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Sex differences in mass loss rate and growth efficiency in Antarctic fur seal (*Arctocephalus gazella*) pups at Macquarie Island

Abstract We investigated the relationship between the mass gained by a pup during a period of maternal attendance (as an index of milk intake) and the duration of the preceding foraging trip in relation to the mass-specific rate of mass loss during fasting periods and the growth rate of Antarctic fur seal (*Arctocephalus gazella*) pups at Macquarie Island. We found that (1) serially weighed male pups grew significantly faster than females pups and that (2) fasting female pups lost mass at a significantly higher rate (2.55% day^{-1}) than male pups (2.12% day^{-1}) of the same mass; (3) during periods of maternal attendance, there were no intersexual differences in the amount of mass gained by pups of the same size, hence (4) female pups required a higher daily mass gain to grow at the same rate as male pups. Our results show that intersexual differences in growth rate may be accounted for by intersexual differences in mass-specific rate of mass loss, because females lost 0.42% more of their total mass per day (i.e. 4.2 g kg^{-1} day^{-1}) compared with male pups of the same body mass. Despite intersexual differences in growth rates, our results indicate equality of maternal expenditure between the sexes. Intersexual differences in the rate of mass loss may be due to differences in the metabolic rate, activity level and/or body composition of male and female pups.

Key words Antarctic fur seal · Maternal expenditure · Sexual dimorphism · Growth rate · Metabolic rate

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Introduction

The larger adult size of males compared with females in many polygynous species may be due to the reproductive advantages accruing to large body size in males (Alexander et al. 1979). Fur seals (Pinnipedia, Otariidae) are highly polygynous and sexually dimorphic and thus a difference in the variance in lifetime reproductive success between sexes is to be expected. Parental-investment theory predicts that if higher maternal investment in male pups affects their lifetime reproductive success more than investment in female pups, then mothers should expend greater resources on the sex with the greatest variance in reproductive success, i.e. males (Fisher 1930; Trivers and Willard 1973; Maynard Smith 1980). In red deer (*Cervus elaphus*), reproductive success of stags was found to be related to body size, early growth and maternal expenditure during the first year of life, while the reproductive success of hinds was not closely related to size or expenditure before weaning (Clutton-Brock et al. 1987). However, the assumption that increased maternal expenditure ultimately translates to larger adult body size and greater survival and/or reproductive success of offspring is not currently supported by any direct evidence in otariids and phocids (see Trillmich 1996 for a review).

Pinnipeds are good subjects for the study of early differential growth and maternal expenditure because neonates are entirely dependent on milk until weaning. Studies of growth in otariids have pointed to greater maternal expenditure on male pups as the primary factor responsible for their larger size at birth (Costa et al. 1988; Boyd and McCann 1989; Cappozzo et al. 1991) and significant differences in the growth rates, calculated from cross-sectional but also longitudinal data sets (see Lunn et al. 1993), of male and female pups have been used to support the hypothesis of differential postnatal maternal expenditure between the sexes in the cape fur seal *Arctocephalus pusillus pusillus* (Rand 1956; Mison-Jooste 1999), the New Zealand fur seal, *A. fosteri*

(Crawley 1975; Mattlin 1981), Antarctic fur seal, *A. gazella* (Doidge et al. 1984; Goldsworthy 1995), the subantarctic fur seal, *A. tropicalis* (Kerley 1985), the Galapagos fur seal, *A. galapagoensis* (Trillmich 1986), northern fur seal, *Callorhinus ursinus* (Boltnev et al. 1998) and California sea lion, *Zalophius californianus* (Boness et al. 1991). On the other hand, in serially weighed pups, no sex differences were found in growth rates of Antarctic (Lunn et al. 1993) and subantarctic (Georges and Guinet, in press) fur seals. Recent investigations of Antarctic fur seals at South Georgia have shown that both male and female neonates contain similar amounts of gross energy (albeit in different forms), indicating that prenatal expenditure (in terms of gross energy) is similar between the sexes (Arnould et al. 1996; Lunn and Arnould 1997), and in a recent review Trillmich (1996) indicated that there was little evidence for differential maternal investment in pinniped pups.

In mammals, neonatal growth results from the difference between the mass gained through milk consumption and the mass lost due to metabolism. This is particularly true in seals, where the growth of the pup is totally dependent on milk because no solid food is provided by the mother and offspring do not generally forage until they are weaned.

To date there has been little investigation into how male and female pups conserve energy and use milk for growth. There is limited evidence that female otariid pups expend greater energy than males. For example, male California sea lions had lower resting metabolic rates than females (Ono and Boness 1996). Similarly, in northern fur seals, female pups expended greater energy than males (Costa and Gentry 1986). We investigated the mass gained by Antarctic fur seal pups during periods of maternal attendance (as an index of milk intake) in relation to the duration of the preceding foraging trips, the mass-specific rate of mass loss during fasting periods, and the growth rate of pups. Our objectives were to examine whether intersexual differences occurred in (1) the mass gained during a period of maternal attendance, (2) the rate of mass loss of fasting pups and (3) the relationship between growth rate and mass gained by the pup during an attendance period.

Methods

Study species

Antarctic fur seals breed on subantarctic islands in the South Atlantic and South Indian Oceans, in the vicinity of the Antarctic Polar Front (Bonner 1981). Pregnant females return to traditional breeding beaches in November and December, give birth within a few days of their arrival and wean their pup in late March/early April (Doidge et al. 1986, Shaughnessy and Goldsworthy 1990; Lunn and Boyd 1991). After parturition, mothers stay ashore for 5–7 days (perinatal attendance period) before mating and departing for sea on the first of many foraging trips. During this phase of lactation, mothers alternate foraging trips at sea with attendance bouts ashore. Pups suckle and increase in mass during the periods of maternal attendance and lose mass when their mothers are

foraging at sea. Males are typically heavier than females at birth, and both Antarctic and northern fur seal pups have the fastest absolute growth rates of all otariids (Scheffer and Wilke 1953; Payne 1979).

Study site

Macquarie Island (54°30′ S, 158°57′ E) is located in the southern Pacific Ocean, north of the Antarctic Polar Front. Antarctic fur seals breed on pebble beaches in a sheltered bay on the east coast of the northern tip of the island (Shaughnessy et al. 1988). The fur seal population is increasing at an annual rate of 13.0% and during the 1996–1997 breeding season about 110 pups were born (S.D. Goldsworthy, unpublished data). The subantarctic fur seal, *A. tropicalis*, also breeds on Macquarie Island and some hybrid pups are born each year (Goldsworthy et al. 1999). Pups of both species and hybrids were identified using morphological criteria (Condy 1978; Shaughnessy and Fletcher 1987; Goldsworthy et al. 1999) and only pups showing all the characteristics of Antarctic fur seals were used for this study. Data reported here were collected between 28 November 1996 and 8 January 1997.

Maternal attendance behaviour

On Macquarie Island, females were identified by uniquely numbered plastic tags applied to the trailing edge of each fore-flipper. Newborn pups were initially identified with paint marks, and later tagged (Dalton, Nettlebed, UK) when they exceeded 7 kg. Females were captured using a hoop net while pups were caught by hand (Gentry and Holt 1982; Erickson et al. 1993).

The attendance behaviour of 15 *A. gazella* lactating females was monitored using small radio transmitters incorporated into flipper tags (Sirtrack, Havelock North, NZ) that were applied to their fore-flipper soon after they gave birth (Goldsworthy, in press). Presence or absence of females ashore was monitored using a scanning receiver [Advanced Telemetry Systems (ATS), 150 and 151 MHZ model 2000B receiver] connected to a programmable data logger (ATS model 5040 data collection computer). Frequencies were monitored sequentially for 60 s and the number of pulses received was logged over a 45-min period.

Maternal attendance was also determined from direct observations of females ashore. Checks were made twice daily, usually at 0830 hours and 1730 hours local time. Data gathered by the automated receiver indicated that the average departure time for females that were still present at the evening check was 1945 hours ± 1 h 17 min and the average arrival time of females before the morning check was 0551 hours ± 1 h 21 min. Thus, we considered that a female had left the colony at 2000 hours if present in the evening check but absent in the morning check, and arrived at 0600 hours when present in the morning check but absent in the previous evening check. When a female was absent in the morning check but present in the evening check, the mid-point between the two observations was used to estimate the arrival time.

When a female was observed ashore in the evening and the following morning, we could not be confident that she had spent the entire night ashore because previous research (Goldsworthy, in press) and results from this study showed that in most cases females were also undertaking overnight foraging trips. Thus, when females were present ashore in the evening and the next morning, maternal attendance data could not be used as we were unable to determine if females had been at sea on an overnight foraging trip or remained onshore.

Pup mass change

Pups were weighed daily using 10 kg × 50 g or 20 kg × 100 g spring balances. When possible, pups were captured just after the departure of their mothers in order to determine mass change over an attendance bout.

Absolute mass gain (AMG, kg) over an attendance period was defined as the difference between the mass of the pup at the

beginning (m_i) and end (m_f) of an attendance bout while the daily mass gain (DMG, kg day^{-1}) was calculated as AMG divided by the duration of the previous foraging trip plus attendance bout duration.

Daily mass loss (DML, kg day^{-1}) was calculated during fasting periods as follows:

$$DML = (m_1 - m_2)/\Delta d$$

where m_1 is the mass (kg) of the pup measured at least 24 h after the departure of the mother to allow for the digestion of milk, m_2 is the subsequent mass (kg) measurement taken during the fasting period, and Δd is the number of days (d) between m_1 and m_2.

The mass-specific rate of mass loss (MSML, % day^{-1}) was calculated as follows:

$$MSML = (\log m_2 - \log m_1)/\Delta d) \times 100$$

The DML and MSML of pups were calculated when the consecutive masses of individual pups were obtained at least 24 h apart to allow a sufficient mass loss in the pup to be measured.

As pup mass change was monitored continuously through the study period, AMG over an attendance period and mass lost by a pup during a foraging trip could be determined on several occasions for a given pup. The most accurate AMG (weighing a pup just before suckling began and just after the departure of the female) obtained for a pup was used for analyses. When several AMG measurements of the same precision and DML were obtained for a given pup, random sampling was conducted to respect the independency criteria for the analysis.

Pup growth rate

Pup growth rates over the study period were determined from least-squares linear regression of mass against age (Doidge et al. 1986; Gentry et al. 1986). Growth rates were only calculated when at least ten mass measurements (range: 10–46) were available throughout the study period for a given pup.

To avoid repeated use of the same individual as independent observations to study the relationship between daily milk intake and growth rate, we used mean values of daily milk intake when repeated observations were available.

Statistical analysis

Analysis of variance (ANOVA), two-factor analysis of covariance (ANCOVA) and comparisons were performed using the SAS (1988) and Systat (1997) statistical packages. We used a stepwise descending covariance analysis (GLIM; Payne 1985) to estimate the impact of the different factors or their interactions on DML and MSML. Initial models included the factors sex, initial mass, fast duration as well as all the possible interactions of these factors. The relative importance of each factor, or interaction of factors, was analysed by removing each factor alternately from the model. For each factor removed, the increase in deviance was tested using F-tests. Once all the factors or interactions of factors had been tested in this manner, the factor(s), or the interaction of factors that caused the smallest increase in deviance in this procedure were removed from the initial model providing a new model for the next step. The same procedure was applied to the new model, and so on, leading to a suite of descending steps. At the end of the procedure, the contribution of factors or combination of factors to DML or MSML was statistically tested for each model and the final model only included statistically significant factors or combinations of factors. Means are given ± SD.

Results

Maternal attendance

A total 160 different foraging trips and 156 attendance bouts were recorded for 15 lactating females fitted with VHF transmitters, 8 with male pups, 7 with female pups. There was no significant change in the duration of foraging trips over the study period ($F_{1,158} = 0.83$, $P = 0.36$). There were also no significant intersexual differences in the duration of foraging trips (males, 2.05 ± 1.48 days, $n = 8$; females, 2.02 ± 1.55, $n = 7$; two-sample t-test $t_{13} = 0.19$, $P = 0.77$), attendance bouts (males, 0.45 ± 0.32 days, $n = 8$; females, 0.49 ± 0.29 days, $n = 7$; two-sample t-test $t_{13} = 0.58$, $P = 0.57$) or foraging cycles (males, 2.50 ± 0.38 days, $n = 8$; females, 2.51 ± 0.21 days, $n = 7$; two-sample t-test $t_{13} = 0.045$, $P = 0.96$). The average departure time for a foraging trip was 1700 hours ± 3 h ($n = 160$) with arrivals occurring at 0940 hours ± 4 h ($n = 160$) (Fig. 1). During attendance bouts, females remained ashore overnight in only 13% of cases. In all the other cases (87%), females undertook a new foraging trip on

Fig. 1 Distribution of the arrival (*black*) and departure times (*white*) throughout the day for female Antarctic fur seals equipped with a VHF transmitter at Macquarie Island between 28 November 1996 and 8 January 1997
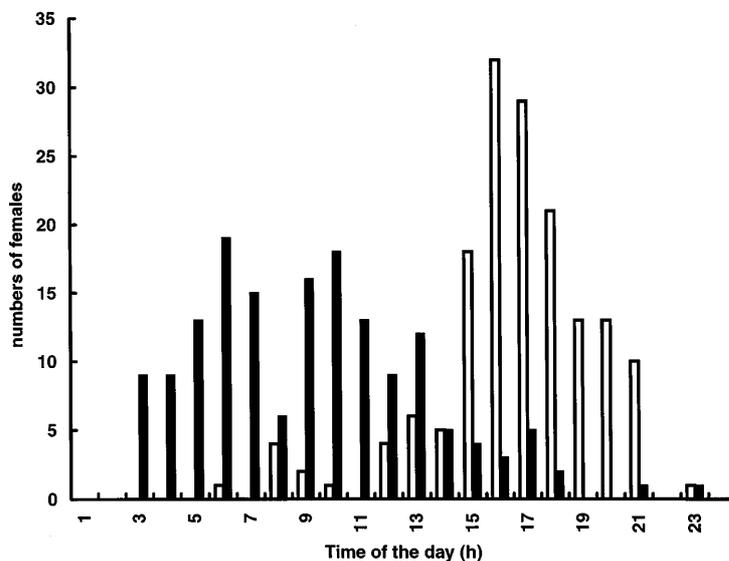
the same night subsequent to their arrival ashore. Out of the 160 foraging trips recorded from the 15 females fitted with transmitters, 56 were overnight foraging trips (35%) while 104 (65%) were extended foraging trips lasting more than 24 h. For extended foraging trips, no differences were detected in the average extended foraging trip duration obtained by telemetry and observation (VHF, 2.8 ± 1.2 days, $n = 15$; observation, 3.1 ± 1.4 days, $n = 57$; two-sample t-test, $t_{70} = 0.89$, $P = 0.39$).

AMG during periods of maternal attendance

AMG was measured for 33 different pups and ranged from 0.35 to 2.6 kg over attendance durations ranging from 5 to 12 h. AMG was analysed using ANOVA. AMG during an attendance bout was significantly related to the duration of the preceding foraging trip ($F_{1,31} = 25.89$, $P < 0.001$; Fig. 2), but was not related to the initial mass ($F_{1,31} = 3.164$, $P = 0.086$), age ($F_{1,31} = 0.229$, $P = 0.636$), sex of the pup ($F_{1,31} = 0.258$, $P = 0.615$) or the duration of the attendance bout ($F_{1,31} = 0.484$, $P = 0.492$).

Factor effects on mass loss rates of fasting pups

Three factors were available for the models, the sex of the pup, the initial mass (m_1) of the pup and the fast duration. Starting with the most comprehensive model (sex × initial mass × fast duration), we parsimoniously removed factors, or the interaction of factors in descending nested steps testing, at the same time, the effect of all of them statistically. The procedure revealed that none of the interactions or fast duration had a significant effect on DML, but that DML was significantly related to both sex and initial mass (Table 1). These results indicate that the linear regressions of DML against initial mass calculated for each sex (Fig. 3) have different intercepts (sex effect) but the same slopes (no significant interaction between sex and initial mass). The same procedure was conducted to test the effect of the factors (sex, initial mass, fast duration) or their inter-

actions on MSML. The sex of the pup was the only factor found to have a significant effect on MSML ($F_{1,28} = 9.056$, $P = 0.005$). MSML was significantly higher ($t = 2.32$, $df = 28$, $P = 0.027$) in female ($2.55 \pm 0.02\%$ day^{-1}, $n = 12$) than male ($2.13 \pm 0.02\%$ day^{-1}, $n = 18$) pups.

Growth rates

Growth rates were calculated for 68 pups over the study period. Male pups grew significantly faster than female pups (males, 0.108 ± 0.036 kg day^{-1}, $n = 38$; females, 0.079 ± 0.045 kg day^{-1}, $n = 30$; two-sample t-test, $t_{66} = 2.94$, $P = 0.004$).

DMG and growth rate

Pup growth rates were analysed using a two-factor ANCOVA with sex as factor and DMG as a covariate. There was no significant effect of the interaction between DMG and sex on pup growth rate ($F_{1,27} = 0.0007$, $P = 0.98$); however, growth rate was significantly related to the DMG ($F_{1,28} = 26.726$, $P < 0.001$) and sex of the pup ($F_{1,28} = 10.34$, $P = 0.003$). The linear regressions between growth rate and DMG calculated for each sex are shown in Fig. 4.

Discussion

The four mains results of our study were (1) the absence of sex differences in pup AMG during attendance bouts, (2) a higher DML and MSML in female than in male pups, (3) higher growth rates in male compared to female pups and (4) that the same DMG allowed males to grow more rapidly than female pups.

Pup mass gain, mass loss and growth

The AMG over an attendance period was related to the duration of the previous foraging trip (Fig. 3) but not to

Fig. 2 Absolute mass gain (AMG) of Antarctic fur seal pups over an attendance bout plotted against the duration of the previous foraging trip. AMG was linearly related to the duration of the preceding foraging trip (FT) by the following equation: AMG = $0.298 + 0.228$FT, $r^2 = 0.490$, $n = 33$, $P < 0.001$
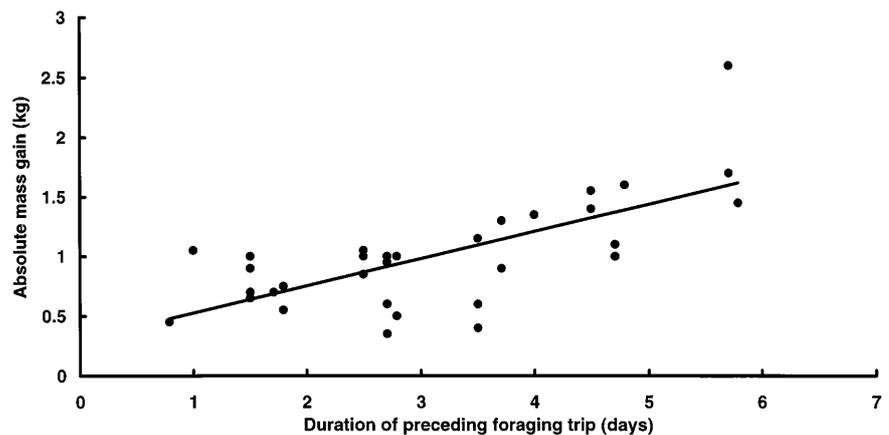
Table 1 Descending multifactorial covariance analysis (see text for details) of the effect of sex, initial mass and fast duration and their interactions on dailymass loss

Factor effect tested	Deviance	df	F	P
Complete model	0.0261	22		
Sex × initial mass × fast duration	0.0272	23	0.942	0.34
Fast duration × initial mass	0.0272	24	0.004	0.95
Sex × fast duration	0.0275	25	0.22	0.64
Sex × initial mass	0.0281	26	0.523	0.48
Fast duration	0.0283	27	0.195	0.66
Initial mass	0.0744	28	44.068	<0.001
Sex	0.0379	28	9.188	0.005

the sex of the pup. Similar results have been found by Goldsworthy (1995) in Antarctic fur seals at Heard Island, although only for male pups. Likewise, Arnould et al. (1996) found that the amount of milk energy consumed per feeding bout was positively related to the duration of the previous foraging trip and the initial mass of the pup, but not to the sex of the pup in Antarctic fur seals at South Georgia. In northern fur seals and Californian sea lions, mass-specific milk intake was found to be related to pup mass, but was not found to differ according to pup sex (Costa and Gentry 1986; Oftedal et al. 1987).

We found that DML of pups increased with their initial mass. We also found that DML and MSML differed according to the sex of the pup, and that fasting female pups were losing about 4.2 g kg^{-1} day^{-1} (i.e. 0.42% of their total mass) more than male pups. The results from two other otariid studies suggest that sex differences in MSML may arise from differences in the metabolic rates of male and female pups. Costa and Gentry (1986) found sex differences in metabolic water production in northern fur seal pups, females producing 25% more water than males. Similarly, using a respira-

tory chamber, Ono and Boness (1996) found that the resting metabolic rates of female California sea lion pups were higher than those of male pups. These observations, plus sex differences in the mass-specific rate of mass loss observed in our study strongly suggest that female and male pups have different energy expenditure. Futhermore, Arnould et al. (1996) found that female and male Antarctic fur seal pups at South Georgia differed in their body composition, females having higher body lipid reserves than male pups, indicating that the energy store may differ with pup sex.

We found that the growth rate of pups was significantly related to their DMG. As expected, faster-growing pups had higher daily mass gains than slower growing pups. Unexpected was the finding that for female pups to grow at the same rate as males, they would require higher daily mass gain. Hence the higher growth rates observed in males likely result from their lower mass-specific rate of mass loss (while fasting) and not their greater milk intake. According to these differences, a 10-kg female pup loses 42 g day^{-1} more than a male pup of the same mass. These differences are within the range of observed intersexual differences in growth rates at Macquarie Island (i.e. 30 g day^{-1}). Furthermore, as we found that DML increased with pup mass, we would also expect that to maintain their growth rate through the whole rearing period, pups should increase their milk intake. A constant daily milk intake would result in decreasing growth rates as pup mass increases and growth rates would be nil when milk intake only compensated for the DML of the pup.

Maternal expenditure

As indicated in the Introduction, several studies in fur seals and other otariids have found differences in birth

Fig. 3 Daily mass loss (*DML*) after the first 24-h fasting period in relation to the initial mass (m_1) for male and female Antarctic fur seal pups at Macquarie Island. DML was linearly related to m_1 by the following equations: male pups, DML $= -0.0770 + 0.0319m_1$, $r^2 = 0.453$, $n = 18$, $P = 0.002$; female pups, DML $= -0.0388 + 0.0319m_1$, $r^2 = 0.789$, $n = 12$, $P < 0.001$
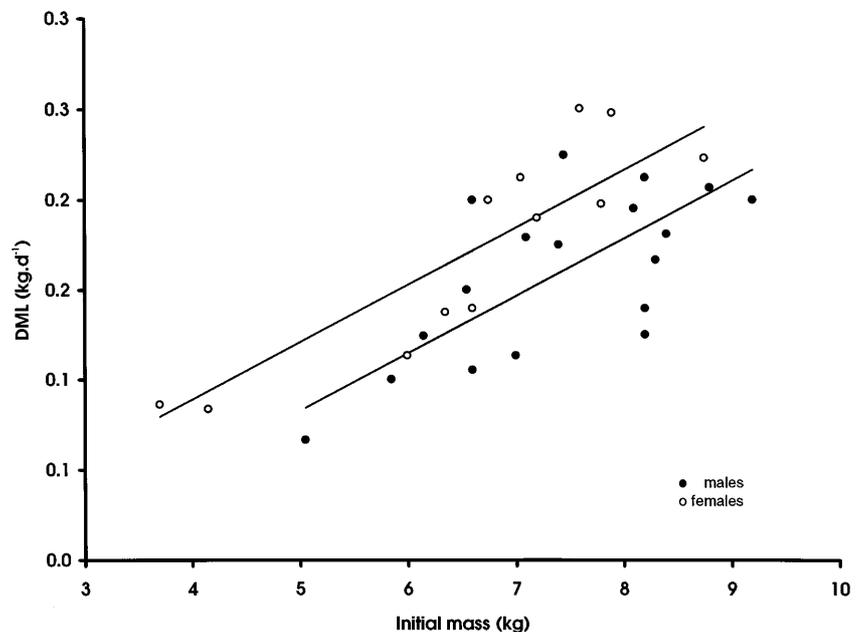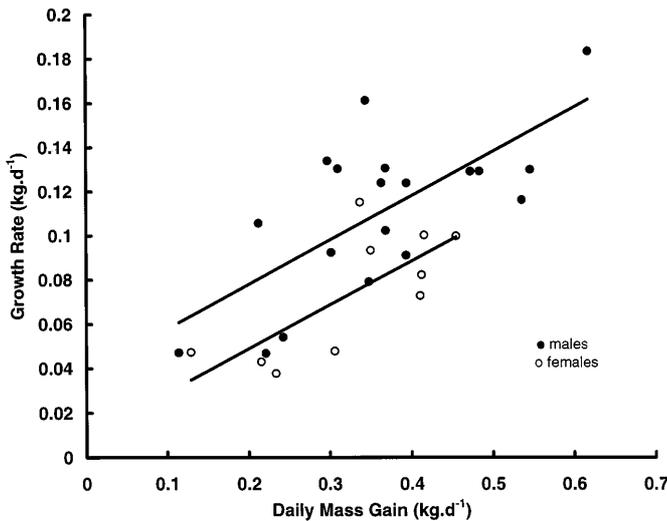
Fig. 4 Growth rate in relation to the daily mass gain (DMG) for male and female Antarctic fur seal pups at Macquarie Island. The growth rates were linearly related to DMG by the following equations: male pups, growth rate $= 0.040 + 0.195\text{DMG}$, $r^2 = 0.483$, $n = 20$, $P = 0.001$; female pups, growth rate $= 0.009 + 0.195\text{DMG}$, $r^2 = 0.547$, $n = 10$, $P = 0.014$

masses and growth rates between female and male pups and this has led to the conclusion that there is differential maternal expenditure between the sexes in these species. However, several recent studies, including this one have shown that male pups do not receive more milk than females per unit of mass (Costa and Gentry 1986; Arnould et al. 1996; Ono and Boness 1996) suggesting an absence of differential postnatal expenditure in terms of milk input or gross energy transfer to the pup by the mother but, nevertheless, male pups grow faster than females pups (Ono and Boness 1996; this study).

Differences in energy expenditure between the sexes as found in California sea lion pups (Ono and Boness 1996) and northern fur seal pups (Costa and Gentry 1986) could account for much of the observed differences in mass loss rates and thus growth rates of male and female pups. In fact, the differences we found in the mass-specific rate of mass loss are sufficient to account for all the differences we found between the growth rates of male and female pups at Macquarie Island. This is an important finding because in previous studies, intersexual differences in growth rates (Crawley 1975; Mattlin 1981; Doidge et al. 1984; Kerley 1985; Trillmich 1986; Boness et al. 1991; Goldsworthy 1992, 1995; Mison-Jooste 1999), and the assumed similarity of metabolic rates and fasting mass losses, may have lead to the incorrect conclusion that males receive more postnatal expenditure than female pups. It should also redirect attention from studies examining maternal expenditure in otariids to potential intersexual differences in fasting mass loss/metabolic rates. Studies which examine pup growth should start from an assumption of equal maternal expenditure and investigate if differential mass loss or metabolic rate can account for any intersexual

differences in growth rates. Few studies have investigated intersexual differences in mammalian metabolic rate, and rarely during the growth stage when the high metabolic rates of young animals may be related to their relatively rapid tissue synthesis. In adult humans and domestic mammals, the metabolic rate of males is generally higher than that of females (Astrand 1960; see Hudson and Christopherson 1985), but this is not always the case with wild ruminants. Although differences in metabolic rates between males and females are sometimes noted, their occurrence is inconsistent, except in a few cases where there are pronounced differences in mass, with the larger males having higher metabolic rates than smaller females (Kautz et al. 1981; see also Hudson and Christopherson 1985).

Recent studies on the Antarctic fur seal population at South Georgia have shown no intersexual differences in milk intake (Arnould et al. 1996) and indicate that in most years, male and female pups grow at similar rates (Lunn and Boyd 1993). For subantarctic fur seals at Amsterdam Island, no differences were found in the rate of mass gain and growth rate (Georges and Guinet, in press) or rates of mass loss (C. Guinet and J.Y. Georges, unpublished data) between male and female pups. This raises the interesting question as to the factors influencing and determining the extent of intersexual differences in the fasting mass loss rates and metabolic rates of pups.

Although results from several studies suggest that female pups have elevated metabolic rates compared with males (Costa and Gentry 1986; Ono and Boness 1996; this study), there is also some evidence to the contrary. Arnould et al. (1996) found no differences in the rate of mass loss between male and female pups and showed that female Antarctic fur seal pups had significantly higher lipid contents than male pups. From these results we would expect that better-insulated females should in fact have lower metabolic rates than less well-insulated leaner male pups. Furthermore, a study on Californian sea lions found no sex differences in the activity level of pups (Ono and Boness 1996). Future studies on maternal expenditure in otariid seals should focus on investigating the factors that may be responsible for differences in energy expenditure between male and female pups, such as differences in metabolic rates, in activity levels and/or body composition. Such studies should be undertaken under a broad range of ecological conditions.

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