pups spent little time in water, and Donohue et al. (2000, 2002) suggested that this was due to their inability to thermoregulate efficiently in water at that age. By contrast, Antarctic fur seal pups in the present study spent considerable amounts of time swimming in shallow water close to the shore (S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data), and similar-aged pups on South Georgia have been recorded as spending up to 50% of their time in the water (McCafferty et al., 1998). It is possible, therefore, that pre-moult Antarctic fur seals are better able to thermoregulate in water than northern fur seal pups. Indeed, the higher body lipid content (22%) of Antarctic fur seal pups in the present study compared with that of northern fur seal pups (15%; Donohue et al., 2000) is likely to provide them with greater subcutaneous thermal insulation.

Unexpectedly, in contrast to Antarctic fur seal pups, in-water SMR of subantarctic fur seal pups was not significantly greater than their in-air RMR. This could indicate that pre-moult subantarctic fur seal pups have better thermoregulatory capabilities than Antarctic fur seal pups. If this was the case, pre-moult subantarctic fur seal pups might be expected to spend considerable amounts of time in water developing important swimming and diving skills (Baker and Donohue, 2000; McCafferty et al., 1998). However, while the 4% greater body lipid content of subantarctic fur seal pups might provide them with some advantage in thermal insulation, they were rarely seen in water during the study (S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data, see below), suggesting that they do not have exceptional thermoregulatory capabilities. An alternative explanation is that pre-moult pups of this species have less developed thermoregulatory ability than Antarctic fur seal pups, and immersion in water, representing a severe thermal challenge they would not normally experience, resulted in metabolic depression (Boily and Lavigne, 1996; Lee et al., 1997). Unfortunately, core body temperature could not be measured in the present study, so this proposition cannot be investigated. Additional studies determining the thermal conductance of subantarctic fur seal pups both in water and in air are required to elucidate the reasons behind the unexpected findings of their similar in-air RMR and in-water SMR.

A further surprising finding of the present study was that Antarctic fur seal pups had a mean in-air mass-specific RMR 21% higher than that of subantarctic fur seal pups. The higher TBL of subantarctic fur seals may have provided them with some thermoregulatory advantage and, conversely, the corresponding higher LBM of Antarctic fur seals would result in a greater metabolically active mass and, thus, higher metabolic costs. On their own, however, these factors are unlikely to account for the large differences in RMR. One possibility is that the higher RMR of Antarctic fur seal pups is related to their generally greater levels of activity (see below). Numerous studies with humans and rats have shown that sustained increases in daily activity levels result in the elevation of RMR (Byrne and Wilmore, 2001; Poehlman and Danforth, 1991; Tremblay et al., 1992).

Concomitant with a higher mass-specific RMR, Antarctic fur seal pups also had a daily energy expenditure 20% greater than that of subantarctic fur seal pups. This is consistent with opportunistic observations at the study site of subantarctic fur seal pups spending significantly less time in both terrestrial and aquatic activities than Antarctic fur seal pups, preferring instead to sleep (S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data). Indeed, the low DEE recorded for subantarctic fur seal pups at Amsterdam Island (see below) has been attributed to their low activity levels (Beauplet et al., 2003). The ratio of DEE to in-air RMR was 1.3 for both species, which is less than the ratio of 1.7 reported for pre-moult Antarctic fur seal pups at South Georgia and northern fur seal pups (Arnould et al., 2001; Donohue et al., 2002). The DEE of Antarctic fur seal pups in the present study (638 kJ kg^{-1} day^{-1}) is less than the DEE reported for free-ranging pre-moult northern fur seal pups (700 kJ kg^{-1} day^{-1}; Donohue et al., 2002) and conspecific pups of similar age on South Georgia (1044 kg^{-1} day^{-1}; calculated from MWP values in Arnould et al., 2001). These differences may reflect the

colder ambient and sea water temperatures during summer at the Pribilof Islands (5°C and 4°C, respectively; http://ingrid.ldeo.columbia.edu/SOURCES/.IGOSS/) and South Georgia (4°C and 3°C, respectively; British Antarctic Survey, unpublished data) in comparison with those during the present study (8°C and 8°C, respectively; http://ingrid.ldeo.columbia.edu/SOURCES/.IGOSS/), leading to higher thermoregulatory costs. Similarly, the difference between the DEEs of pre-moult subantarctic fur seal pups in the present study (533 kJ kg^{-1} day^{-1}) and on Amsterdam Island (416 kJ kg^{-1} day^{-1}; Beauplet et al., 2003) may reflect the substantially warmer summer climate of the latter (17°C and 18°C for ambient and sea water temperatures, respectively; Meteo France, unpublished data).

Errors in calculating DEE from CO_2 production values can arise if incorrect RQ values are assumed (Costa, 1988; Nagy, 1980). Indeed, differences in body composition may reflect differences in metabolic fuel use (Beauplet et al., 2003; Blaxter, 1989) such that differences in calculated DEE could be an artefact of RQ assumptions. In the present study, however, if subantarctic fur seal pups were catabolising proportionately more protein than were Antarctic fur seal pups (as might be suggested by their body composition differences) then the difference in DEE between the species would actually be greater.

Milk consumption and growth strategy

The lack of any significant difference in daily or per bout milk consumption between Antarctic and subantarctic fur seal pups is consistent with the similarity in foraging trip durations of their mothers (S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data). The mean daily milk energy consumption by Antarctic fur seal pups in the present study (1.6 MJ kg^{-1} day^{-1}) is the same as that recorded for pre-moult conspecific pups at South Georgia (1.6 MJ kg^{-1} day^{-1}; Arnould et al., 1996a) and similar to that reported for pre-moult northern fur seal pups (1.4 MJ kg^{-1} day^{-1}; Donohue et al., 2002). By contrast, consumption by subantarctic fur seal pups (1.2 MJ kg^{-1} day^{-1}) is greater than reported for similar-aged pre-moult pups of the Australian fur seal (*A. pusillus doriferus* Jones; 0.8 MJ kg^{-1} day^{-1}), a temperate species with a comparable lactation length (Arnould and Hindell, 2002). Unfortunately, milk consumption estimates are not available for other fur seal species or for subantarctic fur seals at allopatric colonies, so it cannot be ascertained whether pups of this nominally temperate species normally consume such quantities of milk or if this only occurs at the subantarctic breeding sites. Comparison of subantarctic fur seal pup growth rates during the first four months at sympatric colonies (e.g. present study site, 70 g day^{-1}, S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data; Marion Island, 72 g day^{-1}, Kerley, 1985) with those at allopatric colonies further north (Gough Island, 58 g day^{-1}, Kirkman et al., 2002; Amsterdam Island, 54 g day^{-1}, Guinet and Georges, 2000), however, would tend to suggest a greater milk consumption by pups at the subantarctic sites during this period.

As has been reported on Marion and Macquarie islands (Goldsworthy and Crowley, 1999; Kerley, 1985), Antarctic fur seal pup growth rates are significantly greater than those of subantarctic fur seals at the present study site on Possession Island (80 g day^{-1} and 70 g day^{-1}, respectively; S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data). This finding appears inconsistent with the observed parity in milk consumption, especially in conjunction with the observed differences in the rates of energy expenditure. Differences in body composition, however, could account for this apparent contradiction. As adipose tissue is more energy dense than lean mass, its deposition requires greater amounts of nutrition (Blaxter, 1989). This is especially so in infant mammals, where the hydration of lean body mass is 3–4% greater than in physiologically mature adults (Adolph and Heggeness, 1971; Arnould et al., 1996b; Reilly and Fedak, 1990). Furthermore, if the observed body composition differences reflect differences in metabolic substrate use, as has recently been shown for sex-based body composition differences in subantarctic fur seals at Amsterdam Island (Beauplet et al., 2003), preferential lipid catabolism could provide Antarctic fur seals with the additional energy to account for their greater metabolic expenditure. Consequently, it is feasible that equal milk energy consumption could produce the differing growth rates.

A question that the findings of this study pose is why do Antarctic fur seal pups not conserve energy and accumulate greater lipid reserves to sustain them once they are weaned, especially as food availability may be reduced during the colder winter months? Why do they have higher energy expenditure rates than their sympatric congenerics? Pups of this species only have four months in which to develop all the swimming and diving skills necessary to forage independently (Bonner, 1984). While greater lipid reserves would provide some advantages (e.g. thermal insulation, ‘nutritional buffer’), their benefit would be limited if pups did not have any ability to dive and know how to hunt at weaning. Hence, selection should favour the early acquisition of necessary behavioural skills relative to species with longer maternal dependence. Comparison of the diving behaviour of Antarctic and subantarctic fur seal pups at Possession Island indicates that the former do indeed spend greater amounts of time in water and learning to dive at an earlier age (S. P. Luque, J. P. Y. Arnould and C. Guinet, unpublished data). Such increased activity would lead to a higher energy expenditure (Baker and Donohue, 2000; Donohue, 1998). Consistent with this earlier development of diving behaviour in Antarctic fur seals is the finding of the present study that pups of this species have greater mass-specific blood volumes than do subantarctic fur seal pups. As Hb and Hct content did not vary between the species, the larger blood volume translates into greater blood oxygen stores in Antarctic fur seal pups (El-Sayed et al., 1995). Blood oxygen storage capacity in pinnipeds generally increases with age until maturity (Costa et al., 1998; Horning and Trillmich, 1997a; Jorgensen et al., 2001). Consequently, the results of the

present study suggest that physiological development is faster in Antarctic than in subantarctic fur seal pups.

The converse question posed by the findings of the present study is, as pups of both species appear to receive similar amounts of nutrition during the summer overlap in lactation, why do subantarctic fur seal pups not devote more resources to faster behavioural and physiological development? The answer may lie in the 'anticipation' of a reduced rate of nutrient delivery during the winter months. While there is no corresponding information available for the present study site on Possession Island, average winter maternal foraging trips of subantarctic fur seals at both Amsterdam Island and Marion Island are the longest recorded for any otariid species (23–28 days; Georges and Guinet, 2000b; Kirkman et al., 2002). The fasting durations experienced in winter by pups at these sites, therefore, are some of the most extreme for any infant mammal (Guinet and Georges, 2000). Pups endure these fasts by greatly reducing activity, adopting protein conserving pathways and relying mainly on lipid catabolism for metabolic energy (Beauplet et al., 2003). Furthermore, initial body lipid stores and daily mass loss in these pups are, respectively, positively and negatively related to the fasting durations endured (G. Beauplet, unpublished data; Guinet and Georges, 2000). Hence, a strategy of limiting energy expenditure and directing nutritional resources to adipose tissue growth by subantarctic fur seal pups during the summer months may be an adaptation for accumulating sufficient lipid reserves to survive repeated extreme fasts later in lactation.

In summary, the results of the present study indicate that differences exist in the resting metabolic rates, total energy expenditure and development between Antarctic and subantarctic fur seal pups, two closely related congeneric species (Wynen et al., 2001), at a sympatric breeding site. These differences are consistent with adaptations for rapid development of foraging abilities necessary for the earlier nutritional independence in the former and extended periods of fasting during prolonged maternal dependence in the latter. The mechanisms controlling the physiological differences observed between the two species are unknown but are likely to involve thyroid hormones, which are known to play an important role in regulating metabolism and development in neonatal mammals (Bernal and Refetoff, 1977). While thyroid hormones have been shown to vary throughout development, lactation and between seasons in phocid seals (Haulena et al., 1998; John et al., 1987; Little, 1991; Litz et al., 2001; Ortiz et al., 2001; Woldstad and Jenssen, 1999), their dynamics in otariid seals remain to be investigated.

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