Early mortality and perinatal growth in the subantarctic fur seal (*Arctocephalus tropicalis*) on Amsterdam Island

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Abstract

Early mortality and pup growth during the perinatal period were investigated in pups of the subantarctic fur seal *Arctocephalus tropicalis* on Amsterdam Island. Mothers that were shorter in body length and expected to be younger, gave birth earlier in the pupping season, compared with longer/older mothers. Pups born early were often still-born, suggesting that shorter/younger mothers that gave birth early in the season were not able to carry their foetuses to term. Pregnant females arrived ashore 1.4 days before giving birth, regardless of the date and their body condition. There was a positive relationship between maternal body length and pup birth mass. Consistently, birth mass increased throughout the pupping period. After parturition, mothers suckled their pups during an average 8.7-day postnatal period that was significantly shorter in mothers giving birth late in the season. However, the absolute gain in pup mass was 1.5 kg regardless of the birth date, suggesting that mothers did not leave their pups before they had transferred a given amount of body reserves to them. We propose that pups born late grew faster because they were bigger at birth and because their mothers were likely to be more experienced. Mothers in good condition, nursing male pups transferred more milk and therefore greater mass to their pup, whereas mothers in poor condition were unable to do so. Such differences did not occur in smaller female pups, suggesting that pup growth was limited by maternal resources in male pups but not in female pups. The lack of a relationship between birth mass and absolute gain during the perinatal period suggests that mass at birth determined pup body mass after the perinatal period. Body mass is an important factor in growth rate and survival during the period of pup dependence.

Key words: Amsterdam Island, *Arctocephalus tropicalis*, subantarctic fur seal, parturition, perinatal period, mortality

INTRODUCTION

Pinnipeds spend most of their life at sea but have to return to land to breed and nurse their offspring. In phocid (earless) seals, maternal care consists of a short, intensive period of lactation, during which the pup sucks while its mother fasts ashore (Bonner, 1984). During this period, all energy transferred to the pup is derived from maternal body reserves. In contrast, maternal care in otariid seals (eared, including the fur seals) is characterized by a relatively short perinatal period ashore with the newborn pup, followed by a long pup-rearing period (4 months to 3 years) of alternating foraging trips at sea and attendance periods ashore (Gentry & Kooyman, 1986).

Before parturition, pregnant fur seals arrive ashore

with all the necessary nutrients and energy to support themselves and their pups during the perinatal period (Costa & Trillmich, 1988). Pregnant females of all species of fur seals spend on average 1–2 days ashore before giving birth. Several studies, particularly in the Antarctic *Arctocephalus gazella* and northern *Callorhinus ursinus* fur seals, have investigated the timing of birth in otariids in relation to the sex of the pup, maternal age, size, experience and environmental conditions (Boyd & McCann, 1989; Duck, 1990; Trites, 1992a; Lunn & Boyd, 1993a,b; Boyd 1996). Younger Antarctic and northern fur seals give birth to lighter pups later in the pupping season (Trites, 1992a; Lunn & Boyd, 1993a), probably because they implant later compared to older mothers (Boyd, 1996; York & Scheffer, 1997). Consequently, there is a decline in birth mass throughout the pupping period (Boyd & McCann, 1989). Conversely, several studies suggest that in Cape fur seals *A. pusillus pusillus*, longer/older females give

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birth later in the season (Rand, 1955), while birth mass increases with birth date (Mison-Jooste, 1999). After birth and until mating occurs, mothers nurse their pups that then have to store body reserves from maternal milk to survive while the mother is foraging at sea.

The duration of the perinatal period has been described previously for most fur seals (Antarctic fur seals, Doidge, McCann & Croxall, 1986; Goldsworthy, 1992, 1995; Lunn & Boyd, 1993a,b; northern fur seals, Gentry & Holt, 1986; New Zealand fur seals *A. forsteri*, Goldsworthy, 1992; Galapagos fur seals *A. galapagoensis*, Trillmich, 1986a; Cape fur seals, David & Rand, 1986; Juan Fernandez fur seals *A. philippi*. Francis, Boness & Ochoa-Acuña, 1998). However, investigations of the first days of life of the pups have only been conducted for a few species (see Costa & Trillmich, 1988; Lunn & Boyd, 1993a,b; Boltnev, 1994; Boltnev, York & Antonelis, 1998). Factors that affect pup growth during the perinatal period may be important determinants of pup survival during the first fasting period. In northern fur seals, mortality mostly occurs while pups are left unattended for the first time, with the greatest number of deaths occurring probably as a result of starvation just before the mother returns to nurse her pup (Trites, 1992b). Early mortality may also occur with increasing population density, as observed at several colonies of Antarctic and South American *A. australis* fur seals (Doidge, Croxall & Baker, 1984; Harcourt, 1992).

Several factors may affect the timing of birth, the survival of pups and the rate of pup growth. In this paper, we investigate the effects of maternal size and condition on the timing of birth and on the size and growth rate of pups in subantarctic fur seals *A. tropicalis* breeding on Amsterdam Island during two consecutive reproductive seasons. We investigate early mortality in relation to the year, the sex of the pup, and the date of birth. We describe the perinatal period, in relation to the sex of the pup, its birth date, and maternal body condition. We also consider the consequences of these parameters of the perinatal period on pup growth and pup body mass after the perinatal period.

MATERIAL AND METHODS

Study site and animals

This study was carried out during the austral summers 1995–96 and 1996–97 (referred to as 1996 and 1997) at the study colony La Mare aux Elephants, Amsterdam Island in the Indian Ocean (37°55′S, 77°30′E), *c.* 400 km north of the subtropical front. Large colonies of subantarctic fur seals are found on the west and the northeast coasts of the island on a coastline composed of boulders and large blocks of rock (Roux, 1987; Guinet, Jouventin & Georges, 1994). The fur seal population on Amsterdam Island increased annually by 7.8% between 1956 and 1970, and by 15.5% between 1970 and 1982 (Roux, 1986). Between 1982 and 1993 the population

seemed to have stabilized with an annual total pup production in excess of 10 000 (Guinet *et al.*, 1994). From late November to early January, 749 births (438 in 1996 and 311 in 1997) were identified during daylight by continuous scans of the study beach. At birth, new-borns were sexed, weighed (Salter spring scale, ± 0.05 kg) and individually marked with small-mammal ear tags (Chevillot, 81000 Tarbes, France) placed on the trailing edge of the fore flipper. These tags were later replaced in pups heavier than 7 kg, by large numbered plastic tags (Dalton Rototags, Dalton Supply, Nettlebed, U.K.) to monitor pups over the rearing period. Pup mortality was investigated in new-borns and in marked pups that were found dead within their first month of life in 1996 and within their first 2 weeks of life in 1997. Dates were counted as days after 1 November for each year.

Maternal characteristics

Mothers were not captured during the birth period to avoid disturbance of the colony during parturition and bias of the sampling. During the monitoring of parturition in 1996 and 1997, pregnant females were visually evaluated and assigned to one of 3 classes of body condition. These classes were defined by the extent to which pelvis and ribs were visible: poor (highly apparent), medium (poorly apparent) and good (not apparent). No mothers were tagged before December 1995. This visual classification of body condition was later validated by measuring (standard body length, ± 1 cm) and weighing (± 1 kg) mothers during the 1996 season. Before capture a visually evaluated body condition index was assigned to each mother. Mothers were captured using a collar, and were restrained on a wooden plank as described by Gentry & Holt (1982) before measuring. Mothers were not captured in 1997, but a visual body condition index was attributed to them. Maternal body condition was calculated using the residual values of the linear regression between maternal body mass (MBM, kg) and maternal body length (MBL, cm) determined by Georges & Guinet (2000): $MBM = -73.746 + 0.884 \ MBL$, $r = 0.641$, $P = 0.001$, $n = 105$ (Fig. 1). The mean body condition index differed significantly among visual classes (Fig. 2; ANOVA $F_{2,87} = 13.01$, $P < 0.001$). There were significant differences between poor (-1.849 ± 4.519, $n = 23$) or medium (-0.775 ± 3.411, $n = 37$) classes compared with the good (3.481 ± 4.713, $n = 30$) class, but no significant difference between poor and medium classes (Bonferoni post-hoc tests). Consequently, we defined 2 classes of mothers: those in poorer condition at parturition (poor and medium combined: -1.187 ± 3.872, $n = 60$) and those in better condition at parturition (3.481 ± 4.713, $n = 30$, $t = 5.009$, $P < 0.001$). Visual body condition indexes assigned in 1996 and 1997 were considered to be comparable as they were assigned by the same field worker (J.-Y. Georges) in both years. Some of the mothers monitored in 1997 had been tagged in 1996.
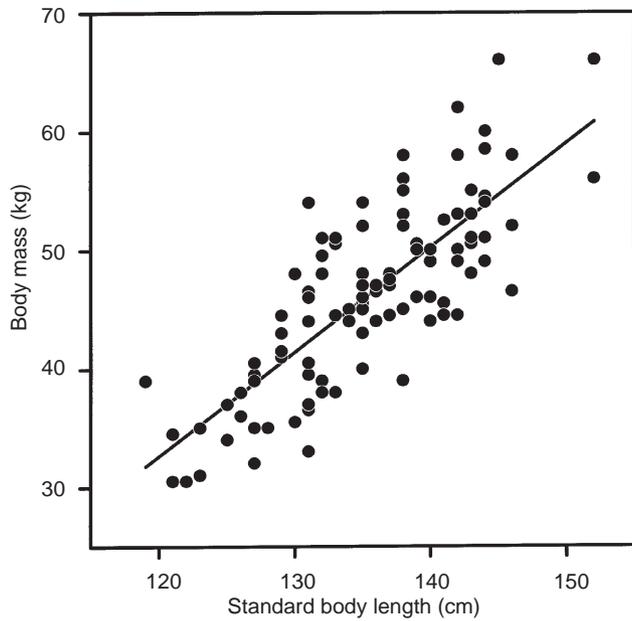
Fig. 1. Linear relationship between body mass and standard body length in lactating subantarctic fur seals breeding on Amsterdam Island during the 1996 reproductive season. Maternal body condition was determined using residual values of this regression.
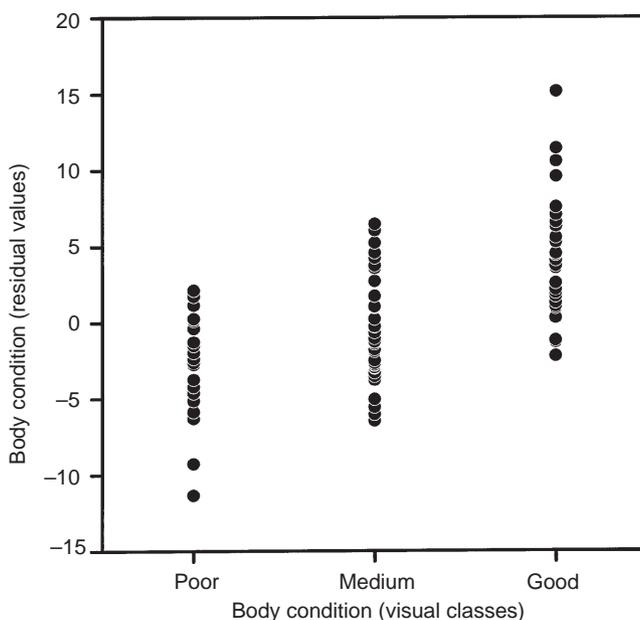

Fig. 2. Validation of the visually evaluated maternal body condition indices using residual values of the linear regression between maternal body mass and body length (see Methods).

Perinatal period

The perinatal period was investigated in 1997 for 94 tagged mother–pup pairs (44 male and 50 female pups). The perinatal period was divided into 2 periods according to Goldsworthy (1992): (1) the prenatal
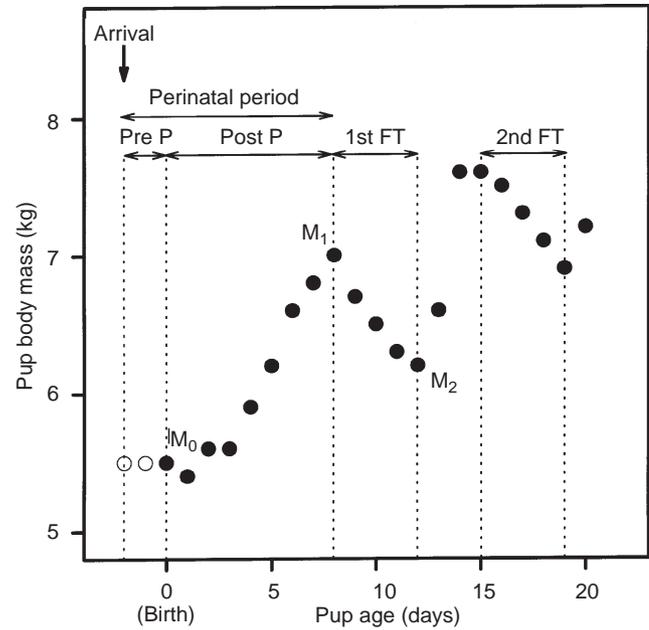

Fig. 3. Schematic representation of the perinatal period with a typical example of records of pup mass changes from birth until a few days after the first foraging trip in a subantarctic fur seal pup (female pup J165 born on 3 December 1997). Mother arrived 2 days before giving birth (pre P: prenatal period). During the postnatal period (Post P), pup body mass was M_0 at birth, decreased typically during the first day of life and then increased to pup body mass after the postnatal period (M_1), corresponding to an absolute pup mass gain M_1–M_0. Pup growth rate during the postnatal period was defined by [M_1–M_0]/Post P. During the first foraging trip (1st FT), the pup fasted and lost mass until M_2, when mother came back ashore.

period was defined from the date of arrival of the pregnant tagged female to the date of parturition; (2) the postnatal period was defined from the date of parturition to the date of first departure of the female (Fig. 3). After birth, new-borns were weighed daily (± 0.1 kg) until the first departure of their mother. The date of departure was determined by checking tagged females every day. Two groups of pups were defined according to date of birth: pups born early in the season, between 1 and 8 December (22 males and 25 females) and pups born late in the season, between 18 and 25 December 1996 (22 males and 25 females). The date of arrival after the first foraging trip was determined by daily attendance checks of tagged mothers to calculate the duration of the trip at sea.

Statistics

Statistical analyses were carried out in accordance with Sokal & Rohlf (1981), using Systat 7.0 statistical software (Systat, SPSS Inc.). Values are given as means $\pm$ SD. All tests were 2-tailed and differences were considered significant at $P < 0.05$.

Table 1. Birth sex ratio (males/females), and birth date, body mass, body length and body condition in male and female subantarctic fur seal new-borns on Amsterdam Island during the 1996 and 1997 pupping seasons. Values are means ± SD (sample size). Comparisons of means between sexes and between years (*t*-test) are given for each variable

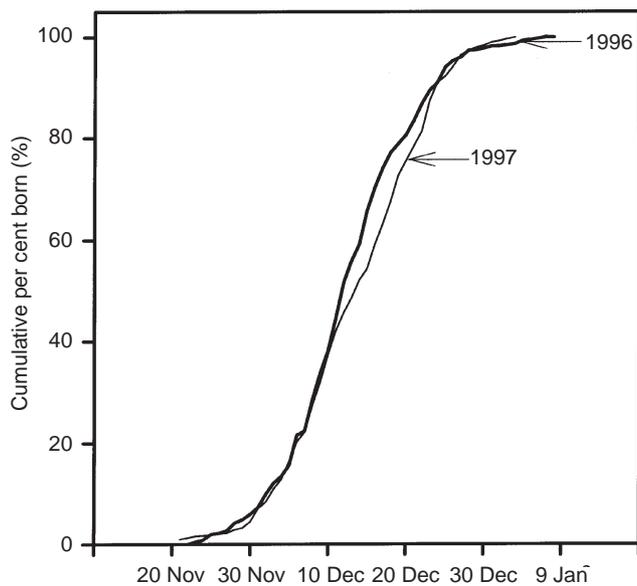|	1996	1997	1996 *vs* 1997
Sex ratio at birth	222/216	138/173	
Birth date			
Male pups	14 Dec ± 8.3 (222)	13 Dec ± 8.0 (138)	$t = 0.368$, $P = 0.713$
Female pups	14 Dec ± 8.9 (216)	14 Dec ± 8.0 (173)	$t = 1.391$, $P = 0.165$
Male *vs* female	$t = 0.942$, $P = 0.347$	$t = 0.061$, $P = 0.951$	
Birth mass (kg)			
Male pups	5.1 ± 0.6 (220)	4.9 ± 0.6 (131)	$t = 2.627$, $P = 0.009$
Female pups	4.5 ± 0.5 (214)	4.4 ± 0.5 (165)	$t = 2.0$, $P = 0.046$
Male *vs* female	$t = 10.245$, $P < 0.001$	$t = 7.81$, $P < 0.001$	

Fig. 4. Cumulative percentage of pups born in relation to date for the 1996 (heavy line) and 1997 (light line) reproductive seasons.

RESULTS

Parturition period

Births occurred from 21 November to 8 January, median birth dates being 12 December in 1996 and 14 December in 1997 (Fig. 4). Median birth dates were similar to mean birth dates (Table 1). There were no differences in mean birth dates between sexes for each year and between years (Table 1). In 1996 mothers were measured and the date of parturition was positively related to maternal body length ($F_{1,89} = 4.748$, $r^2 = 0.051$, $P = 0.032$).

The sex ratio at birth did not differ from unity (Table 1; 1996 $\chi_1^2 = 0.018$, $P = 0.892$; 1997 $\chi_1^2 = 1.756$, $P = 0.185$) and did not vary throughout the pupping seasons for both years (logistic regression: $\chi_1^2 = 0.356$, $P = 0.551$). Male pups were significantly heavier than female pups at birth for each year (Table 1). Birth mass was positively related to birth date for each sex except for male

pups in 1997 (Fig. 5; 1996: males $F_{1,218} = 19.549$, $r^2 = 0.082$, $P < 0.001$, females $F_{1,212} = 31.364$, $r^2 = 0.129$, $P < 0.001$; 1997: males $F_{1,129} = 1.343$, $r^2 = 0.01$, $P = 0.249$, females $F_{1,163} = 9.797$, $r^2 = 0.057$, $P = 0.002$). Males and females born in 1996 were significantly heavier than in 1997 (Table 1). In 1996, birth mass was positively related to maternal body length (males $F_{1,39}^2 = 11.725$, $r^2 = 0.231$, $P = 0.001$; females $F_{1,45} = 14.226$, $r^2 = 0.240$, $P < 0.001$).

Pup mortality

Among the 443 pups monitored in 1996, 3.2% ($n = 14$) died in the first 30 days of life. Pup mortality did not differ between males ($n = 7$) and females ($n = 7$), but pup mortality tended to be higher (*G*-test: $G = 3.095$, $P = 0.079$) in pups born before the median date of birth (4.5% of 269 pups) than in pups born after the median date of birth (1.1% of 174 pups).

Among the 331 pups monitored in 1997, significantly more died in the first 15 days of life (9.0%, $n = 28$) than in 1996 during 1 month ($G = 10.6$, $P = 0.001$). Mortality in female pups ($n = 16$) was twice that of male pups ($n = 8$) but differences were not significant ($G = 1.871$, $P = 0.171$). In 1997, mortality in pups born before the median date of birth was 11.7% of 143, i.e. twice that of pups born later (6.0% of 140), but the difference was not significant ($G = 2.458$, $P = 0.117$). In 1997, the cause of death was identified but sex was not determined for the four still-born pups found before the median date of birth (Table 2). For pups born before the median date of birth, 11 (58%) of 19 dead pups were still-born or died in the first day of life, while only one (11%) of the nine pups born later was still-born. Death was also attributed to starvation, crushing, and drowning (see Table 2). There were not enough data to investigate pup mortality in relation to maternal characteristics.

Perinatal period

In this study, the perinatal period (prenatal + postnatal periods; Fig. 3) was monitored in 34 mother–pup pairs, and the postnatal period (from birth to departure at sea
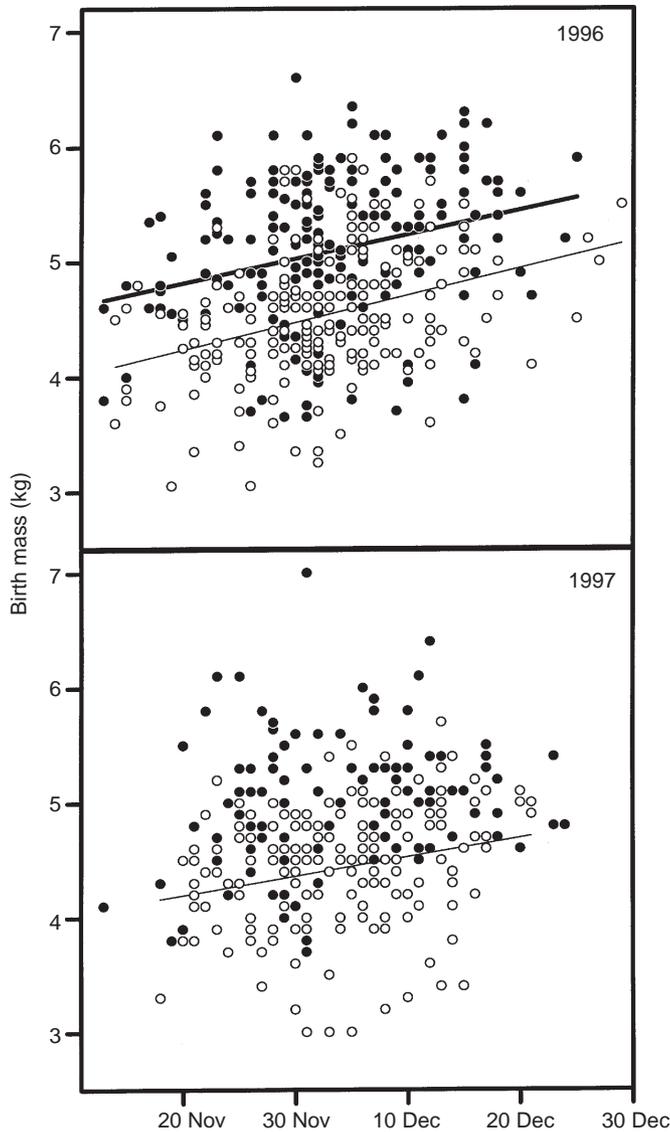
Fig. 5. The relationship between birth date and birth mass in male (closed circles) and female (open circles) pups for the 1996 and 1997 reproductive seasons.

of the mother) was monitored in an additional 60 mother–pup pairs (i.e. $n = 94$).

Prenatal period

Of the 34 mothers (17 male pups and 17 female pups), body condition was visually evaluated as poor in eight and good in 26. The prenatal period lasted on average 1.4 ± 0.9 days. There were no differences in the prenatal period duration according to the sex of the pup ($t_{17,17} = 0.19$, $P = 0.85$), or to maternal body condition ($t_{8,26} = 0.866$, $P = 0.406$). For both sexes, the duration of the prenatal period was not related to the date of arrival ($F_{1,32} = 0.035$, $r = 0.001$, $P = 0.938$).

Postnatal period

Body masses at birth and after the perinatal period were significantly higher in male pups than in female pups, but pup growth rate during the perinatal period and the duration of the postnatal period and first foraging trip did not differ between sexes (Table 3). Furthermore, absolute pup mass gain did not differ between sexes (Table 3), and was not related to birth mass (males $F_{1,40} = 0.235$, $r^2 = 0.006$, $P = 0.63$; females $F_{1,43} = 1.034$, $r^2 = 0.023$, $P = 0.315$). Thus, pup body mass after the perinatal period was positively related to birth mass in both sexes ($F_{1,85} = 74.45$, $r^2 = 0.467$, $P < 0.001$).

When pups born early were compared with those born late, results were similar (Table 3). Despite the increase in birth mass throughout the pupping period (Fig. 5), there were no differences between pups born early and those born late in the season (Table 3). This may be related to the relatively low sample size of the considered subsample or to differences in statistical power between univariate regression and comparison of means (Sokal & Rohlf, 1981). Pup body mass after the perinatal period tended to be higher in male pups than in female pups. Pups born early were suckled during a longer postnatal period, but there were no differences in absolute pup mass gain between pups born early and late, so that growth rate was slower in pups born early than in pups born late (Table 3). The time mothers spent ashore after their pups reached their maximum mass during the perinatal period was shorter in mothers giving birth early ($3.5 \pm 9.0\%$ of the whole postnatal period duration, $n = 42$) than in mothers giving birth late ($8.0 \pm 12.0\%$ of the whole postnatal period duration, $n = 43$; MANOVA $F_{3,81} = 3.361$, $P = 0.07$) regardless of the sex of the pup ($F_{3,81} = 0.203$, $P = 0.654$). The duration of the first foraging trip was not significantly different between mothers giving birth early and those giving birth late in the season (Table 3).

When considering maternal body condition, there were no differences in date of parturition between mothers in poor condition and those in good condition

Table 2. Causes of death (still-born, starved to death, others) in pups dead before 15 days of age in male and female pups according to their birth date during the 1997 pupping season

	Early			Late		
	Still-born	Starvation	Others	Still-born	Starvation	Others
Males	4	0	1	1	2	0
Females	3	5	2	0	3	3
Unsexed	4	0	0	0	0	0
Total	11	5	3	1	5	3

Table 3. Maternal body condition, birth mass, mass after the postnatal period (PP), absolute mass gain, daily growth rate during the postnatal period, duration of the postnatal period and of the first foraging trip (FT) in subantarctic fur seals at Amsterdam Island during the 1997 perinatal period, according to birth date. Values are means ± SD (sample sizes)

	All pups	Early	Late	Early *vs* late [a]
Birth mass (kg)				
Male pups	5.0 ± 0.5 (44)	5.0 ± 0.5 (22)	5.1 ± 0.6 (27)	$t = 0.266$, $P = 0.792$
Female pups	4.4 ± 0.5 (50)	4.4 ± 0.5 (25)	4.4 ± 0.5 (29)	$t = 0.404$, $P = 0.688$
Males *vs* females	$t = 5.928$, $P < 0.001$	$t = 4.404$, $P < 0.001$	$t = 3.929$, $P < 0.001$	
Mass after PP (kg)				
Male pups	6.4 ± 0.9 (42)	6.4 ± 1.1 (21)	6.5 ± 0.7 (21)	$t = 0.184$, $P = 0.855$
Female pups	5.9 ± 0.9 (45)	5.9 ± 0.8 (23)	6.0 ± 0.9 (22)	$t = 0.461$, $P = 0.647$
Males *vs* females	$t = 2.667$, $P = 0.009$	$t = 1.856$, $P = 0.07$	$t = 1.874$, $P = 0.068$	
Mass gain (kg)				
Male pups	1.4 ± 0.7 (42)	1.4 ± 0.9 (21)	1.4 ± 0.5 (21)	Sexes pooled
Female pups	1.5 ± 0.6 (45)	1.5 ± 0.6 (23)	1.6 ± 0.7 (22)	$t^* = 0.143$, $P = 0.866$
Males *vs* females	$t = 0.701$, $P = 0.485$	$t = 0.164$, $P = 0.871$	$t = 0.916$, $P = 0.365$	
Growth rate (g/day)				
Male pups	170 ± 81 (42)	154 ± 90 (21)	185 ± 70 (21)	Sexes pooled
Female pups	180 ± 82 (45)	160 ± 63 (23)	201 ± 95 (22)	$t^* = 2.14$, $P = 0.035$
Males *vs* females	$t = 0.596$, $P = 0.553$	$t = 0.243$, $P = 0.809$	$t = 0.632$, $P = 0.531$	
Duration of PP (days)				
Male pups	8.6 ± 2.0 (42)	9.6 ± 1.8 (21)	7.8 ± 1.6 (21)	Sexes pooled
Female pups	8.8 ± 2.2 (45)	9.3 ± 1.7 (23)	8.4 ± 2.4 (22)	$t^* = 3.376$, $P = 0.001$
Males *vs* females	$t = 0.35$, $P = 0.727$	$t = 0.678$, $P = 0.501$	$t = 0.983$, $P = 0.332$	
Duration of FT (days)				
Male pups	5.9 ± 2.3 (41)	6.1 ± 2.1 (21)	5.8 ± 2.7 (20)	Sexes pooled
Female pups	5.6 ± 2.8 (44)	5.0 ± 2.0 (23)	6.2 ± 3.4 (21)	$t^* = 0.759$, $P = 0.444$
Males *vs* females	$t = 0.603$, $P = 0.548$	$t = 1.706$, $P = 0.096$	$t = 0.465$, $P = 0.645$	

[a] Sexes were pooled for comparisons between early and late pups (t^*) when there were no significant differences between sexes.

Table 4. Birth mass, mass after the postnatal period (PP), absolute mass gain, daily growth rate during the postnatal period, duration of the postnatal period in subantarctic fur seals at Amsterdam Island during the 1997 perinatal period, according to maternal body condition. Values are means ± SD (sample sizes)

	Male pups	Female pups
Birth mass (kg)		
Poor condition	4.8 ± 0.5 (25)	4.4 ± 0.5 (31)
Good condition	5.3 ± 0.5 (19)	4.5 ± 0.5 (19)
Poor *vs* good	$t = 2.373$, $P = 0.022$	$t = 0.784$, $P = 0.437$
Mass after PP (kg)		
Poor condition	6.1 ± 0.8 (25)	5.8 ± 0.9 (29)
Good condition	6.9 ± 0.9 (17)	6.1 ± 0.7 (16)
Poor *vs* good	$t = 2.645$, $P = 0.012$	$t = 1.154$, $P = 0.256$
Mass gain (kg)		
Poor condition	1.3 ± 0.7 (25)	1.5 ± 0.7 (29)
Good condition	1.6 ± 0.7 (17)	1.6 ± 0.5 (16)
Poor *vs* good	$t = 1.711$, $P = 0.097$	$t = 0.714$, $P = 0.479$
Growth rate (g/day)		
Poor condition	163 ± 86 (25)	177 ± 95 (29)
Good condition	180 ± 74 (17)	186 ± 54 (16)
Poor *vs* good	$t = 0.7$, $P = 0.488$	$t = 0.404$, $P = 0.688$
Duration of PP (days)		
Poor condition	8.3 ± 2.1 (25)	8.9 ± 2.5 (29)
Good condition	9.2 ± 1.7 (17)	8.6 ± 1.5 (16)
Poor *vs* good	$t = 1.501$, $P = 0.141$	$t = 0.45$, $P = 0.655$

($t_{56,38} = 0.706$, $P = 0.482$). Mothers in good condition had heavier male pups than mothers in poor condition at birth and after the perinatal period, but there was no relationship between pup mass and maternal body condition in female pups (Table 4). Male pups of mothers in good condition had a higher absolute mass gain than male pups of mothers in poor condition but this difference was not found for female pups (Table 4). Pup growth rate and duration of the perinatal period did not differ according to maternal body condition ($t_{54,33} = 0.758$, $P = 0.451$, and $t_{54,33} = 0.698$, $P = 0.487$, respectively).

Perinatal period

For the 34 mothers for which the perinatal period (prenatal + postnatal periods) was investigated, there were no differences in the perinatal period duration according to the sex of the pup ($t_{17,17} = 0.293$, $P = 0.772$), or to maternal body condition ($t_{8,26} = 0.75$, $P = 0.463$). For both sexes, the duration of the perinatal period was negatively related to the date of arrival ($F_{1,32} = 7.038$, $r^2 = 0.18$, $P = 0.012$).

DISCUSSION

In pinnipeds, large body size is an important factor in fighting ability, mate acquisition, and ultimately for reproductive success in adult males, but body size is less related to reproductive success in adult females (McCann, 1982; Anderson & Fedak, 1985). Furthermore, high birth mass increases the probability of survival during the first stages of life (Calambokidis &

Gentry, 1985; Boltnev, York & Antonelis, 1998). This selection for large body size in males appears to begin during gestation, as has also been found in northern fur seals (Trites, 1991). In subantarctic fur seals breeding on Amsterdam Island, births occurred over a 50-day period. At birth, males were heavier than females, and the sex ratio did not vary throughout the pupping season. This is consistent with previous studies on otariids (Antarctic fur seal, Doidge, McCann & Croxall, 1986; northern fur seal, Trites, 1993; Galapagos fur seal, Trillmich, 1986b; subantarctic fur seal, Bester & Van Jaarsveld, 1994) and more generally in pinnipeds (southern elephant seal *Mirounga leonina*, Anderson & Fedak, 1985; grey seal *Halichoerus grypsus*, Kovacs & Lavigne, 1986; McCann, Fedak & Harwood, 1989; harbour seals *Phoca vitulina*, Bowen *et al.*, 1994). Interestingly, Mison-Jooste (1999) showed that in Cape fur seals, the sex ratio changes through the pupping period, males being born later than female pups.

On Amsterdam Island, pup mortality was two to four times higher in pups born early (before the median date of birth) than in pups born later in the season, and did not differ between sexes. Most of the mortality in pups born early was as still-births, whereas still-birth occurred only once in pups born after the median date of birth in 1997. In northern fur seals, birth is stimulated by the act of hauling out (Bigg, 1984). The higher incidence of still-births early in the season may be because some females returned to shore before their pups were near term. In fur seals, body length increases throughout life (Trites & Bigg, 1996), and longer individuals are expected to be older and more experienced (Lunn, Boyd & Croxall, 1994). Our findings suggest that female subantarctic fur seals that were shorter, and therefore probably younger, gave birth earlier in the season. These results suggest that higher mortality in pups born early may reflect the inability of young/inexperienced mothers to carry the foetus to term. Our results are consistent with those for Cape fur seals, where high birth mass is associated with a decrease in newborn mortality throughout the pupping period (Mison-Jooste, 1999).

On Amsterdam Island, pup mortality also occurred by crushing and drowning. The study site La Mare aux Elephants is one of the densest colonies of Amsterdam Island (Guinet *et al.*, 1994), with the highest density occurring from 1 December to 1 January (Roux, 1986). Consequently, the density at the colony is high (75–100% of the maximum density) from the beginning to the end of the pupping season (Roux, 1986). Our results indicate that pup mortality caused by crushing by adults or drowning was similar for pups born early and for those born late in the season. One could expect that as pups born early spend more time in the colony during the period of high density, this would increase their risk of being crushed by adults compared to pups born later. However, at a given date, pups born early are also older and more agile so they may avoid encounters with aggressive adults. In Antarctic and South American fur seals, higher mortality in pups born late in the season

compared with pups born earlier results from density-dependent mortality in these species (Doidge, Croxall & Baker, 1984; Harcourt, 1992). In South Georgia and Peru, beaches are mostly flat and composed of pebbles (Doidge *et al.*, 1984: plates 1 & 2; R. Harcourt & J. Francis, pers. comm.) with only occasional large boulders, and do not provide refuge for pups (R. Harcourt & J. Francis, pers. comm.). Our results suggest that on Amsterdam Island, density does not influence pup mortality as it does in other localities. On Amsterdam Island La Mare aux Elephants is composed of large boulders and blocks of rock (Roux, 1986; Guinet *et al.*, 1994), where subantarctic fur seal pups are usually found hidden as soon as they are born. Hence on Amsterdam Island, beach topography reduces the risk of crushing by adults, whereas Antarctic and South American fur seal pups have nowhere to hide in South Georgia and Peru during their first weeks of life.

Pup mortality differed between years. The higher pup mortality in 1997 was associated with lower birth mass and a lower pup growth rate during the whole 11-month pup rearing period (32.7 ± 12.0 g/day, $n = 101$) compared to 1996 (37.4 ± 12.8 g/day, $n = 54$; Georges & Guinet, 2000; $t_{54,101} = 2.208$, $P = 0.03$). Lunn, Boyd, Barton & Croxall (1993) showed that in Antarctic fur seals, a reduction in pup growth rate occurs during years of low food availability. The reduced pup growth rate in 1997 suggests that environmental conditions were poorer than in 1996. Our results suggest that such annual changes in environmental conditions may be detected on Amsterdam Island by monitoring pup mortality and birth mass in subantarctic fur seals.

In 1996, when mothers were measured, there was an increase in birth mass that was associated with an increase in maternal body length throughout the pupping period. Similarly, longer Cape fur seals that are older than shorter individuals give birth later in the season (Rand, 1955). Consistently, a recent study showed that birth mass increases throughout the pupping season in Cape fur seals (Mison-Jooste, 1999). Conversely, in Antarctic and northern fur seals, birth mass decreases throughout the pupping period and this is associated with a decrease in maternal body length (Bigg, 1986; Boyd & McCann, 1989; Lunn & Boyd, 1993a; Boyd, 1996). Since the timing differs between species, these covariances are consistent with the positive relationship found between maternal length and pup body mass at birth in both species by Boyd & McCann (1989) and in our study.

In Antarctic and northern fur seals, the pup rearing period lasts 4 months (Doidge *et al.*, 1984; Gentry & Holt, 1986) so that mothers spend 8–9 months at sea between the weaning of one pup and the birth of the next. Such a long period spent at sea suggests that pregnant females are likely to return ashore with replenished body reserves before giving birth. Lunn & Boyd (1993a) showed that old Antarctic fur seals return earlier in the pupping season to occupy the most suitable sites when density at the colony is low. Bigg (1986) suggested that pregnant northern fur seals that

Table 5. Comparison in birth mass, prenatal (Pre P) and (Post P) postnatal period duration, duration of the first trip after parturition, pup growth rate during the perinatal period, and pup rearing period duration between fur seal species. Values are given as means ± SD (sample size)

Species	Birth mass (kg) Males	Birth mass (kg) Females	Pre P duration (days)	Post P duration (days)	First trip duration (days)	Pup growth rate (g/day) Males	Pup growth rate (g/day) Females	Pup rearing period	References
C. ursinus	6.1 ± 0.8 (1347)	5.5 ± 0.7 (1349)	1.1 ± 0.6 (8[a])	7.1 ± 0.6 (5[a])	5.0 ± 1.4 (10[a])	55 ± 20[b] (215)	40 ± 19[b] (155)	4 months	a, b
A. forsteri	4.2 ± 0.5 (6)	4.0 ± 0.2 (4)	1.9 ± 1.6 (6)	7.9 ± 2.5 (18)				10–11 months	c, d
A. galapagoensis	3.7 ± 0.3 (3[a])	3.3 ± 0.1 (3[a])		7.3 ± 1.2 (12)		102 ± 46 (15)		1–3 years	e, f, g
A. gazella	5.5 ± 0.2 (12[a])	4.9 ± 0.2 (12[a])	1.8 ± 0.4 (4[a])	6.1 ± 0.8 (4[a])		205 ± 13 (70)	154 ± 13 (73)	4 months	e, h, i, j
A. philippi	6.1 ± 0.8 (120)	5.5 ± 0.7 (118)		11.3 ± 3.3 (49)	10.2 ± 5.6 (47)			7–11 months	k, l
A. pusillus	6.2 ± 0.7 (504)	5.2 ± 0.4 (535)	1.4 ± 1.5 (10)	4.3 ± 3.3 (33)				9–11 months	m, n
A. tropicalis	5.6 ± 0.3 (3[a])	4.9 ± 0.6 (3[a])	2.1 ± 1.8 (6)	11.6 ± 9.6 (9)				10–11 months	d
A. tropicalis	5.0 ± 0.2 (2[a])	4.5 ± 0.1 (2[a])	1.4 ± 0.9 (34)	8.7 ± 2.1 (87)	5.7 ± 2.6 (85)	170 ± 81 (42)	180 ± 82 (45)	10–11 months	This study

[a] Means ± SD calculated from *n* years and localities.
[b] Means ± SE values.

a, Gentry & Holt (1986); b, Boltnev *et al.* (1998); c, Miller (1974); d, Goldsworthy (1992); e, Costa & Trillmich (1988); f, Trillmich (1986*a*); g, Trillmich (1986*b*); h, Doidge, McCann & Croxall (1986); i, Lunn & Boyd (1993*a*); j, Lunn & Boyd (1993*b*); k, Francis *et al.* (1998); l, Ochoa-Acuna, Francis & Boness (1998); m, David & Rand (1986); n, Mison-Jooste (1999).

arrive late are probably young with a less-developed homing instinct than other females. In contrast, in subantarctic and Cape fur seals, the pup rearing period lasts 10 months (Rand, 1955; Bester, 1981) and mothers spend only 1–2 months at sea before the next parturition (Table 5). One may suggest that longer/older individuals that are also more experienced may increase the amount of body reserves they store at sea by maximizing the time spent at sea between weaning and parturition. In doing so, they may also increase the probability of giving birth to a bigger new-born than individuals spending less time at sea before parturition. In Antarctic fur seals, the date of parturition has been related to maternal body condition, which is expected to affect the timing of implantation, with older females that are also in good condition implanting and giving birth earlier than younger ones (Lunn & Boyd, 1993a; Boyd, 1996). However, our results suggest that this relationship may be different for subantarctic fur seals on Amsterdam Island.

Subantarctic fur seals arrived 1.4 days before pupping, spent an average of 8.7 days with their pups before leaving for their first foraging trips of 5.7 days. This attendance pattern is similar to those described in other fur seals (Table 5). However, subantarctic fur seals giving birth early in the season spent 9.5 days with their pups, whereas mothers giving birth late spent 8.0 days ashore after parturition. Shorter postnatal period in mothers giving birth late in the season have also been observed in Antarctic fur seals (Lunn & Boyd, 1993a). We found that subantarctic fur seals which gave birth late seemed to compensate for the shorter postnatal period by increasing the growth rate of their pup. As a result, absolute gain in pup mass after the postnatal period was 1.5 kg both in pups born early and late in the pupping season. This suggests that old mothers that gave birth later in the season were more efficient at transferring energy to their pups compared with other mothers. Furthermore, the higher birth mass in pups born later in the season may allow them a higher mass gain, as Georges & Guinet (2000) showed that body mass is a limiting factor for mass gain in young subantarctic fur seal pups. As females leave the colony after copulation (Riedman, 1983), the differences in postnatal periods also suggest that oestrus occurs 1.5 days later in young mothers giving birth early in the season compared with old mothers giving birth later.

In Antarctic fur seals, it has been suggested that differences in the duration of the perinatal period between years reflect differences in maternal condition due to environmental conditions (Duck, 1990). Our results suggest the time spent ashore before and after parturition was not related to maternal condition in subantarctic fur seals.

During the 8-day postnatal period, pups have to store body reserves (on average 1.5 kg, i.e. 30% of their birth mass), and particularly fatty tissue, to survive the first fasting period of 6 days. This is particularly important as we found that when pups were left unattended, the main cause of pup mortality was starvation, as also observed in northern fur seals (Trites, 1992b). We found that for the same duration, absolute mass gain and body mass after the perinatal period were higher in male pups whose mothers were in good condition compared with those whose mothers were in poor condition, but this relationship was not found in female pups. This suggests that during the first days of life, pup growth was limited by maternal resources in male pups but not in female pups. At birth, male fur seal pups seem to be leaner than female pups (Arnould, Boyd & Socha, 1996). Consequently, male pups have to store comparatively more fat reserves than female pups, as well as to increase their probability of survival. Our results suggest that the lower amount of fatty tissue observed at birth in male pups may be compensated for by higher absolute mass gain observed for male pups with mothers in good condition. Such compensation would be less essential for female pups that are possibly fat enough to survive the first fasting period without the additional mass gain.

The absence of a relationship between birth mass and absolute gain in pup mass, as also found in other fur seals (Doidge, McCann & Croxall, 1986; Boltnev et al., 1998), indicates that body mass at the end of the perinatal period was directly related to birth mass for both male and female pups. Consequently, birth mass and thus body mass at the end of the perinatal period are probably important factors for survival of subantarctic fur seal pups which have to fast for long periods because of the protracted foraging cycles in this species on Amsterdam Island (Georges & Guinet, 2000). Furthermore, during the first 3 months of age, pup growth rate is size-dependent in subantarctic fur seals, the larger pups growing at a higher rate than smaller ones because they can ingest more milk (Georges & Guinet, 2000). Thus, our results indicate that mothers have to produce pups that are as large as possible at birth to enhance pup body mass during the perinatal period. This will enhance pup growth during the first stages of life (Georges & Guinet, 2000) and consequently their probability of survival as shown in northern fur seals (Calambokidis & Gentry, 1985; Boltnev et al., 1998).

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