

Mass change in Antarctic fur seal (*Arctocephalus gazella*) pups in relation to maternal characteristics at the Kerguelen Islands

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Abstract: Maternal allocation to growth of the pup was measured in Antarctic fur seals (*Arctocephalus gazella*) at the Kerguelen Islands during the 1997 austral summer. Absolute mass gain of pups following a maternal foraging trip was independent of the sex of the pup but was positively related to foraging-trip duration and maternal length. However, daily mass gain (i.e., absolute mass gain of the pup divided by foraging-trip duration) decreased with increasing foraging-trip duration but increased with maternal length. While the pup were fasting, their daily mass loss was related to their sex and initial body mass: both heavier pups and female pups lost more mass per day than lighter pups and male pups. The mass-specific rate of mass loss was significantly higher in female than in male pups. Over the study period, the mean growth rate was zero, with no difference between female and male pups. The growth rate in mass of the pup was positively related to maternal length but not to maternal condition, and negatively related to the foraging-trip duration of the mother and the initial mass of the pup. This indicates that during the study period, heavier pups grew more slowly because of their higher rate of daily mass loss during periods of fasting. Interestingly, for a given maternal length, the mean mass of the pup during the study period was higher for male than for female pups, even though the rate of daily mass gain was the same. Such differences are likely to result from sex differences in the mass-specific rate of mass loss. As female pups lose a greater proportion of their mass per day, a zero growth rate (i.e., mass gain only compensating for mass loss) is reached at a lower mass in female pups than in male pups. Our results indicate that maternal allocation does not differ according to the sex of the pup, but suggest that the two sexes follow different growth strategies.

Résumé : L'allocation des ressources de la mère à son petit a été étudié chez l'Otarie de Kerguelen (*Arctocephalus gazella*) aux Îles Kerguelen pendant l'été austral 1997. Le gain de masse absolu du petit après une excursion alimentaire de sa mère était indépendant de son sexe, mais était significativement relié à la durée de l'excursion et à la longueur de la mère. Cependant, le gain de masse quotidien (i.e., le gain de masse absolu du petit divisé par la durée en jours de l'excursion alimentaire de la mère) diminuait avec l'augmentation de la durée des séjours en mer mais augmentait en fonction de la longueur de la mère. Pendant les périodes de jeûne, la perte de masse quotidienne du petit dépendait de son sexe et de sa masse initiale, les taux de perte de masse étant plus élevés chez les femelles et les petits les plus lourds. La perte de masse spécifique était également significativement plus élevée chez les petites femelles comparée aux petits mâles. Pendant la période d'étude, le taux de croissance pondérale moyen était nul, et aucune différence n'a été observée entre les petits mâles et les petites femelles. Le taux de croissance pondérale était en corrélation avec la longueur de la mère, mais pas avec sa condition et en corrélation négative avec la durée de l'excursion alimentaire de la mère et avec la masse initiale du petit. Ces résultats indiquent que les petits les plus lourds ont grossi plus lentement que les petits plus légers du fait de leur taux de perte de masse plus important. Pour une longueur donnée de la mère, la masse moyenne des petits au cours de la période d'étude était plus élevée chez les petits mâles que chez les petites femelles, malgré le même gain moyen quotidien. Cette différence résulte probablement des différences de pertes de masse spécifiques en fonction du sexe du petit. Comme les petites femelles perdent quotidiennement une plus grande proportion de leur masse que les petits mâles, un taux de croissance nul (i.e., où le gain de masse compense tout juste la perte de masse) est atteint à une masse pondérale moins élevée chez les petites femelles que chez les petits mâles. Nos résultats indiquent qu'il n'y a pas de différences d'allocation en fonction du sexe du petit, mais suggèrent que mâles et femelles ont des stratégies de croissances différentes.

Introduction

The level of parental investment in offspring can be estimated from the overall cost to the parent of ensuring a given

allocation to the offspring, i.e., the amount of milk/mass or energy received by the offspring and, ultimately, its growth rate (Evans 1990). Evans (1990) indicated that for a given allocation of resources by the parents, the investment in an

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offspring may differ according to environmental conditions. For example, when environmental conditions are unfavourable, increasing investment costs may be associated with a decrease in the allocation of parental resources to the offspring (Trivers 1974; Evans 1990). In addition, age-related changes in ability to exploit resources could produce a similar effect (Evans 1990). Nevertheless, from the offspring's perspective, parental investment, and consequently the growth rate, which are correlated with weaning mass, are likely to be important in influencing offspring survival, as was found in red deer (*Cervus elaphus*) (Clutton-Brock et al. 1987), particularly during the initial period of nutritional independence after weaning. They may, therefore, still prove to be proximate correlates of fitness.

Fur seals are sexually dimorphic, with a polygynous reproductive system. Hence, they are considered good models for critical assessment of theories of differential investment between the sexes, as (i) females produce only one pup per season, (ii) all parental care is maternal, and (iii) neonates are nutritionally dependent on the milk produced by their mother until weaning. Parental-investment theory predicts that if higher maternal investment affects lifetime reproductive success in male pups more than in female pups, then mothers should expend greater resources on the sex with the greatest variance in reproductive success, i.e., males (Trivers and Willard 1973; Williams 1979). In polygynous animals, it is assumed that males exhibit the greatest variance in reproductive success, and that in sexually dimorphic species the reproductive success of males is closely allied to their large size and mass. However, in a review, Trillmich (1996) indicated that there is little evidence for differential allocation of maternal resources in relation to pup sex in pinnipeds and that ecological conditions, such as variability in resource abundance and maternal size, age, and experience, account for most of the variance in pup development to weaning. Thus, for any given year, differences in pup growth may reflect some differences between the sexes but also inter-individual differences in maternal characteristics and foraging efficiency.

The aim of this study was to investigate, for a given year (i.e., under the same environmental conditions), (i) the factors affecting gain in pup mass in relation to maternal and pup characteristics, (ii) differences in growth rate between the sexes and (iii) whether such differences result from differential gain in pup mass and (or) differential use of maternal resources by pups of each sex.

Methods

Study species

The Antarctic fur seal breeds in the South Atlantic and Indian oceans, in the vicinity of the Antarctic Polar Front (Bonner 1981). From mid-November until mid-December, females give birth to a single pup within a few days of their arrival. Pups are weaned in late March – early April (Doidge et al. 1986; Shaughnessy and Goldsworthy 1990; Lunn and Boyd 1991). As in other otariids, males are typically heavier than females at birth, and growth rates of *Arctocephalus gazella* pups, along with *Callorhinus ursinus* pups, are amongst the fastest recorded for all otariids (Scheffer and Wilke 1953; Payne 1979). After parturition mothers stay ashore for 5–7 days (perinatal attendance period) before mating and departing to sea on the first of many foraging trips. During this phase of the

lactation period mothers alternate foraging trips at sea with attendance bouts ashore.

Study sites

The Kerguelen Islands (49°00'S, 70°00'E) are located in the South Indian Ocean, near the Antarctic Polar Front. The fur seal population is increasing rapidly within the Kerguelen Islands: the number of breeding females at the Îles Nuageuses increased from approximately 300 individuals in the late 1960s to more than 10 000 in the late 1980s, which represents an annual rate of increase of 17% (Jouventin and Stonehouse 1985; Guinet et al. 1996). The present study took place between 4 February and 11 March 1998 at Cap Noir on the northeastern coast of the Courbet Peninsula. The study period was restricted because of logistic constraints and therefore does not encompass the 4-month breeding season entirely. The colony comprises approximately 400 mother-pups pairs.

Data collection

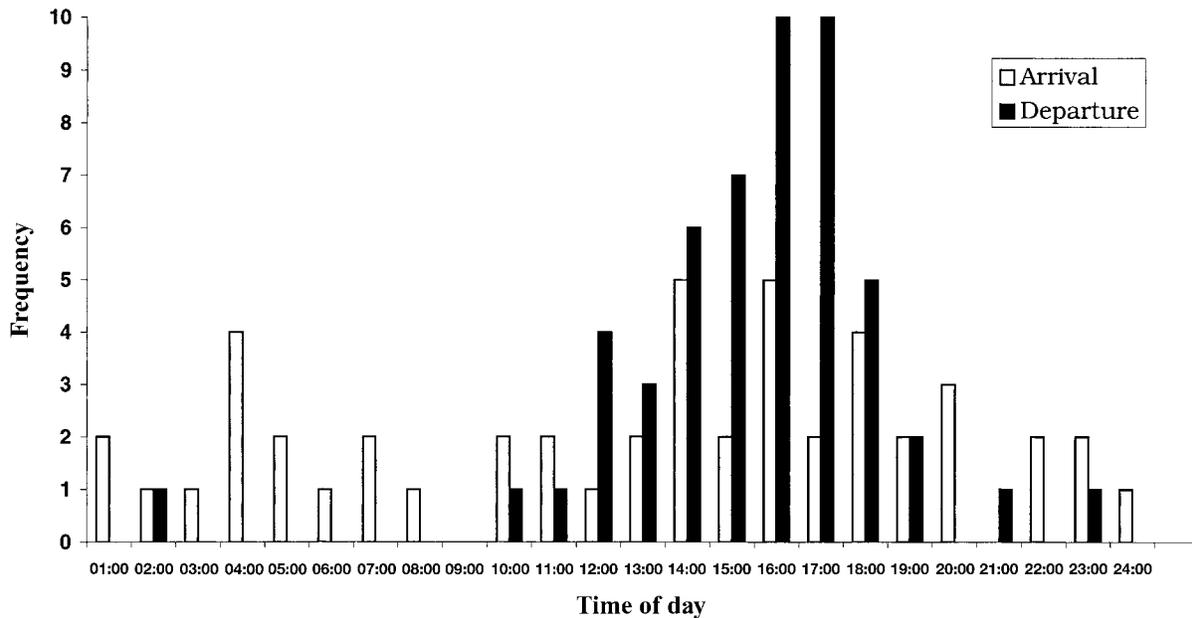
One hundred and four pups were caught on arrival throughout the colony and tagged using numbered plastic tags (size 1 Supertags, Dalton Supplies Pty Ltd., U.K.) applied to the trailing edge of each foreflipper. Pups were weighed using a 20 × 0.1 kg spring balance (Salter Industrial Measurement Ltd., West Bromwich, U.K.) and their standard length (horizontally from the tip of the nose to the tip of the tail) was measured to the nearest centimetre. Mothers of tagged pups ($n = 79$) were caught with a hoop net and marked with serial numbers by bleaching the fur on their rump with peroxide hair dye (Clairol Born Blonde®, Bristol-Myers Squibb Ltd., West Ryde, N.S.W., Australia) or by using Nyanzol. Standard length of mothers was measured to the nearest centimetre and weighed to the nearest 0.2 kg using a 50 × 0.2 kg capacity scale (Salter Industrial Measurement Ltd.). Body condition of females and pups was determined from the residual value of the linear regression of mass (kg) against standard length (cm). The use of the residual values of the regression of mass against standard length was found to be independent of the length of the mothers and pups ($P = 0.99$ in both cases) and was preferred to the usual ratio, mass (kg) / standard length (cm), as the latter body-condition index is not independent of adult female length ($r^2 = 0.40$, $n = 78$, $P < 0.001$) or pup length ($r^2 = 0.49$, $n = 104$, $P < 0.001$). To determine the change in body condition over the study period, one measurement of mass and length per pup was randomly sampled in order to respect the independence criteria. The body-condition index of the pup was calculated as the difference between the observed mass and the expected mass of the pup according to its length. The expected mass (μ) of the pup was calculated according to the following equation:

$$\mu = 0.271x - 11.712 \quad (r^2 = 0.55, n = 104, P < 0.001)$$

where x is the length of the pup in centimetres and μ is the expected mass of the pup in kilograms.

The provisioning attendance patterns of 20 pups of the pups monitored during this study were monitored by fitting their mother with a 20-g 150-MHz radio transmitter (Sirtrack Ltd., Havelock North, New Zealand). Presence or absence of mothers was monitored using a DCC II scanning receiver (Model 2000B receiver, range 150–151 MHz, Advanced Telemetry Systems Inc., Isanti, MN 55040, U.S.A.) connected to a programmable data logger (Model 5040, Advanced Telemetry Systems Inc.). Frequencies were monitored sequentially for 30 s and the number of pulses received was logged during that period. Maternal attendance was also determined by direct observation of 76 females without a radio transmitter. Checks of the whole colony were made twice daily, between 08:00–09:00 and 18:00–19:00. Exact arrival and departure

Fig. 1. Distribution of arrival and departure times for 20 female Antarctic fur seals fitted with VHF transmitters at the study colony during the study period.



times were recorded if possible, otherwise they were estimated using the median arrival and departure times recorded for the 20 mothers fitted with VHF tags (Fig. 1). Arrival and departure times were estimated as the median time elapsed between morning and evening checks.

Pup mass change

All tagged pups were weighed every 6 d during the study period. A subsample of pups were also weighed daily during a whole foraging cycle, which was defined as the sum of the foraging-trip duration and the following attendance bout of the mother. While the mother foraged at sea the pup fasted on land and thus lost body mass, and while the mother was ashore the pup was suckling and gained mass (Fig. 2). Observers were present in the study colony during the entire day and whenever possible, pups were weighed just prior to reunion with their mother and just after the mother's departure in order to determine, as precisely as possible, the mass increase during an attendance period.

For calculating the rate of mass loss of the pups while their mothers were foraging at sea, the initial mass of the pup was measured a minimum of 24 h after the departure of the mother (to allow for digestion of the milk retained in the stomach) and then following the return of the mother but before suckling began again. The mass-specific rate of mass loss (%/d) was calculated according to the following relationship:

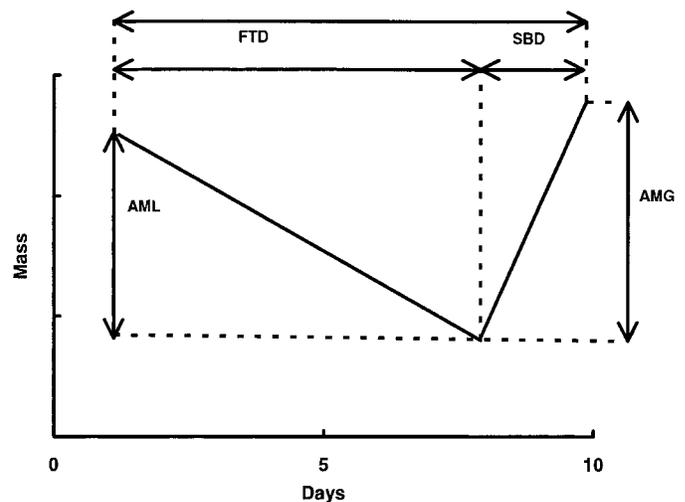
mass-specific rate of mass loss

$$= \left[\frac{(\log M_f - \log M_i)}{\Delta t} \right] \times 100$$

where M_i is initial mass, M_f is final mass, and t is time expressed in days.

Daily mass gain was calculated as the absolute mass gain of the pup during an attendance period divided by the cycle duration (Fig. 3).

Fig. 2. Schematic representation of pups' mass change during a foraging cycle (FC), which is defined as the foraging-trip duration (FTD) plus the subsequent maternal shore-bout duration (SBD). Pups lose mass during the fast, which corresponds to the maternal FTD. The absolute mass loss (AML) corresponds to the total mass lost during one foraging trip. The absolute mass gain (AMG) corresponds to the total amount of mass gained by the pup during one maternal shore bout.



Pup growth rates

Pup growth rates over the study period were determined from least square linear regression of mass, standard length, and body-condition index against time.

Analysis of variance (ANOVA), and multiple analysis of covariance (ANCOVA) were performed using the SAS (SAS Institute Inc., U.S.A.) and SYSTAT statistical packages (SYSTAT, 7.0 statistics, SPSS, Inc., U.S.A.). We used a stepwise descending covariance analysis (GLIM; Payne 1985) to estimate the impact of the different factors or their interactions on the studied variable.

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 an F test. 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 on the tested variable was statistically tested for each model, and the final model only included statistically significant factors or combinations of factors. To avoid repeated use of the same individual as independent observations for studying foraging-trip duration and shore-bout duration, we used mean foraging-trip and shore-bout durations over the study period.

Results

Maternal attendance

Of the 20 lactating females fitted with a VHF transmitter, 9 produced male pups and 11 produced female pups. There were no differences in the mean foraging-trip durations in days (combined mean = 8.90 d, SD = 2.72 d, $n = 96$) determined either from direct observation ($n = 76$) or using VHF transmitters ($n = 20$) ($F_{[1,94]} = 0.57$, $P = 0.45$), or according to the sex of the pup ($F_{[1,94]} = 1.09$, $P = 0.299$). Mean foraging-trip duration, however, was negatively related to maternal length according to the following equation:

$$y = -0.118x + 22.450 \quad (r^2 = 0.074, n = 77, \\ P = 0.017)$$

where x is maternal length and y is foraging-trip duration. We found significant differences between the duration of attendance bouts determined from direct observation (mean = 1.52 d, SD = 0.49 d, $n = 68$), and using VHF transmitters (mean = 1.88 d, SD = 0.59 d, $n = 20$; $t = 2.454$, $P = 0.008$), while pup sex ($F_{[1,86]} = 0.018$, $P = 0.89$) and maternal length ($F_{[1,71]} = 0.06$, $P = 0.80$) had no effect on shore-bout duration. There was no difference in cycle duration (mean = 10.74 d, SD = 2.83 d, $n = 86$) determined by direct observation or VHF transmitters ($F_{[1,84]} = 0.616$, $P = 0.435$), or according to pup sex ($F_{[1,84]} = 0.018$, $P = 0.89$). The duration of the entire foraging cycle, however, was negatively related to maternal length according to the following equation:

$$y = -0.130x + 25.728 \quad (r^2 = 0.076, n = 71, \\ P = 0.019)$$

where y is foraging-cycle duration (d) and x is maternal length (cm).

Effect of female length and body condition on pup length

The initial length of pups when tagged at the beginning of the study was significantly related to maternal length ($F_{[1,77]} = 50.48$, $P < 0.001$), maternal body condition ($F_{[1,77]} = 7.13$, $P < 0.001$), and their sex ($F_{[1,77]} = 11.71$, $P < 0.001$). None of the interactions were found to have a significant effect on the initial length of the pup ($P > 0.05$ in all cases). The initial mass of pups when tagged was found to be significantly related to maternal length ($F_{[1,77]} = 48.87$, $P < 0.001$) but not

to maternal condition ($F_{[1,77]} = 2.58$, $P = 0.11$) or their sex ($F_{[1,77]} = 2.18$, $P = 0.14$). None of the interactions were found to have a significant effect on the initial mass of the pup ($P > 0.05$ in all cases).

Mass loss rates of fasting pups

The effect of three factors (sex, initial mass, and fast duration of the pup) and all the possible interactions on mass loss rates of fasting pups was tested.

Daily mass loss was found to differ according to the sex of the pup ($F_{[1,80]} = 4.31$, $P = 0.041$), its mass ($F_{[1,80]} = 184.92$, $P < 0.001$), and its fast duration ($F_{[1,80]} = 22.12$, $P < 0.001$), while no significant interactions were found between these factors ($P > 0.05$ in all cases). The daily rate of mass loss was found to increase significantly with respect to the initial mass of the pup and decrease with increasing fast duration (Table 1).

The mass-specific rate of mass loss was related to the sex of the pup ($F_{[1,80]} = 4.96$, $P = 0.03$) and its fast duration ($F_{[1,80]} = 3.85$, $P = 0.053$) but not to the initial mass of the pup ($F_{[1,80]} = 1.14$, $P = 0.53$). No significant interactions were found between these factors ($P > 0.05$ in all cases). The mass-specific rate of mass loss was significantly higher in female pups (mean = 2.95%/d, SD = 0.038%/d, $n = 42$) than in male pups (mean = 2.70%/d, SD = 0.038%/d, $n = 40$; $t_{[1,80]} = 2.80$, $P = 0.006$).

Mass gain

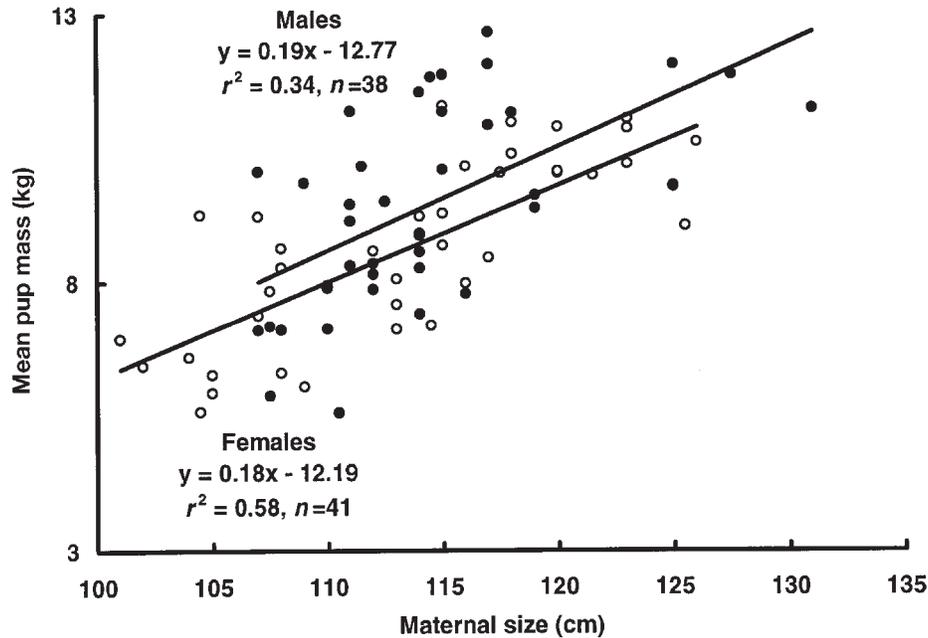
The effects of four factors (pup sex, foraging-trip duration, and maternal length and body condition) and their interactions on absolute mass gain and daily mass gain of the pup were tested.

Absolute mass gain during an attendance bout was measured for 28 male and 27 female pups for whom maternal length and body condition were known. Absolute mass gain did not vary according to pup sex ($F_{[1,53]} = 0.92$, $P = 0.34$) or maternal body condition ($F_{[1,53]} = 0.45$, $P = 0.51$) but was significantly positively related to maternal length ($F_{[1,53]} = 10.14$, $P = 0.002$) and the duration of the previous foraging trip ($F_{[1,53]} = 10.14$, $P = 0.002$), while no interactions had a significant effect on absolute mass gain ($P > 0.05$ in all cases). Absolute mass gain during an attendance bout was found to be positively related to maternal length and to the duration of the previous foraging trip (Table 2).

The daily rate of mass gain was not related to pup sex ($F_{[1,53]} = 0.06$, $P = 0.80$) or maternal body condition ($F_{[1,53]} = 0.47$, $P = 0.49$) but was related to foraging-trip duration ($F_{[1,53]} = 3.80$, $P = 0.049$) and maternal length ($F_{[1,53]} = 5.33$, $P = 0.026$). No interactions were found to have a significant effect on the daily rate of mass gain ($P > 0.05$ in all cases). The daily rate of mass gain decreased with increasing foraging-trip duration but increased with maternal length (Table 2).

Growth rates

The rate of mass change (mean = 0.0029 kg·d⁻¹, SD = 0.0454 kg·d⁻¹, $n = 79$) was not significantly different from zero (modified t test (Dixon and Massey 1969), $t = 0.56$, $P = 0.58$), indicating a lack of pup growth in mass over the study period. Since pups were not growing, we used a mean value for body mass over the study period. The mean mass of the

Fig. 3. Mean pup mass during the study period as a function of maternal length for male (●) and female (○) Antarctic fur seal pups.**Table 1.** Multiple regression analysis by pup sex of daily mass loss and mass-specific rate of mass loss in relation to pup's initial mass and maternal foraging-trip duration (i.e., pup's fast duration).

Dependent variable	Pup sex	Model			Independent variable ^a	
		<i>r</i> ²	<i>P</i>	<i>n</i>	Initial pup mass	Foraging-trip duration
Daily mass loss	Male	0.98	<0.001	40	26.91	-3.14
					0.028	-0.004
	Female	0.77	<0.001	42	10.28	-4.22
					0.022	-0.006
				<i>P</i> < 0.001	<i>P</i> < 0.001	

^aFor each variable studied, the values given are the *t* value, the coefficient of the slope, followed by the probability (*P*) value; *n*, sample size.

pups (females: mean = 8.60 kg, SD = 1.65 kg, *n* = 41; males: mean = 9.40 kg, SD = 1.87 kg, *n* = 38) was significantly related to maternal length ($F_{[1,77]} = 65.80$, $P < 0.001$) (Fig. 3), maternal body condition ($F_{[1,77]} = 5.99$, $P = 0.017$), and pup sex ($F_{[1,77]} = 5.41$, $P = 0.022$). There were no sex differences in the slope of mean body mass of the pups over the study period in relation to maternal length (ANCOVA, $F_{[1,76]} = 0.07$, $P = 0.78$) or maternal body condition (ANCOVA, $F_{[1,76]} = 0.22$, $P = 0.63$).

The rate of mass change of the pups (Table 3) over the study period was positively related to maternal length ($F_{[1,77]} = 6.19$, $P = 0.015$) and negatively related to the mean duration of maternal foraging trips ($F_{[1,77]} = 6.19$, $P = 0.011$) and the initial mass of the pup ($F_{[1,77]} = 18.38$, $P < 0.001$). We found no effect of pup sex ($F_{[1,77]} = 1.40$, $P = 0.24$) or maternal body condition ($F_{[1,77]} = 1.55$, $P = 0.21$) on the rate of mass change of pups.

The rate of change in length of the pup (mean = 0.196 cm·d⁻¹, SD = 0.070 cm·d⁻¹, *n* = 77) over the study period was not related either to its sex ($F_{[1,75]} = 0.09$, $P = 0.76$) or to maternal body condition ($F_{[1,75]} = 0.04$, $P = 0.83$), but

tended to be positively related to maternal length ($F_{[1,75]} = 3.34$, $P = 0.07$) and negatively related to the mean duration of maternal foraging trips ($F_{[1,75]} = 3.17$, $P = 0.08$). It was also negatively related to the initial length of the pup ($F_{[1,75]} = 9.17$, $P = 0.003$; Table 3).

The rate of change in the body-condition index of pups over the study period (mean = -0.047 kg·d⁻¹, SD = 0.039 kg·d⁻¹, *n* = 77) was not related to their sex ($F_{[1,75]} = 0.07$, $P = 0.78$), to the maternal body-condition index ($F_{[1,75]} = 0.13$, $P = 0.718$), or to maternal length ($F_{[1,75]} = 0.146$, $P = 0.70$) but was negatively related to the pups' initial body-condition index ($F_{[1,75]} = 9.87$, $P < 0.001$) and to the mean duration of maternal foraging trips ($F_{[1,75]} = 8.49$, $P = 0.005$; Table 3).

Discussion

Within the body-mass range of our study pups we were unable to detect any significant change in the mass-specific rate of mass loss in relation to the initial mass of the pup, while the mass-specific rate of mass loss tended to decrease with increasing duration of fasting periods. Interestingly, we

Table 2. Multiple regression analysis of absolute mass gain against daily mass gain in relation to maternal length and duration of the preceding foraging trip.

Dependent variable	Model			Categorical variable (sex)	Independent variable ^a	
	r ²	P	n		Maternal length	Foraging-trip duration
Absolute mass gain	0.437	<0.001	55	ns	3.534	5.903
				—	0.041	0.159
				P = 0.341	P = 0.002	P < 0.001
Daily mass gain	0.261	<0.001	55	ns	3.180	-2.150
				—	0.004	-0.006
				P = 0.256	P = 0.003	P = 0.036

^aFor each variable studied, the values given are the *t* value, the coefficient of the slope, followed by the probability (*P*) value; ns, not significant; *n*, sample size.

Table 3. Multiple regression analysis of growth rate in mass and length in relation to maternal length, initial mass, length, and body-condition index (BCI) of the pup, and mean maternal foraging-trip duration.

Dependent variable	Model				Independent variable ^a		
	r ²	P	n	Categorical variable (sex)	Maternal length	Initial mass of pup	Foraging-trip duration
Growth rate in mass	0.272	<0.001	79	P = 0.241	2.229	-3.977	-2.395
					0.002	-0.012	-0.003
					P = 0.027	P < 0.002	P = 0.019
Growth rate in length	0.198	<0.001	77	P = 0.764	Maternal length	Initial length of pup	Foraging-trip duration
					2.001	-3.585	-1.842
					0.003	-0.007	-0.004
					P = 0.049	P < 0.001	P = 0.069
Rate of change in BCI	0.298	<0.001	77	P = 0.780	Maternal length	Initial BCI of pup	Foraging-trip duration
					1.47	-4.92	-2.127
					—	-0.019	-0.003
					ns	P < 0.001	P = 0.003

^aFor each variable studied, the values given are the *t* value, the coefficient of the slope, followed by the probability (*P*) value; ns, not significant; *n*, sample size.

found that female pups had a higher mass-specific rate of mass loss than male pups over the range of fast durations observed in our study. Similar results were found at Macquarie Island (Guinet et al. 1999). This is an important finding because in previous studies of fur seals, intersexual differences in growth rates (Crawley 1975; Mattlin 1981; Doidge et al. 1984; Kerley 1985; Trillmich 1986; Boness et al. 1991; Goldsworthy 1995; Mison-Jooste 1999), and the assumed similarity of metabolic rates and fasting mass losses, may have led to the incorrect conclusion that males receive a greater postnatal allocation of maternal resources than female pups. Other studies of otariids suggest the existence of at sex differences in metabolic rates of pups. Costa and Gentry (1986) found that female northern fur seal pups had a water-production rate 25% greater than that of males. Similarly, using a respiratory 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, in addition to sex differences in the mass-specific rate of mass loss observed in our study, suggest that male and female Antarctic fur seal pups may have different metabolic rates. In addition, male and female pups may also differ in their behaviour during fasting periods.

More information on intersexual differences in activity budgets (percentage of time spent swimming in the water and resting on land) is required to examine whether female and male pups have different fasting strategies in relation to fast duration.

We found that the rate of daily mass loss increased with the mass of the pup. This indicates that in order to maintain their mass and to grow at the same rate, heavier pups require an increasing quantity and or quality of milk to support their larger mass relative to lighter ones. Thus, with increasing mass, the growth rate of pups should decrease progressively with constant daily mass gain, and should be zero when mass gain only compensates for mass lost.

The mass gained by the pup was not related to its sex but was related to the duration of the mother's previous foraging trip. This result is consistent with those of other studies, which indicate a positive relationship between absolute mass gain or milk intake of the pup and the duration of the preceding foraging trip (Goldsworthy 1995; Arnould et al. 1996; Georges and Guinet 2000; Guinet et al. 1999).

However, we observed that the pups' daily mass gain decreased significantly with increasing foraging-trip duration, indicating that their rate of mass gain decreased with

increasing foraging-trip duration. This is confirmed by the negative relationship we found between the rate of increase in mass, length, and the change in body-condition index, and increasing foraging-trip duration. Lunn et al. (1993) found no relationship between foraging-trip duration and growth rate except in one year, 1990–1991, which was characterised by low food abundance and abnormally long foraging trips. The results obtained at the Kerguelen Islands are consistent with those obtained at South Georgia in a year of low food availability, as indicated by the lack of any growth in mass of pups (although they were still growing in length) and a decrease in pups' body-condition index throughout our study (a negative rate of change in body-condition index). This is further supported by the mean duration of foraging trips (8.8 d), which were 1.5 d longer than the longest mean foraging trip observed for the same species at South Georgia in years of low food availability (Lunn et al. 1993). These observations suggest that under poor environmental conditions, mothers are unable to maintain or to increase the rate of milk supply to their pups to allow them to grow. Furthermore, we found that under these conditions, shorter mothers had longer foraging trips than longer mothers, and for a given foraging-trip duration, the daily mass gain of pups increased with maternal length. This indicates that under the environmental conditions experienced by Antarctic fur seals at the Kerguelen Islands during the 1997–1998 austral summer, longer females (which are likely to be older; see Lunn and Boyd 1993) were more efficient (mass gain relative to maternal foraging-trip duration, i.e., maternal expenditure) than shorter (younger) females. Foraging efficiency may be improved through experience and this factor may be particularly important in years of low food availability. Older mothers may therefore be more efficient per foraging trip or have more suitable attendance schedules in relation to the needs of their pups than younger mothers (see Georges and Guinet 2000). As pups of longer mothers had a higher daily mass gain and their mothers undertook shorter foraging trips, pups of longer mothers grew in mass and tended to grow in length more than pups of shorter females. This result is consistent with the finding of Georges and Guinet (2000), who found that the growth rate of sub-Antarctic fur seal (*Arctocephalus tropicalis*) pups at Amsterdam Island, which is characterised by low provisioning rates, was positively correlated with the length of the mother and negatively related to the duration of foraging trips.

At South Georgia, Lunn et al. (1993) found no effect of maternal length, age, or experience on growth rates of the pups in any of their study years. However, they found that the reproductive performance of experienced multiparous female Antarctic fur seals was greater than that of younger (primiparous) females because they had higher natality rates, gave birth to heavier pups earlier in the season, and had greater weaning success (Lunn et al. 1994). We found no effect of maternal length on the pups' rate of body-condition change, suggesting that growth in length of pups is favoured over change in body condition.

We also found that the mean mass of the pups over the study period was related to both maternal length and body condition. Similarly, at Amsterdam Island, sub-Antarctic fur seal mothers in better condition had pups with higher growth

rates (Georges and Guinet 2000). However, in this study, we found no relationship between maternal condition and pup mass gain or rates of change in mass, length, and body condition. The presence or absence of relationships between pup characteristics (mass, length, and growth rate) and maternal body condition should be considered with caution because the mass of each female fur seal was not measured systematically at the exact time of arrival ashore in our study. Large variations in females' mass, and consequently body condition, occur over an attendance period, as they lose mass rapidly while suckling their pups (Georges and Guinet 2000).

As the mothers' ages were not known in our study, we were unable to determine the respective effects of age and length on the reproductive performance of our study females. However, the effect of maternal length and foraging-trip duration explained only 26% of the total variation in pups' daily mass gain, and other factors such as foraging efficiency and pup energy expenditure are likely to have contributed to growth-rate differences among pups.

We found that for a given maternal length the growth rate of the pup decreased with its initial mass. This is consistent with our findings of greater absolute daily expenditure by pups with increasing body mass. Furthermore, we observed that for a given maternal length, the mean mass of female pups was lower than that of male pups. This may be due to two factors: first, the smaller length and body mass of female pups at birth, as is generally the case in fur seals (Costa et al. 1988; Boyd and McCann 1989; Mison-Jooste 1999), and secondly, higher mass-specific rates of mass loss in female pups than in male pups, which result in a lower equilibrium mass in female pups for the same rate of mass gain, as they exhibit a higher rate of mass loss. These findings lead to the conclusion that there is no differential postnatal energy expenditure in Antarctic fur seal pups at the Kerguelen Islands under the conditions of our study, which took place in a year of low food availability. Similar results were found at Macquarie Island (Guinet et al. 1999) in a year of normal food availability. These results suggest that female and male pups have different growth strategies, with female pups requiring more energy than male pups to grow in mass at the same rate, and that factors such as body composition of the pup (see Arnould et al. 1996) or its energy expenditure (Costa and Gentry 1986; Ono and Boness 1996) are more important in determining sex differences in growth rate than are differences in maternal expenditure (see Trillmich 1996; Lunn and Arnould 1997). Our results, in the light of those found in Antarctic fur seals at South Georgia (Lunn et al. 1993) and sub-Antarctic fur seals at Amsterdam Island (Georges and Guinet 2000), suggest that the effect of maternal characteristics such as length on pup growth rates may differ among localities and (or) with environmental conditions, and that under low food availability conditions, pup growth rates may be influenced by the length of the female, but this may not be the case under conditions of high food availability.

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References

- Arnould, J.P.Y., Boyd, I.L., and Socha, D.G. 1996. Milk consumption and growth efficiency in Antarctic fur seal (*Arctocephalus gazella*) pups. *Can. J. Zool.* **74**: 254–266.
- Boness, D.J., Oftedal, O.T., and Ono, K.A. 1991. The effect of El Niño on pup development in the California sea lion (*Zalophus californianus*) I. Early postnatal growth. *In* Pinnipeds and El Niño: responses to environmental stress. *Edited by* F. Trillmich and K.A. Ono. Springer-Verlag, Berlin, Heidelberg, and New York. pp. 173–179.
- Bonner, W.N. 1981. Southern fur seals *Arctocephalus* (Geoffroy Saint Hillaire and Cuvier 1826). *In* Handbook of marine mammals. *Edited by* S.H. Ridgway and R.J. Harrison. Academic Press, New York. pp. 161–208.
- Boyd I.L., and McCann, T.S. 1989. Pre-natal investment in reproduction by female Antarctic fur seals. *Behav. Ecol. Sociobiol.* **24**: 377–385.
- Clutton-Brock, T.H., Guinness, F.E., and Albon, S.D. 1987. Red deer, behavior and ecology of two sexes. The University of Chicago Press, Chicago.
- Costa, D.P., and Gentry, R.L. 1986. Free-ranging energetics of northern fur seals. *In* Fur seals: maternal strategies on land and at sea. *Edited by* R.L. Gentry and G.L. Kooyman. Princeton University University Press, Princeton, N.J. pp. 19–101.
- Costa, D.P., Trillmich, F., and Croxall, J.P. 1988. Intraspecific allometry of neonatal size in the Antarctic fur seal (*Arctocephalus gazella*). *Behav. Ecol. Sociobiol.* **22**: 361–364.
- Crawley, N.C. 1975. Growth of New Zealand fur seal pups. *N.Z. J. Mar. Freshwater Res.* **9**: 539–545.
- Doidge, D.W., Croxall, J.P., and Ricketts, C. 1984. Growth rates in the Antarctic fur seal *Arctocephalus gazella* at South Georgia. *J. Zool.* (1965–1984), **203**: 87–93.
- Doidge, D.W., McCann, T.S., and Croxall, J.P. 1986. Attendance behavior of Antarctic fur seals. *In* Fur seals: maternal strategies on land and at sea. *Edited by* R.L. Gentry and G.L. Kooyman. Princeton University University Press, Princeton, N.J. pp. 102–114.
- Evans, R.M. 1990. The relationship between parental input and investment. *Anim. Behav.* **39**: 797–813.
- Georges, J.-Y., and Guinet, C. 2000. Maternal provisioning strategy and pup growth in subantarctic fur seals on Amsterdam Island. *Ecology*, **81**: 295–308.
- Goldsworthy, S.D. 1995. Differential expenditure of maternal resources in Antarctic fur seals, *Arctocephalus gazella*, at Heard Island, southern Indian Ocean. *Behav. Ecol.* **6**: 218–228.
- Guinet, C., Cherel, Y., Ridoux, V., and Jouventin, P. 1996. Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: changes in relation to consumer biomass 1962–85. *Antarct. Sci.* **8**: 23–30.
- Guinet, C., Goldsworthy, S., and Robinson, S. 1999. Sex differences in mass loss rate and growth efficiency in Antarctic fur seal (*Arctocephalus gazella*) pups at Macquarie Island. *Behav. Ecol. Sociobiol.* **46**: 157–163.
- Jouventin, P., and Stonehouse, B. 1985. Biological survey of Ile de Croy, Iles Kerguelen, *Polar Rec.* **22**: 688–691.
- Kerley, G.I.H. 1985. Pup growth in the fur seals *Arctocephalus tropicalis* and *A. gazella* on Marion Island. *J. Zool. Ser. A*, **205**: 315–324.
- Lunn, N.J., and Arnould, J.P.Y. 1997. Maternal investment in Antarctic fur seals: evidence for equality in the sexes. *Behav. Ecol. Sociobiol.* **40**: 351–362.
- Lunn, N.J., and Boyd, I.L. 1991. Pupping-site fidelity of Antarctic fur seals at Bird Island, South Georgia. *J. Mammal.* **74**: 908–919.
- Lunn, N.J., and Boyd, I.L. 1993. Influence of maternal characteristics and environmental variation on reproduction in Antarctic fur seals. *Symp. Zool. Soc. Lond. No. 66*. pp. 115–129.
- Lunn, N.J., Boyd, I.L., Barton, T., and Croxall, J.P. 1993. Factors affecting the growth rate and mass at weaning of Antarctic fur seals at Bird Island, South Georgia. *J. Mammal.* **74**: 908–919.
- Lunn, N.J., Boyd, I.L., and Croxall, J.P. 1994. Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. *J. Anim. Ecol.* **63**: 827–840.
- Mattlin, R.H. 1981. Pup growth of the New Zealand fur seal *Arctocephalus fosteri* on the Open Bay Islands, New Zealand. *J. Zool.* (1965–1984), **193**: 305–314.
- Mison-Jooste, V. 1999. Contribution à l'étude de la biologie des populations de l'otarie à fourrure du cap (*Arctocephalus pusillus pusillus*). Les soins maternels diffèrent-ils en fonction du sexe du jeune? Thèse de Doctorat, Université Claude-Bernard (Lyon I), Lyon, France.
- Ono, K.A., and Boness, D.L. 1996. Sexual dimorphism in sea lion pups: differential maternal investment, or sex-specific differences in energy allocation? *Behav. Ecol. Sociobiol.* **37**: 31–41.
- Payne, M.R. 1979. Growth in the Antarctic fur seal (*Arctocephalus gazella*). *J. Zool.* (1965–1984), **187**: 1–20.
- Payne, C.D. 1985. The GLIM system, Release 3.77, manual. Royal Statistical Society, London.
- Scheffer, V.B., and Wilke, F. 1953. Relative growth in the northern fur seal. *Growth*, **17**: 129–145.
- Shaughnessy, P.D., and Goldsworthy, S.D. 1990. Population size and breeding season of the Antarctic fur seal *Arctocephalus gazella* at Heard Island—1987/1988. *Mar. Mamm. Sci.* **6**: 292–304.
- Trillmich, F. 1986. Maternal investment and sex-allocation in the Galapagos fur seal *Arctocephalus galapagoensis*. *Behav. Ecol. Sociobiol.* **19**: 157–164.
- Trillmich, F. 1996. Parental investment in pinnipeds. *Adv. Study Behav.* **25**: 533–577.
- Trivers, R.L. 1974. Parent–offspring conflict. *Am. Zool.* **14**: 249–264.
- Trivers, R.L., and Willard, D.E. 1973. Natural selection of parent ability to vary the sex ratio of offspring. *Science* (Washington, D.C.), **179**: 90–92.
- Williams, G.C. 1979. The question of adaptative sex ratio in out-crossed vertebrates. *Proc. R. Soc. Lond. B Biol. Sci.* **205**: 567–580.