

MATERNAL CARE IN THE SUBANTARCTIC FUR SEALS ON AMSTERDAM ISLAND

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Abstract. This paper reports the first study of maternal input and care from birth to weaning in a fur seal with a long pup-rearing period: the subantarctic fur seal *Arctocephalus tropicalis* breeding on the temperate Amsterdam Island, Indian Ocean. The protracted weaning period provided the opportunity for examination of maternal care in relation to seasonal changes in the requirements of the mother–pup pair and environmental conditions. During the reproductive season 1995–1996, maternal care was investigated in terms of provisioning (maternal attendance) pattern while diving effort was investigated using time depth recorders in summer and winter. Maternal input was calculated in terms of the absolute rate of pup mass gain and, ultimately, pup growth rate and pup body mass at weaning. Lactating subantarctic fur seals perform one of the longest attendance cycles described in fur seals, spending on average 11–23 d at sea from summer to winter. The time mothers spend ashore suckling their pup is also long (~4 d) but remains constant throughout the year. Throughout the year, maternal input should be described as follows: mothers spending a long time at sea store a large amount of body reserves that provide them a good body condition. Consequently, they spend a long time ashore to transfer their body reserves to their pups. However, mothers spending short attendance periods increase the mass transfer efficiency, probably by decreasing their metabolic overhead. In summer, maternal care was mostly controlled by pup traits: maternal absences appeared to be controlled by pup fasting ability, while maternal input was controlled by pup ingestion ability, i.e., pup body size and the time the pup was suckling. In fall, pups were no longer limited in milk ingestion, and maternal input was mostly controlled by maternal traits (e.g., body length and experience). In winter, maternal input decreased as the pup became older despite an increase in maternal diving effort. We propose that, in winter, maternal requirements increase, probably in response to increasing costs of gestation and because of a decrease in food resource availability. Pups whose mother performed short and regular foraging trips grew faster and were heavier at weaning than other pups. This is discussed in term of pup fasting endurance and maternal experience. Finally, we found a window of foraging trip durations that maximizes the net rate of energy acquisition of the pup, suggesting that in subantarctic fur seals there may not exist one optimal maternal attendance pattern, but a range of patterns promoting the same maternal fitness.

Key words: *Arctocephalus tropicalis*; foraging effort; maternal care; maternal input; Otariidae; Pinnipedia; provisioning pattern; pup growth rate; subantarctic fur seal.

INTRODUCTION

In the evolutionary concept of life history theory, natural selection is supposed to maximize parental fitness (Stearns 1976). To maximize their fitness, parents are expected to adjust their expenditure on parental care in relation to variations in benefits to their offspring and in costs to themselves (Winkler 1987). Furthermore, changes of parental care for the offspring observed in long-living animals could result from the predicted trade-off between present and future reproduction (Ricklefs 1990). Throughout an animal's lifetime, the reproductive success can be divided into two com-

ponents: (1) the survival and future reproduction of the offspring (i.e., offspring fitness) currently cared for, and (2) the parent's future reproduction in subsequent breeding attempts. Offspring fitness derives from maternal input, i.e., the amount of parental care and resources received by current offspring regardless of cost to the parents (Evans 1990). Environmental changes may influence the effects of parental expenditure on offspring fitness: when environmental conditions are poor, an increase in parental investment may be associated with a decrease in parental input to the young (Trivers 1972, Evans 1990). The theory of state-dependent life history evolution predicts that mothers of different physiologic states might have different tactics to conduct maternal care (McNamara and Houston

1996). For example, body condition acts as a determinant in the current breeding attempt in Blue Petrels (Chastel et al. 1995). During reproductive events, parental strategies are expected to maximize the rate of energy acquisition of the offspring (Stearns 1976). In central place foragers, parental care consists of alternating foraging trips to acquire energy, and attendance periods to transfer it to the young. According to central place foraging theory, parents are expected to show an optimal cycle duration to do so (Krebs and Davies 1987, Ydenberg et al. 1994). Parental input will promote inclusive fitness of the parents (Cézilly et al. 1991), i.e., growth rate, weaning mass (Lunn et al. 1993), and ultimately survival and future reproductive success (Fedak and Anderson 1982) of the offspring.

It is generally agreed that among pinnipeds, the pup is totally dependant on maternal care and milk, i.e., there is no paternal care (Bartholomew 1970). In phocid (earless) seals, maternal care consists of a short intense period of lactation during which the pup suckles while the mother fasts ashore. In otariid (eared) seals, maternal care consists of a long period (4 months to 3 years) of alternating foraging trips at sea and fasting visits ashore to suckle the pup. Because of this temporal and spatial segregation of maternal foraging and nursing, otariids are central place foragers. Lactating females have to balance the time required to replenish their body reserves against the time the pup is left alone fasting ashore. Thus, maternal care comprises three components: the time period between provisioning events (i.e., maternal attendance pattern), the mass/energy of milk delivered during each provisioning event (e.g., pup absolute mass gain, rate of pup mass gain), and the quality of milk. Few studies consider that mothers can promote the same growth rate in their pup by different ways: for example, a decline in provisioning rate may be compensated for by an increase in quality and/or mass of milk provided per delivery or vice versa (Gentry et al. 1986, Trillmich and Lechner 1986). According to central place foraging theory, maternal provisioning tactics are expected to maximize the rate of energy acquisition to the offspring, i.e., its growth rate. Consequently, pup growth rate should reflect the provisioning tactic adopted by the mother (Gentry et al. 1986). However, several studies indicate that in the best known species, the Antarctic fur seal *Arctocephalus gazella*, the way maternal provisioning tactics affect pup growth rate depends on environmental conditions. During years of normal food availability, the duration of foraging trips was not related either to the rate of energy delivery nor to the pup growth rate at South Georgia (Boyd et al. 1991, Arnould and Boyd 1995, Arnould et al. 1996a). However, when food resources were scarce, long foraging trips were associated with reduced pup growth rate (Lunn et al. 1993). Interestingly, the same negative relationship was found in Antarctic fur seals on Heard Island (Goldsworthy 1995) and in New Zealand fur seals, *A. forsteri* (Lea and Hindell 1997).

This paper presents the first study of maternal care during the whole reproductive season in a fur seal with a long pup-rearing period: the subantarctic fur seal *Arctocephalus tropicalis* breeding on Amsterdam Island during the reproductive season 1995–1996. Subantarctic fur seals breed in the south Atlantic and Indian oceans, mostly north of the polar front on the subantarctic islands of Marion, Prince Edward, Macquarie, Crozet, and north of the subtropical front on the temperate islands of Gough, Saint Paul, and Amsterdam (Bester 1981, Guinet et al. 1994). Births occur from late November to early January and the rearing period lasts 10 months (Kerley 1985, Roux 1986). In temperate latitudes, such a long period includes seasonal changes in environmental conditions. First, we investigated maternal input (in terms of absolute and rate of pup mass gains, pup growth rate, and ultimately pup weaning mass) in relation to maternal provisioning tactics, and maternal (body length and condition) and pup (sex, age, and mass) characteristics. Maternal provisioning tactics were studied according to maternal attendance pattern, maternal foraging efficiency (rate of resource acquisition, i.e., rate of maternal mass gain), and diving effort using time depth recorders. Second, we investigated if maternal effort changed throughout the rearing period, and if so, how it affects maternal input.

MATERIALS AND METHODS

Study site and animals

The study was carried out on the colony "La Mare aux Elephants," Amsterdam Island (37°55' S, 77°30' E), Indian Ocean, during the whole 1995–1996 reproductive season. Amsterdam Island lies 3000 km from Africa, 3000 km from Australia, 400 km north from the subtropical front. The study period was divided into three seasons of three months: the "summer" from December 1995 to end of February 1996 corresponded to the period from birth to 3 mo of age, the "fall" from March to May, 1996 and the "winter" from June to August 1996.

From late November to early January, births were identified by continuous observations during daytime. Pups were marked using temporary codes glued on their fur after pup-mother recognition had occurred just after birth. Then they were sexed and weighed (± 0.05 kg) before suckling began. At ~ 1 mo of age, each marked pup was double-tagged in the web of the fore flippers with a plastic tag (Rototag: Dalton, Nettlebed, UK). From birth to early September, the study colony was checked daily and all tagged pups found were weighed using a rope attached on a spring scale (20.0 ± 0.1 kg and 25.0 ± 0.1 kg). The weaning process was investigated by two checks of the colony and weighing of tagged pups every week from September to November, and the last measure of pup body mass during that period was considered to be weaning mass. During the whole period, lactating females were captured using a

collar and restrained on a wooden plank as described by Gentry and Holt (1982). All mothers used in this study were double-tagged (Rototag: Dalton, Nettlebed, UK), sized (standard body length from nose to tail, ± 1 cm), and weighed using a spring scale (200 ± 1 kg) fixed on the restrained board. Mothers were weighed (1) when arriving ashore before suckling began, (2) during the suckling event, and/or (3) before departure, at the conclusion of suckling. Continuous observations of the study site allowed us to catch mothers as soon as they arrived ashore (case 1). To confirm that the last weighing corresponded to that at departure (case 3), the data set was compared to that of the pup body mass: mothers were considered to have been caught at the conclusion of suckling if their pup did not gain mass during the subsequent days. When the mass of the mothers at arrival (case 1) and at departure (case 3) was known and when the pup was weighed before and after suckling for the same attendance period, we calculated a mass transfer equation. From this equation, we calculated the mass at arrival and at departure for mothers that were weighed only once during the other attendance periods (case 2). Maternal body condition was calculated using the residuals values of the linear regression between maternal body mass (MBM) and maternal body length (MBL) as used by Trites (1991). For lactating subantarctic fur seals breeding on Amsterdam Island, the relation was: $\text{MBM (kg)} = -73.746 + 0.884(\text{MBL (cm)})$, $r^2 = 0.641$, $P = 0.001$, $n = 105$. Positive residual values corresponded to individuals in good condition while negative residual values corresponded to individuals in poor condition (Trites 1991).

Maternal attendance was calculated from analyses of pup body mass changes assuming that pups do not feed themselves before weaning. These calculations were controlled using the data set of direct observations of tagged mothers: mothers were assumed to be at sea from the first day of pup mass loss or when they were not observed for an entire day; mothers were assumed to be ashore as soon as the pup gained mass or was observed directly. Mothers that were seen ashore once in a day were scored as spending the entire day ashore, and mothers that were not sighted were scored as spending a day at sea. To assess the accuracy of our methodology, we compared maternal attendance pattern in 24 mother-pup pairs whose females were equipped with VHF radio transmitters and whose pup was daily weighed at the same time from January to September. There were no significant differences between both methods in the calculation of foraging trip durations (paired t test, $t = 0.348$, $P = 0.201$, $n = 23$) and attendance period durations (paired t test, $t = 0.095$, $P = 0.54$, $n = 21$). This indicates that (1) pup mass changes can be used to calculate maternal attendance pattern and (2) subantarctic fur seal pups lose mass continuously when fasting (i.e., they do not feed themselves when their mothers are at sea). The different periods of maternal attendance and the nomenclature relative to the mother and her pup used in this paper

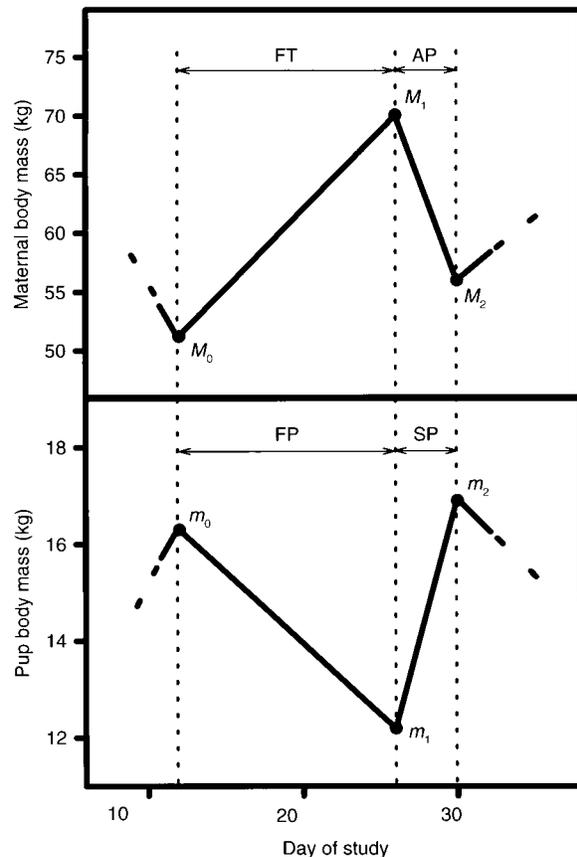


FIG. 1. Maternal and pup mass changes during one maternal attendance cycle. The foraging trip of the mother (FT) corresponds to the pup fasting period (FP). The rate of maternal mass gain was defined as the absolute maternal mass gain divided by the duration of the foraging trip ($(M_1 - M_0)/\text{FT}$). The time spent ashore by the mother (attendance period, AP) corresponds to the pup suckling period (SP). During the attendance period, maternal mass at arrival M_1 decreases to M_2 (absolute maternal mass loss, $M_1 - M_2$) while pup mass before suckling m_1 increases to m_2 (absolute pup mass gain, $m_2 - m_1$). The rate of pup mass gain was defined as the absolute pup mass gain divided by the duration of the previous foraging trip ($(m_2 - m_1)/\text{FT}$). Both rates of mass gain were used as indexes of maternal efficiency when the mother was foraging at sea. The index of provisioning variability was the coefficient of variation ($\text{CV} = \text{SD}/\text{mean}$) of foraging trip duration.

are summarized in Fig. 1. The perinatal period (i.e., time spent ashore just after birth and subsequent foraging trip) was excluded from analysis.

Foraging effort was investigated in eight different lactating females, which were captured and equipped with MK5 time depth recorder TDR (Wildlife Computers, Redmond, Washington, USA). Maternal characteristics are summarized in Table 9. TDRs were glued on the back of the fur seals using fast-setting epoxy resin. TDRs were programmed to sample depth (± 1 m) at 10-s intervals when fur seals were at sea. They were recovered after one foraging trip. Four mothers were equipped in early February and four in early July.

TABLE 1. Maternal attendance and mass changes in lactating subantarctic fur seals and their pups in summer, fall, and winter during the reproductive season 1995–1996 on Amsterdam Island.

Variable	Summer			Fall			Winter		
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
Foraging trip duration (d)	10.8	3.1	85	14.4	4.0	79	22.7	6.6	24
Attendance period duration (d)	3.8	1.1	85	3.8	1.1	79	3.7	1.1	24
Pup absolute mass gain (kg)	2.7	0.7	85	3.6	1.1	79	3.7	1.2	24
Pup mass gain rate (kg/d at sea)	0.274	0.084	85	0.273	0.074	79	0.171	0.042	24
Maternal body mass at arrival (kg)	49.6	7.2	78	51.7	7.7	64	51.5	9.0	11
Maternal body mass at departure (kg)	41.2	6.3	78	42.0	6.2	64	43.6	8.9	11
Maternal absolute mass loss (kg)	8.4	2.4	78	9.7	2.8	64	7.9	2.8	11
Maternal absolute mass gain (kg)	8.4	3.6	44	9.3	4.7	38	10.5	3.2	2
Maternal mass gain rate (kg/d at sea)	0.695	0.301	44	0.639	0.283	38	0.464	0.125	2

Only dives >3 m were analyzed. Diving effort was studied using three parameters: (1) cumulative diving distance was the sum of maximum depths reached during the whole trip; (2) cumulative diving duration was the total of time spent underwater, and (3) diving frequency was the number of dives per hour of night. Fur seals feed at night (Gentry and Kooyman 1986) and thus, cumulative diving distance, cumulative diving duration, and diving frequency were calculated per hour of night because of changes in night duration between seasons. Night duration according to the date of foraging trip was calculated using SUNTAB shareware (A. Lysell, Huddinge, Sweden) for the latitude of Amsterdam Island.

Statistical analyses

Statistics were calculated using SAS 6.03 (SAS Institute Incorporated, Cary, North Carolina, USA), following the procedures recommended by Sokal and Rolf (1981). Values are given as mean \pm 1 SD. Statistical significance was considered to be at $P < 0.05$. During this one-year study, 78 mother–pup pairs were monitored regularly, and 11 more pups were monitored whereas their mothers were not studied (i.e., 89 pups were regularly monitored). Any mother whose pup died during the study period was excluded from the analysis. Data on maternal attendance and mass changes were calculated and then averaged for each mother–pup pair for each season. Thus, all data used in the analyses are means of repeated measures of mother–pup pairs and the analyses constitute high-order analyses. However, for several analyses where the studied variables were related to initial characteristics of the mother–pup pairs, we employed a random sampling procedure to consider one attendance cycle by season for each mother–pup pair. When analyzing the equation of mass transfer according to the seasons (summer and fall), we employed a random sampling procedure to use the same mother–pup pairs in summer and fall, each mother–pup pair being considered once per season. This analysis allowed us to test the season effect while avoiding pseudoreplication. Comparisons of means among seasons were investigated using analysis of variance (ANOVA). Comparisons between sexes were

investigated using Student's *t* test. Correlations were analyzed using general linear model (GLM) when multivariate analyses were run. Tables only include the contribution of significant factors to the model and the slope *b* corresponds to the model after stepwise backward analysis (level of significance $P < 0.1$).

RESULTS

Maternal attendance pattern

During the study period, 89 pups (42 males and 47 females) were monitored to calculate 85, 79, and 24 attendance cycles (foraging trip at sea + attendance period ashore) in summer, fall, and winter, respectively (Table 1). For each season, the mean durations of the foraging trips and attendance periods did not differ according to the sex of the pup (*t* test, $P > 0.15$ in all cases), except for attendance periods in summer (*t* test $t = 2.002$, $P = 0.049$; males, 3.6 ± 1.1 , $n = 41$; females, 4.1 ± 1.2 , $n = 44$).

The duration of the foraging trips increased throughout the year (ANOVA, $F_{2,186} = 82.7$, $P < 0.001$), while the duration of the attendance periods remained constant ($F_{2,186} = 0.5$, $P = 0.628$, Table 1). For each season, the duration of the attendance periods was positively related to the duration of the foraging trip (linear regression, summer, $r^2 = 0.083$, $P = 0.007$, $n = 85$; fall, $r^2 = 0.162$, $P < 0.001$, $n = 79$; and winter, $r^2 = 0.516$, $P < 0.001$, $n = 24$). The durations of the foraging trips and attendance periods were not related to maternal body length (linear regression, foraging trip, summer, $r^2 = 0.001$, $P = 0.747$, $n = 84$; fall, $r^2 = 0.004$, $P = 0.564$, $n = 78$; winter, $r^2 = 0.016$, $P = 0.562$, $n = 24$; attendance period, summer, $r^2 = 0.001$, $P = 0.782$, $n = 84$; fall, $r^2 = 0.011$, $P = 0.36$, $n = 78$; winter, $r^2 = 0.014$, $P = 0.584$, $n = 24$). The duration of the foraging trips was positively related to pup body mass but neither the sex of the pup, nor the interaction had significant effect in the model (Table 2). This suggests that the duration of the foraging trips was mostly controlled by pup requirement rather than by its sex.

Maternal mass changes

During the study period, maternal body mass was monitored for 78, 64, and 11 mothers in summer, fall,

TABLE 2. Analysis (general linear model) of mean duration of foraging trip by lactating subantarctic fur seals in relation to variables during the reproductive season 1995–1996 on Amsterdam Island.

Seasons	<i>n</i>	<i>r</i> ²	Source of variation	% Contr.‡	<i>b</i> §
Summer	85	0.158	pup mass (kg)	99.7***	1.039
			pup sex	NS	...
			mass × sex	NS	...
Fall	79	0.285	pup mass (kg)	97.3***	1.245
			pup sex	NS	...
			mass × sex	NS	...
Winter	24	0.181	pup mass (kg)	99.4†	1.317
			pup sex	NS	...
			mass × sex	NS	...

† $P < 0.10$; *** $P < 0.001$. NS = not significant ($P > 0.10$).

‡ Percentage of contribution to the global model.

§ Slope (only given for significant effects after stepwise backward analysis).

and winter, respectively (Table 1). The maternal body mass at arrival ashore tended to increase from summer to fall (t test, $t = 1.725$, $P = 0.087$) while maternal body mass at departure to sea remained constant ($t = 0.761$, $P = 0.448$). The absolute maternal mass loss ashore increased between summer and fall ($t = 3.107$, $P = 0.002$). However, from fall to winter, maternal body mass at arrival and at departure remained constant ($t = 0.083$, $P = 0.934$, and $t = 0.739$, $P = 0.462$, respectively) while absolute maternal mass loss tended to decrease ($t = 1.963$, $P = 0.05$). In summer, the absolute maternal mass gain was related neither to maternal body length ($r^2 = 0.016$, $P = 0.414$, $n = 44$) nor to the foraging trip duration ($r^2 = 0.049$, $P = 0.149$, $n = 44$). However, in fall, the absolute maternal mass gain tended to be positively related to maternal body length ($r^2 = 0.094$, $P = 0.061$, $n = 38$) and was positively related to the duration of the foraging trips ($r^2 = 0.142$, $P = 0.020$, $n = 38$). The rate of maternal mass gain (mass gained by the mother per day at sea) did not differ between summer and fall ($t = 0.869$, $P = 0.387$, Table 1). The rate of maternal mass gain was positively related to maternal body length in summer ($r^2 = 0.126$, $P = 0.018$, $n = 44$) and in fall ($r^2 = 0.133$, $P = 0.024$, $n = 38$). Winter comparisons were not conducted due to small sample sizes.

Mass transfer equation

An equation of mass transfer from the mother to her pup was calculated according to a multiple linear model with 56 mother–pup pairs monitored in summer and fall, each mother–pup pair being considered once per season (see *Methods*). A multiple linear model (with absolute maternal mass loss as dependent variable, and pup sex, pup age, pup body mass before suckling, absolute pup mass gain, maternal body length, duration of the attendance period, and season as factors) indicated that maternal mass loss (MML, kilograms) was positively related to pup mass gain (PMG, kilograms), maternal body length (MBL, centimeters), and duration

of the attendance period (AP, days), while season had no effect. The mass transfer equation between the mother and her pup for both summer and fall was deduced as:

$$\text{MML} = -3.4 + 1.715(\text{PMG}) + 0.025(\text{MBL})$$

$$+ 0.879(\text{AP}),$$

($r^2 = 0.932$, $P < 0.001$, $n = 112$; Table 3).

We defined mass transfer efficiency as the ratio of absolute pup mass gain divided by absolute maternal mass loss for these 56 mother–pup pairs. The mass transfer efficiency was significantly higher in fall than in summer (paired t test, $t = 3.638$, $P < 0.001$, $n = 56$; summer, $34.5\% \pm 6.6\%$; fall, $38.5\% \pm 6.0\%$). Multiple regression analyses (with mass transfer efficiency as dependent variable and pup sex, pup age, pup body mass before suckling, maternal body length, and attendance period duration as factors) were calculated per season. For each season (Table 4), mass transfer efficiency (%) was related neither to pup sex, pup age, pup body mass before suckling, nor to maternal body length and it was negatively related to the duration of the attendance period (AP; days) (summer, efficiency = $41.1 - 1.6[\text{AP}]$, $r^2 = 0.201$, $P = 0.001$, $n = 56$; fall, efficiency = $48.7 - 2.6[\text{AP}]$, $r^2 = 0.446$, $P < 0.001$, $n = 56$). Differences were found in slopes and intercepts between summer and fall (Tessier comparison: gradient $T = 3.077$, $P < 0.001$; intercept $T = 5.772$, $P < 0.001$).

Maternal body condition during two consecutive cycles

For both summer and fall, there was a positive relationship between maternal body condition at arrival before suckling and the duration of attendance periods (linear regression, summer, $r^2 = 0.09$, $P = 0.007$, $n = 78$; fall, $r^2 = 0.234$, $P < 0.001$, $n = 64$; winter, $r^2 = 0.018$, $P = 0.694$, $n = 11$). When considering an attendance period, maternal body condition at departure after suckling was positively related to maternal body condition at arrival ($r^2 = 0.647$, $P < 0.001$, $n = 47$, Fig. 2). Distribution of the residuals values did not differ from normal distribution (Kolmogorov Smirnov statistic: $W = 0.984$, $P = 0.876$). Residual values were used as an index of the change of maternal body condition throughout this attendance period to define two groups of mothers: individuals with negative residuals corresponded to mothers whose body condition deteriorated strongly (group a) while those with positive residuals corresponded to mothers whose body condition deteriorated minimally (group b). Mass-specific mass loss was higher in mothers whose body condition deteriorated strongly, compared to other mothers (t test, $t = 5.293$, $P < 0.001$, Table 5). The duration of the consecutive foraging trip did not differ between groups ($t = 1.247$, $P = 0.219$), but the absolute maternal mass gained during the consecutive foraging trip was significantly higher in mothers whose body condition deteriorated strongly, compared to mothers whose con-

TABLE 3. Analysis (general linear model) of maternal absolute mass loss in lactating subantarctic fur seals, in relation to variables for one attendance period during the reproductive season 1995–1996 on Amsterdam Island. Analyses were run for 56 mother–pup pairs randomly sampled once in summer and in fall.

Seasons	<i>n</i>	<i>r</i> ²	Independent variable	% Contr.‡	<i>b</i> §
Summer	56	0.866	pup sex	NS	...
			pup age (d)	NS	...
			pup mass (kg)	NS	...
			pup mass gain (kg)	62.0***	1.824
			maternal length (cm)	1.1†	0.031
			attendance period (d)	36.5***	0.765
Fall	56	0.996	pup sex	NS	...
			pup age (d)	NS	...
			pup mass (kg)	NS	...
			pup mass gain (kg)	48.9***	1.563
			maternal length (cm)	1.0***	0.035
			attendance period (d)	48.9***	1.054
Both seasons	112	0.932	pup sex	NS	...
			pup age (d)	NS	...
			pup mass (kg)	NS	...
			pup mass gain (kg)	57.0***	1.715
			maternal length (cm)	0.7†	0.025
			attendance period (d)	17.0**	0.130
			season	NS	...

† *P* < 0.10; ** *P* < 0.01; *** *P* < 0.001. NS = not significant (*P* > 0.10).

‡ Percentage contribution to the global model.

§ Slope (only given for significant effects after stepwise backward analysis).

dition did not deteriorate (*t* = 2.425, *P* = 0.019, Table 5). This suggests that females whose body condition deteriorated during one attendance period did not lengthen the consecutive foraging trip, but they increased their absolute mass gain, i.e., their foraging efficiency during the consecutive foraging trip.

Pup absolute and daily mass gain

For each season, there were no differences between sexes in absolute pup mass gain (summer, *t* = 1.335, *P* = 0.185; fall, *t* = 0.506, *P* = 0.614; winter, *t* = 1.79, *P* = 0.096) and the rate of pup mass gain (summer, *t* = 0.405, *P* = 0.687; fall, *t* = 0.763, *P* = 0.448; winter,

t = 0.818, *P* = 0.422). For both sexes, the absolute pup mass gain increased from summer to fall (*t* = 6.445, *P* < 0.001) but remained constant from fall to winter (*t* = 0.601, *P* = 0.549). However, the rate of pup mass gain did not differ between summer and fall (*t* = 0.193, *P* = 0.847) but decreased from fall to winter (*t* = 6.443, *P* < 0.001, Table 1).

Multiple regression analyses were used to investigate the relationships between absolute pup mass gain and the rate of pup mass gain with the following factors: pup sex, pup age and body mass before suckling, maternal body length and body condition at arrival, and duration of the previous foraging trip and of the current

TABLE 4. Analysis (general linear model) of mass transfer efficiency in subantarctic fur seals, in relation to variables during the reproductive season 1995–1996 on Amsterdam Island.

Season	<i>n</i>	<i>r</i> ²	Independent variable	% Contr.†	<i>b</i> ‡
Summer	56	0.201	pup sex	NS	...
			pup age (d)	NS	...
			pup mass (kg)	NS	...
			maternal length (cm)	NS	...
			attendance period (d)	54.8**	−1.616
			Fall	56	0.446
pup age (d)	NS	...			
pup mass (kg)	NS	...			
maternal length (cm)	NS	...			
attendance period (d)	83.1***	−2.636			

** *P* < 0.01, *** *P* < 0.001. NS = not significant (*P* > 0.10).

† Percentage contribution to the global model.

‡ Slope (only given for significant effects after stepwise backward analysis).

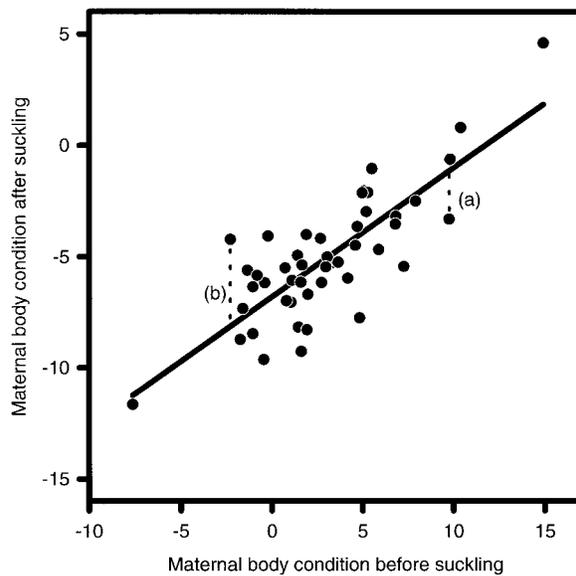


FIG. 2. Relationship between maternal body condition before and after suckling for a given attendance period. Residual values were used to define mothers whose body condition deteriorated strongly (case a, negative residual values) and minimally (case b, positive residual values) during one attendance period.

attendance period. Analyses were performed by seasons, using one attendance cycle randomly sampled once by season (see *Methods*: Statistical analyses). For each season, absolute pup mass gain (Table 6) was positively related to maternal body condition at arrival and positively related to the duration of the previous foraging trip. The sex of the pup was never a significant factor in the models. The absolute pup mass gain was positively related to the pup body mass before suckling and to attendance period duration in summer, positively related to maternal body length in fall, and negatively related to pup age in winter. Similarly, for each season, the rate of pup mass gain (Table 6) was positively related to maternal body condition at arrival but negatively related to the duration of the previous foraging trip except in winter. The sex of the pup was never a significant factor in the models. The rate of pup mass gain was positively related to pup mass before suckling, the attendance period duration in summer, maternal body length in fall, and pup body mass before suckling

and negatively related to pup age and maternal body length in winter.

When considering mean values of the rate of pup mass gain and the mean duration of foraging trip by seasons (Fig. 3), the quadratic relationship appeared to fit better than the linear relationship in summer and in fall but not in winter (Table 7). These relationships indicated that there was a window of foraging trip durations corresponding to a maximum rate of pup mass gain. During summer and fall, the maximum rate of pup mass gain was on average about ~ 300 g/d, corresponding to trips of 9 and 13 d for summer and fall, respectively. In winter, the relationship was linear, indicating that the rate of pup mass gain tended to decrease with increasing foraging trip duration (Fig. 3).

Pup growth rate and weaning mass

Body mass of 38 pups (14 males and 24 females) was monitored until weaning to estimate the date of maximum mass, which was 227 d of age for both sexes, i.e., around 29 July 1996. Pup growth rate until the date of maximum body mass was calculated for 54 pups (25 males and 29 females). Furthermore, pup body mass at weaning was monitored in 70 pups (29 males and 41 females).

There were no significant differences in pup growth rate from birth to the date of maximum body mass between sexes (*t* test, $t = 0.289$, $P = 0.774$; growth rate in male pups, 37 ± 14 g/d, $n = 25$, range, 19–75 g/d; growth rate in female pups, 38 ± 12 g/d, $n = 29$, range, 6–61 g/d). A multiple regression analysis (with pup growth rate as dependent variable and pup sex, date of birth, mass at birth, maternal body length, mean foraging trip duration, and index of provisioning variability as factors) indicated that pup growth rate was negatively related to the mean duration of foraging trips and variability of provisioning and positively related to maternal body length (Table 8). Similarly, pup body mass at weaning did not differ between sexes ($t = 0.498$, $P = 0.620$; males, 11.4 ± 2.1 kg, $n = 29$, range, 6.4–15.0 kg; females, 11.1 ± 2.2 kg, $n = 41$, range, 5.5–14.2 kg). A multiple regression analysis indicated that pup body mass at weaning was negatively related to the mean duration of foraging trips, variability of provisioning, and positively related to maternal body length (Table 8). This suggests that pups whose mother was large and performed short and regular foraging trips grew faster and had a higher body mass at weaning than other pups.

TABLE 5. Comparisons between mothers with different body conditions for mass-specific mass loss during the attendance period, duration of the consecutive foraging trip, and absolute maternal mass gain during the consecutive foraging trip.

Variable	Strongly deteriorated			Minimally deteriorated		
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
Mass-specific mass loss (%)	19.5	3.5	24	14.1	3.4	23
Consecutive foraging trip (d)	14.3	4.4	24	12.7	4.6	23
Maternal absolute mass gain (kg)	9.4	3.6	24	6.9	3.4	23

TABLE 6. Analyses (general linear model) of mass gain in subantarctic fur seal pups in relation to variables during the 1995–1996 season on Amsterdam Island.

Season	Dependent variable	<i>n</i>	<i>r</i> ²	Independent variable	% Contr.‡	<i>b</i> §
Summer	absolute pup mass gain	78	0.594	pup sex	NS	...
				pup mass (kg)	6.2†	0.206
				pup age (d)	NS	...
				maternal length (cm)	NS	...
				maternal condition	45.9***	0.100
				foraging trip (d)	26.9***	0.104
	rate of pup mass gain	78	0.563	attendance period (d)	17.0**	0.130
				pup sex	NS	...
				pup mass (kg)	14.6**	0.025
				pup age (d)	NS	...
				maternal length (cm)	NS	...
				maternal condition	21.0**	0.007
Fall	absolute pup mass gain	63	0.588	foraging trip (d)	54.1***	-0.012
				attendance period (d)	7.4†	0.01
				pup sex	NS	...
				pup mass (kg)	NS	...
				pup age (d)	NS	...
				maternal length (cm)	16.3**	0.048
	rate of pup mass gain	63	0.566	maternal condition	69.8***	0.163
				foraging trip (d)	6.7†	0.06
				attendance period (d)	NS	...
				pup sex	NS	...
				pup mass (kg)	NS	...
				pup age (d)	NS	...
Winter	absolute pup mass gain	13	0.848	maternal length (cm)	6.6†	0.003
				maternal condition	28.4***	0.009
				foraging trip (d)	59.4***	-0.012
				attendance period (d)	NS	...
				pup sex	NS	...
				pup mass (kg)	NS	...
	rate of pup mass gain	13	0.724	pup age (d)	22.9†	-0.038
				maternal length (cm)	NS	...
				maternal condition	35.4†	0.129
				foraging trip (d)	66.5**	0.092
				attendance period (d)	NS	...
				pup sex	NS	...
pup mass (kg)	16.5†	0.018				
pup age (d)	20.0†	-0.001				
maternal length (cm)	35.3†	-0.005				
maternal condition	NS	...				
foraging trip (d)	NS	...				
attendance period (d)	NS	...				

† $P < 0.10$; ** $P < 0.01$; *** $P < 0.001$. NS = not significant ($P > 0.10$).

‡ Percentage contribution to the global model.

§ Slope (only given for significant effects after stepwise backward analysis).

|| Duration of previous foraging trip.

Maternal diving effort

Cumulative diving distances and diving time and number of dives increased from summer to winter (Mann-Whitney $U = 0$, $P < 0.025$, for each variable, Table 9). All dives were at night so diving effort was calculated in relation to nighttime duration for each foraging trip. Because nights lengthened from summer

to winter, diving effort was corrected by night duration. Cumulative diving distances per hour of night and the diving frequency were significantly higher in winter than in summer ($U = 0$, $P < 0.025$, Fig. 4). The cumulative diving time per hour of nighttime tended to be higher in winter than in summer ($U = 2$, $P = 0.083$, Fig. 4).

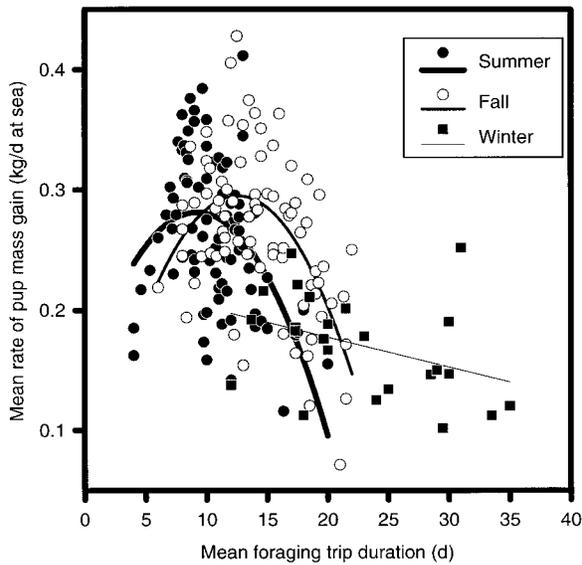


FIG. 3. Quadratic relationships between mean foraging trip duration and mean rate of pup mass gain suggest that in summer and fall, there is a window of foraging trip durations that promote the same rate of energy delivery to the pups (see also Table 7).

DISCUSSION

Provisioning pattern

This study presents the first results of maternal care from birth to weaning in an otariid with a protracted weaning period: the subantarctic fur seal, breeding on Amsterdam Island during the 1995–1996 reproductive season. Maternal care in fur seals is characterized by a long period of offspring dependence (4 to 36 mo, King 1983), when mothers alternate between long foraging

TABLE 7. Results of the linear and quadratic relationships between the mean rate of pup mass gain and the mean duration of foraging trip in subantarctic fur seals in summer ($n = 86$), fall ($n = 79$), and winter ($n = 24$) during the reproductive season 1995–1996 on Amsterdam Island.

Relation- ships	Statistical values	Season		
		Summer	Fall	Winter
Linear	r^2	0.118	0.147	0.152
	P	0.001	0.0005	0.059
Quadratic	r^2	0.251	0.314	0.166
	P	<0.0001	<0.0001	0.148

trips to feed and short attendance periods to nurse their pup (King 1983). In subantarctic fur seals, the weaning period lasts 10–11 months (Tollu 1974). Maternal provisioning effort was investigated in terms of foraging trip duration, absolute and rate of mass gains in the mother and her pup, taking into account seasonal changes.

Foraging trip duration increased throughout the pup-rearing period from, on average, 11 d in summer, to 14 d in fall and 23 d in winter, while the mean duration of attendance period (3–4 d) remained constant. The attendance pattern of the subantarctic fur seals breeding on Amsterdam Island is one of the longest reported for any otariid (compared with Gentry and Kooyman 1986; Croxall et al. 1988, Lunn et al. 1993, Goldsworthy 1995 for Antarctic fur seal *A. gazella*; Lea and Hindell 1997 for New Zealand fur seals *A. forsteri*; Higgins et al. 1988, Merrick and Loughlin 1997 for Steller sea lion *Eumetopias jubatus*; Bester and Bartlett 1990, Goldsworthy 1992 for subantarctic fur seals). Only the temperate Guadalupe *A. townsendi* and Juan Fernandez *A. philippi* fur seals present similar cycle durations,

TABLE 8. Analysis (general linear model) of pup growth rate and pup body mass at weaning in subantarctic fur seal pups in relation to variables during the reproductive season 1995–1996 on Amsterdam Island.

Dependent variable	n	r^2	Independent variable	% Contr. ‡	b §
Growth rate	54	0.404	pup sex	NS	...
			pup mass at birth (kg)	NS	...
			pup date of birth (d)	NS	...
			maternal length (cm)	11.9†	0.432
			foraging trip (d)	21.2**	–1.647
			provisioning variability	53.2***	–50.2
Mass at weaning	70	0.352	pup sex	NS	...
			pup mass at birth (kg)	NS	...
			pup date of birth (d)	NS	...
			maternal length (cm)	17.7†	0.125
			foraging trip (d)	39.4**	–0.198
			provisioning variability	32.7**	–5.364

† $P < 0.10$; ** $P < 0.01$; *** $P < 0.001$. NS = not significant ($P > 0.10$).

‡ Percentage contribution to the global model.

§ Slope (only given for significant effects after stepwise backward analysis).

TABLE 9. Time depth recorder (TDR) data and diving effort for eight (four in summer and four in winter) lactating subantarctic fur seals during the reproductive season 1995–1996 on Amsterdam Island.

TDR no.	Maternal body length (cm)	Maternal body mass (kg)	Date of departure	Hour of departure	Foraging trip duration (h)	Night duration per day (h)	Cumulative nighttime duration per trip (h)	Sum of maximum depths reached per trip (m)	Sum of diving duration per trip (min)	Dives per trip (no.)
Summer										
TDR01	131.0	49.0	31 Jan	0400	219.0	9.4	75.3	19 385	1488.3	1623
TDR02	144.0	39.0	04 Feb	0310	408.2	9.4	149.2	16 804	982.2	1417
TDR03	143.0	45.0	30 Jan	2210	555.8	9.4	211.0	34 535	2196.7	2364
TDR04	133.0	40.0	05 Feb	0050	387.0	9.4	140.3	23 216	1340.2	2886
Winter										
TDR05	137.0	52.0	10 Jul	1930	335.5	13.2	169.1	64 497	3304.4	5271
TDR06	142.0	45.0	29 Jun	1500	333.0	13.2	171.0	65 408	3700.2	4319
TDR07	135.0	51.0	11 Jul	1800	323.5	13.2	169.5	47 220	2449.5	5343
TDR08	142.0	55.0	21 Jul	0900	381.5	13.2	197.3	87 916	6041.2	4876

spending on average 11 and 12 d at sea in summer (Figueroa 1994, Francis et al. 1998). Unfortunately, data are not available for later seasons in these species. The pattern of maternal attendance described in our study appears to be normal on Amsterdam Island, as the same patterns were observed in 1994–1995 and 1996–1997 (Guinet and Georges 1999; C. Guinet and J.-Y. Georges, *unpublished data*) without consequent high pup mortality (Roux 1986). Such very long foraging trips suggest that on Amsterdam Island, coastal resources were not sufficient or appropriate for lactating females, which have to forage in distant oceanic waters. This is confirmed by data from animals fitted with satellite devices or sea temperature recorders (Georges et al. 1999). Furthermore, very long absences of the mothers without their pups starving to death suggest that metabolic adaptations in the pups exist.

Lactating females alternate foraging trips at sea to acquire energy with attendance periods ashore to transfer it to their pup. On the one hand, when mothers feed at sea, one might expect a relationship between maternal energy acquisition and foraging trip duration, which may be adjusted according to fasting ability in the pup. On the other hand, when mothers suckle their pup ashore, duration of the attendance period may be controlled by the amount of milk the mother is able to produce and the rate of milk ingestion of the pup. In subantarctic fur seals, the duration of the attendance period was positively related to the duration of the foraging trip, as observed in other fur seals (Boyd et al. 1991, Lea and Hindell 1997, Francis et al. 1998). Furthermore, mothers arriving ashore with a good body condition (i.e., with large amount of body reserves) performed long attendance periods. This suggests that after long foraging trips, mothers spend a long time suckling their pups to transfer the large amount of body reserves they stored when feeding at sea. Consistently, for each season, we found that the absolute amount of mass transferred to the pup increased with the foraging trip duration. This is consistent with the positive relationship found between milk production over an at-

tendance period and the duration of the previous foraging trip in Antarctic fur seals (Arnould et al. 1996b). Interestingly, the mass transfer from the mother to the pup was more efficient when mothers performed short attendance periods. A short stay ashore should reduce the metabolic overhead paid in the form of fasting maintenance metabolism (Fedak and Anderson 1982) and thus spare the amount of energy available for milk production. It is therefore advantageous for the pup to consume milk as rapidly as possible, as found in northern fur seals *Callorhinus ursinus* (Costa and Gentry 1986). We found that mothers performed longer foraging trips as their pup grew heavier whatever the sex of the pup. This increase in foraging trip duration has also been observed in northern fur seals (Gentry and Holt 1986), Antarctic fur seals (Boyd et al. 1991, Lunn et al. 1994, Goldsworthy 1995), and Steller sea lions (Merrick and Loughlin 1997) and suggests that maternal care is more controlled by the mass of the pup (i.e., its requirements) rather than by its sex.

Seasonal changes in provisioning pattern

Throughout the year, the proportion of time spent foraging increased from 74% in summer to 86% in winter. We also found that maternal input (Evans 1990) was related to maternal body condition. Mothers in better condition transferred a larger amount of body reserves to their pup than other mothers. Such results emphasize the importance of the organism's physiological state on individual optimization of life history decisions (McNamara and Houston 1996). Throughout the long pup-rearing period, maternal input changed, according to seasonal changes in provisioning pattern, and maternal and pup characteristics.

In summer, we found that mothers came back ashore with a lower absolute mass gain compared to fall, as also found in terms of absolute pup mass gain. Interestingly, maternal foraging efficiency (i.e., the rate of maternal mass gain in relation to the rate of pup mass gain/day the mother is at sea) did not differ between these two seasons, indicating that mothers did not come

TABLE 9. Extended.

Sum of maximum depths reached per night (m)	Sum of diving duration per night (min)	Dives per night (no.)	Cumul. diving distance per hour of night (m)	Cumul. diving duration per hour of night (min)	Dives per hour of night (no.)
2423.1	186.0	202.9	257.3	19.8	21.5
1060.8	62.0	89.5	112.7	6.6	9.5
1541.3	98.0	105.5	163.7	10.4	11.2
1558.8	90.0	193.8	165.5	9.6	20.6
5022.4	257.3	410.5	381.5	19.5	31.2
5036.3	284.9	332.6	382.5	21.6	25.3
3668.0	190.3	415.0	278.6	14.5	31.5
5868.5	403.3	325.5	445.7	30.6	24.7

back ashore lighter because they were less efficient in summer but because they spent less time at sea compared to fall. In Antarctic fur seals, lactating females do not return to feed their pup until they have replenished their own reserves (Costa et al. 1989). Our results suggest that in summer, subantarctic fur seals do not completely restore their body reserves as they do in fall, in response (1) to the limited ingestion ability and (2) to the limited fasting ability of the young pup. First, we found that in summer, absolute and rate of pup mass gains were positively related to pup body mass before suckling. This is consistent with several studies that indicate that the quantity of milk consumed by the pup is positively related to its body mass (Costa and Gentry 1986, Gentry and Holt 1986, Higgins et al. 1988, Arnould et al. 1996b, Higgins and Gass 1997). This suggests that bigger pups are bigger because they receive more milk, or that they receive more milk because they are bigger, or both. Furthermore, pup mass gain in summer was positively related to the duration of the attendance period, indicating that pups suckled during a long attendance period gained more mass. Finally, in summer, mothers spent more time ashore suckling their pup (relative to the duration of foraging trips), while transferring their reserves 15% less efficiently to their pup compared to fall (Table 1). All these findings indicate that during the early stage of pup growth, milk ingestion is likely to be limited by the small size of the pup as suggested by Costa and Gentry (1986). Second, the lack of relationship between absolute maternal mass gain and the duration of the foraging trip in summer suggests that mothers do not come back ashore as a result of replenishing their body reserves. One may suggest that mothers end their foraging trips according to pup fasting ability. Furthermore, there is probably no advantage, rather a cost for the mothers to spend a long time at sea and completely replenish their body reserves in the early stage of pup growth: in doing so, their pups would fast longer than their fasting ability permits and pups would be unable to efficiently use all maternal reserves. Consequently, in summer the maternal attendance pattern appears to be mostly controlled by pup fasting ability and the limited pup ingestion ability.

In fall, no relationships were found between pup (absolute and rate) mass gains and pup body mass before suckling and attendance period duration, suggesting that after four months of age, pups were no longer limited in milk ingestion by their size. Consistently, mass transfer efficiency increased by 15% from summer to fall. Furthermore, pup mass gains were positively related to maternal body length. As body size increases throughout life in fur seals, longer mothers are likely to be older (Trites and Bigg 1996) and consequently more experienced than smaller ones (Lunn et al. 1994). Fall appears to be a period where pup acquisition is mostly controlled by maternal traits (size, condition, and foraging trip duration), with large mothers in good condition promoting high growth rate in their pup. Probably in response to greater ingestion ability in the pups, mothers increased the time spent at sea to come back ashore with more body reserves, which they acquired at the same rate as in summer. As a consequence, the total amount of mass gained by the pup was higher in fall than in summer (3.6 and 2.7 kg, respectively). Furthermore, by increasing the duration of the foraging trips, mothers increase the proportion of time spent foraging vs. the time spent traveling. Mothers that seem to be older (and thus more experienced) appear to be more efficient when foraging, as suggested by the positive relationship we found between maternal body length and the rate of mass gain. Longer mothers may also be able to store more body reserves than smaller ones.

In winter, to allow the same amount of mass gain in their pup, females have to spend seven more days at sea than in fall, which was related with a lower rate of pup mass gain. Interestingly, we found a negative relationship between pup (absolute and rate) mass gains and pup age, indicating that the amount of mass gained by the pup decreased as the pup became older. In Antarctic fur seal pups, Arnould et al. (1996b) found that

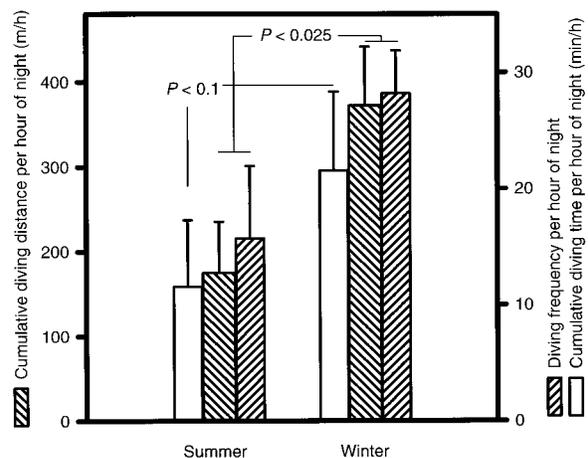


FIG. 4. Cumulative diving distance per hour, cumulative diving time per hour, and diving frequency per hour of night during summer ($n = 4$) and winter ($n = 4$) for subantarctic lactating female fur seals breeding on Amsterdam Island during the 1995–1996 reproductive season.

milk consumption decreases in the last stages of the rearing period as a consequence of preweaning processes. In our study, the weaning process should not have been initiated, as weaning occurs in mid-October (Tollu 1974) while our monitoring of mass changes ended in September. We propose two alternative explanations, which are not exclusive. In winter, most of the lactating subantarctic fur seals are pregnant while still suckling the pup of the year. Pregnancy is associated with an increase in maternal requirements (Robbins and Robbins 1979, Oftedal 1985, Blaxter 1989), in particular in the last months of gestation (Millar 1977, Trites 1991 [for northern fur seals]). The negative relationship between pup age and maternal input may be related to a change in maternal care, mothers reallocating their body reserves toward the fetus rather than to the pup of the year. Furthermore, the negative relationship between pup mass gain and maternal body length suggests that such a reallocation was more important in long (i.e., old) mothers than in short (young) ones. This suggests that in winter, older and more experienced mothers began to invest in their fetus more intensively than younger ones. While metabolic requirements of mothers may increase in winter because of pregnancy (Robbins and Robbins 1979, Oftedal 1985, Blaxter 1989), the costs of gestation are small compared to lactation in fur seals (Boyd and McCann 1989). Thus gestation costs would be insufficient to explain the increase in foraging trip duration and the decrease of 40% in the rate of pup mass gain between fall and winter. The data on diving behavior indicate that lactating subantarctic fur seals dive during the night as widely observed in otariids (see Gentry and Kooyman 1986). Furthermore, we found that for eight mothers equipped with time depth recorders, the amount of time spent foraging increased with lengthening night between summer and winter; and even if night duration was taken into account, the diving effort per hour of night was higher in winter than in summer, while the foraging efficiency (rate of mass gain) decreased. Increase in the diving effort through seasons has been also found in New Zealand fur seals (Mattlin et al. 1998) and suggests that prey availability declined throughout the year, as suggested by Merrick and Loughlin (1997). Under two different food resource conditions, lactating northern fur seals maintain foraging trip duration by increasing metabolic rate (Costa and Gentry 1986) while Antarctic females maintained their metabolic rate and increased foraging trip duration (Costa et al. 1989). It should be interesting to study field metabolic rates in lactating subantarctic fur seals as our results suggest that subantarctic females stay longer at sea and have a greater diving effort late in the season.

Provisioning pattern and foraging theory

According to optimal foraging theory, foragers that have to return to a fixed site may have an optimal cycle duration that maximizes the rate of delivery of food to the offspring (Krebs and Davies 1987). Consistently,

mothers may adopt an optimal provisioning pattern to maximize pup growth rate, which should correspond to Boyd's et al. (1991) expectations; mothers may have a minimum net energy gain, which must be satisfied before they return to feed their pup, while there may be a maximum length for foraging trip set by the fasting ability of the pup and the energy storage capacity of the mother.

For each season, the results of general linear models indicate that the pup absolute mass gain and the rate of mass gain increased and decreased with lengthening foraging trip, respectively (see Table 8). The negative relationship between the rate of pup mass gain and the foraging trip duration has been found in Antarctic fur seals during years of low food availability (Croxall et al. 1988, Lunn et al. 1993), suggesting that mothers performing long foraging trips are unable to acquire energy at a sufficient rate. Interestingly, there were no relationships between the rate of pup mass gain and the foraging trip duration during years of normal food availability (Boyd et al. 1991, Arnould and Boyd 1995). It must be pointed out that in Antarctic fur seals, the pup rearing period occurs during the short (four months) subpolar summer (King 1983). On Amsterdam Island, and over the wide range of foraging trip durations observed within and between seasons, we found that the best univariate relationship between the rate of pup mass gain and the foraging trip duration was a curvilinear relationship (Fig. 3). This suggests that there is a window of foraging trip durations, corresponding to a maximum rate of food delivery to the pup. Within the window, the rate of food delivery does not vary, as observed in Antarctic fur seals during years of normal food availability (Boyd et al. 1991, Arnould and Boyd 1995). This window (7–11 days in summer) shifted to longer durations in fall (11–15 days) as mothers were able to spend more time and store more reserves in response to the increase in pup ingestion ability. According to Trillmich and Lechner (1986), mothers performing foraging trips within this window may compensate longer absences by increasing the fat content of their milk. However, when foraging trip durations exceed the window, the rate of food delivery decreases, as observed during years of low food availability (Croxall et al. 1988, Lunn et al. 1993). One may suggest that outside the window, the increase in milk quality is not enough to compensate long absences of the mothers. We suggest that when studying subantarctic fur seals on Amsterdam Island, the wide range in foraging trip durations may allow us to observe this general relationship, which in the case of Antarctic fur seals in South Georgia can only be reported for contrasting levels of prey abundance, i.e., good and bad years. A similar pattern should occur in other temperate fur seals like Guadalupe and Juan Fernandez fur seals.

On Amsterdam Island, subantarctic male and female pups grew at the same rate during the study year (37–38 g/d, from birth date to the date of maximum mass, i.e., 230 days of age in both sexes). We found that pup growth rate and mass at weaning did not vary according to the sex, birth date, and birth mass of the pups but they were mostly determined by maternal characteristics

and attendance pattern. Basically, pups whose mother was (1) large, and performed (2) short and (3) regular foraging trips grew faster and were heavier at weaning than other pups. First, large mothers should transmit a "large size" phenotype although such a relation has not been observed in southern elephant seals (Fedak et al. 1996). Furthermore, our results indicate that large mothers were more efficient when foraging (in terms of maternal absolute and rate of mass gain), which can be related to individual performances as observed in Antarctic fur seals' (Boyd et al. 1991) age and experience. Second, the negative relationship between pup growth rate and the mean foraging trip duration has previously been found in New Zealand fur seals (Lea and Hindell 1997), and Antarctic fur seals in Heard Island (Goldsworthy 1995) and in South Georgia during years of low food availability (Croxall et al. 1988, Lunn et al. 1993). However, such a relationship was not found in Antarctic fur seals during years of normal food abundance (Boyd et al. 1991, Arnould and Boyd 1995, Arnould et al. 1996a). Third, our results indicate that a parameter never considered in previous studies acts on pup growth rate and mass at weaning: the provisioning variability, defined by the coefficient of variation (cv) of the foraging trip duration. For a given mean duration of foraging trips, pups that were regularly suckled grew faster than pups that were suckled irregularly. Provisioning variability can be discussed from two distinct points of view. From the mother's point of view, provisioning variability may indicate different foraging experience between individuals. On the one hand, experienced mothers that have the knowledge of the location of the permanent foraging grounds would be able to reach them regularly, even far from the island. On the other hand, mothers foraging in unpredictable patches increase the risks of losing them between two consecutive foraging trips, and then reduce the probability of being regular in provisioning by searching for a new patch. From the pup's point of view, the long absences of the mother correspond to long fasting periods (up to 23 days on average in winter). Subantarctic fur seal pups are able to fast for considerably longer periods than northern and Antarctic fur seal pups, which would starve to death in such conditions. On Amsterdam Island, subantarctic fur seals appear to be adapted either to a low food availability or to remote food resources as foraging trip duration is intrinsically very long. Furthermore, mothers seem to reduce as much as possible the time they spend at sea: when their body condition deteriorated after one suckling event, they did not spend more time at sea but they would be more efficient in restoring their body condition during the consecutive foraging trip, probably by increasing their diving effort. Since pup requirements and metabolism are out of the scope of this paper, recent data indicate that on Macquarie Island, mass-specific mass loss is ~30% lower in subantarctic pups compared to Antarctic pups of the same age and body mass (S. Robinson, C. Guinet, and S. Goldsworthy, unpublished data). Furthermore, Guinet and Georges (1999) found that pup mass loss is related to the duration of the foraging trip, suggesting that pups change their metabolism

according to the duration of the fast period in course: metabolism can be modified by changes in activities such as sleeping, playing ashore, and swimming. Thus, one may expect that in pups whose mother's absences are of regular duration, the pattern of mass loss would differ from that of pups whose fast duration is very variable or unpredictable.

Lactating subantarctic fur seals can promote similar growth rate and body mass at weaning to their pups in different ways, i.e., using different provisioning patterns. A mother of average body size (135 cm length) performing long (16 days) and regular (cv = 0.3) foraging trips will enable the same growth rate for her pup (43 g/d) as a mother of the same size performing shorter (10 days) and less regular (cv = 0.5) foraging trips (Table 8). Pup fasting endurance and milk quality may have a significant role in this pattern. While optimal foraging theory predicts that there is an optimal cycle duration that maximizes the net rate of delivery of food to offspring (Krebs and Davies 1987), this study suggests that in subantarctic fur seals, there may not exist one optimal strategy but a range of maternal attendance patterns promoting the same maternal fitness.

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LITERATURE CITED

- Arnould, J. P. Y., and I. L. Boyd. 1995. Temporal pattern of milk production in Antarctic fur seals (*Arctocephalus gazella*). *Journal of Zoology*, London **237**:1–12.
- Arnould, J. P. Y., I. L. Boyd, and D. G. Socha. 1996b. Milk consumption and growth efficiency in Antarctic fur seal (*Arctocephalus gazella*) pups. *Canadian Journal of Zoology* **74**:254–266.
- Arnould, J. P. Y., I. L. Boyd, and J. R. Speakman. 1996a. The relationship between foraging behaviour and energy expenditure in Antarctic fur seals. *Journal of Zoology*, London **239**:769–782.
- Bartholomew, G. A. 1970. A model for the evolution of pinnipeds polygyny. *Evolution* **24**:546–559.
- Bester, M. N. 1981. Seasonal changes in the population composition of the fur seal *A. tropicalis* at Gough Island. *South African Journal of Wildlife Research* **11**:49–55.
- Bester, M. N., and A. Bartlett. 1990. Attendance behaviour of Antarctic and subantarctic fur seal females at Marion Island. *Antarctic Science* **2**:309–312.
- Blaxter, K. 1989. *Energy metabolism in animals and man*. Cambridge University Press, Cambridge, UK.
- Boyd, I. L., N. J. Lunn, and T. Barton. 1991. Time budget and foraging characteristics of lactating Antarctic fur seals. *Journal of Animal Ecology* **60**:577–592.
- Boyd, I. L., and T. S. McCann. 1989. Prenatal investment in reproduction by female Antarctic fur seals. *Behavioral Ecology and Sociobiology* **24**:377–385.
- Cézilly, F., B. Brun, and H. Hafner. 1991. Foraging and fitness. *Acta Oecologica* **12**:683–696.

- Chastel, O., H. Weimerskirch, and P. Jouventin. 1995. Influence of body condition on reproductive decision and reproductive success in the blue petrel. *Auk* **112**:964–972.
- Costa, D. P., J. P. Croxall, and C. D. Duck. 1989. Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology* **70**:596–606.
- Costa, D. P., and R. L. Gentry. 1986. Free-ranging energetics of northern fur seals. Pages 79–101 in R. L. Gentry and G. L. Kooyman, editors. *Fur seals: maternal strategies on land and at sea*. Princeton University Press, Princeton, New Jersey, USA.
- Croxall, J. P., T. S. McCann, P. A. Prince, and P. Rothery. 1988. Reproductive performance of seabirds and seals at South Georgia and Signy Island, South Orkney Islands, 1976–1987: implications for Southern Ocean monitoring studies. Pages 261–285 in D. Sahrhage, editor. *Antarctic Ocean and resources variability*. Springer-Verlag, Berlin, Germany.
- Evans, R. M. 1990. The relationship between parental input and parental investment. *Animal Behaviour* **39**:797–813.
- Fedak, M. A., and S. S. Anderson. 1982. The energetics of lactation: accurate measurements from a large wild mammal, the grey seal (*Halichoerus grypus*). *Journal of Zoology, London* **198**:473–479.
- Fedak, M. A., T. Arbom, and I. L. Boyd. 1996. The relation between the size of southern elephant seal mothers, the growth of their pups and the use of maternal energy, fat and protein during lactation. *Physiological Zoology* **69**:887–911.
- Figuerola, A. L. 1994. Early lactation and attendance behavior of the Guadalupe fur seal females (*Arctocephalus townsendi*). Thesis. University of California, Santa Cruz, California, USA.
- Francis, J., D. Boness, and H. Ochoa-Acuña. 1998. A protracted foraging and attendance cycle in female Juan Fernandez fur seals. *Marine Mammal Science* **14**(3):552–574.
- Gentry, R. L., D. P. Costa, J. P. Croxall, J. H. M. David, R. W. Davis, G. L. Kooyman, P. Majluf, T. S. McCann, and F. Trillmich. 1986. Synthesis and conclusions. Pages 220–264 in R. L. Gentry and G. L. Kooyman, editors. *Fur seals: maternal strategies on land and at sea*. Princeton University Press, Princeton, New Jersey, USA.
- Gentry, R. L., and J. R. Holt. 1982. Equipment and techniques for handling northern fur seals. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Technical Report National Marine Fisheries Service 758, Seattle, Washington, USA.
- Gentry, R. L., and J. R. Holt. 1986. Attendance behavior of Northern fur seals. Pages 41–60 in R. L. Gentry and G. L. Kooyman, editors. *Fur seals: maternal strategies on land and at sea*. Princeton University Press, Princeton, New Jersey, USA.
- Gentry, R. L., and G. L. Kooyman. 1986. *Fur seals: maternal strategies on land and at sea*. Princeton University Press, Princeton, New Jersey, USA.
- Georges, J.-Y., F. Bonadonna, and C. Guinet. 1999. Foraging habitat and diving activity of lactating subantarctic fur seals in relation to sea surface temperatures at Amsterdam Island. *Marine Ecology Progress Series, in press*.
- Goldsworthy, S. D. 1992. Maternal care in three species of southern fur seals (*Arctocephalus* spp.). Thesis. Monash University, Melbourne, Australia.
- Goldsworthy, S. D. 1995. Differential expenditure of maternal resources in Antarctic fur seals, *Arctocephalus gazella*, at Heard Island, southern Indian Ocean. *Behavioral Ecology* **6**: 218–228.
- Guinet, C., and J.-Y. Georges. 1999. Growth in pups of the subantarctic fur seal (*Arctocephalus tropicalis*) on Amsterdam Island. *Journal of Zoology, London, in press*.
- Guinet, C., P. Jouventin, and J.-Y. Georges. 1994. Long term population changes of fur seals *Arctocephalus gazella* and *Arctocephalus tropicalis* on subantarctic (Crozet) and subtropical (St. Paul and Amsterdam) islands and their possible relationship to El Niño Southern Oscillation. *Antarctic Science* **6**:473–478.
- Higgins, L. V., D. P. Costa, and B. J. Le Boeuf. 1988. Behavioral and physiological measurements of maternal investment in the Stellar sea lion, *Eumetopias jubatus*. *Marine Mammal Science* **4**:44–58.
- Higgins, L. V., and L. Gass. 1997. Birth to weaning: parturition, duration of lactation and attendance cycles of Australian sea lions (*Neophoca cinerea*). *Canadian Journal of Zoology* **71**: 2047–2055.
- Kerley, G. I. H. 1985. Pup growth rate in the fur seals *Arctocephalus tropicalis* and *A. gazella* on Marion Island. *Journal of Zoology, London* **205**:315–324.
- King, J. E. 1983. *Seals of the world*. Cornell University Press, Ithaca, New York, USA.
- Krebs, J. R., and N. B. Davies. 1987. *An introduction to behavioural ecology*. Second edition. Blackwell Scientific, Alden, Osney Mead, Oxford, UK.
- Lea, M.-A., and M. A. Hindell. 1997. Pup growth and maternal care in New Zealand fur seals, *Arctocephalus forsteri*, at Maatsuyker Island, Tasmania. *Wildlife Research* **24**:307–318.
- Lunn, N. J., I. L. Boyd, T. Barton, and J. P. Croxall. 1993. Factors affecting the growth rate and mass at weaning of Antarctic fur seals at Bird Island, South Georgia. *Journal of Mammalogy* **74**:908–919.
- Lunn, N. J., I. L. Boyd, and J. P. Croxall. 1994. Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. *Journal of Animal Ecology* **63**:827–840.
- Mattlin, R. H., N. J. Gales, and D. P. Costa. 1998. Seasonal dive behaviour of lactating New Zealand fur seals (*Arctocephalus forsteri*). *Canadian Journal of Zoology* **76**:350–360.
- McNamara, J. M., and A. I. Houston. 1996. State-dependent life histories. *Nature* **380**:215–221.
- Merrick, R. L., and T. R. Loughlin. 1997. Foraging behavior of adult female and young-of-the-year Stellar sea lions in Alaskan waters. *Canadian Journal of Zoology* **75**:776–786.
- Millar, J. S. 1977. Adaptive features of mammalian reproduction. *Evolution* **31**:370–386.
- Oftedal, O. T. 1985. Pregnancy and lactation. Pages 215–239 in R. J. Hudson and R. G. White, editors. *Bioenergetics of wild herbivores*. CRC Press, Boca Raton, Florida, USA.
- Ricklefs, R. E. 1990. Seabirds life histories and the marine environment: some speculations. *Colonial Waterbirds* **13**:1–6.
- Robbins, C. T., and B. L. Robbins. 1979. Fetal and neonatal growth pattern and maternal reproductive effort in ungulates and subungulates. *American Naturalist* **114**:101–116.
- Roux, J. P. 1986. Sociobiologie de l'otarie *Arctocephalus tropicalis*. Thesis. Université des Sciences et Techniques du Languedoc, Montpellier, France.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. Second edition. W. H. Freeman, San Francisco, California, USA.
- Stearns, S. C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* **51**:3–47.
- Tollu, B. 1974. L'otarie de l'île Amsterdam *Arctocephalus tropicalis* (Gray 1872). Thesis. Université Paris VII, Paris, France.
- Trillmich, F., and E. Lechner. 1986. Milk of the Galapagos fur seal and sea lion, with a comparison of the milk of eared seals (Otariidae). *Journal of Zoology, London* **209**:271–277.
- Trites, A. W. 1991. Fetal growth of northern fur seals: life history strategy and sources of variation. *Canadian Journal of Zoology* **69**:2608–2617.
- Trites, A. W., and M. A. Bigg. 1996. Physical growth of northern fur seals (*Callorhinus ursinus*): seasonal fluctuations and migratory influences. *Journal of Zoology London* **238**:459–482.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136–179 in B. Campbell, editor. *Sexual selection and the descent of man*. Aldine, Chicago, Illinois, USA.
- Winkler, D. W. 1987. A general model for parental care. *American Naturalist* **130**:526–543.
- Ydenberg, R. C., C. V. J. Welham, R. Schmid-Hempel, P. Schmid-Hempel, and G. Beauchamp. 1994. Time and energy constraints and the relationships between currencies in foraging theory. *Behavioral Ecology* **5**:28–34.