Milking Strategy in Subantarctic Fur Seals *Arctocephalus tropicalis* Breeding on Amsterdam Island: Evidence from Changes in Milk Composition

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ABSTRACT

Milk composition was investigated throughout the 10-mo pup-rearing period in subantarctic fur seals (*Arctocephalus tropicalis*) breeding on Amsterdam Island. The mean milk composition was 42.8% ± 5.7% lipid, 12.1% ± 1.5% protein, and 42.6% ± 7.3% water. Subantarctic fur seals breeding on Amsterdam Island produced one of the richest milks ever reported in otariids (20.4 ± 2.9 kJ/g), with lipid content contributing 85% of total gross energy. The high lipid levels measured in the milk of subantarctic fur seals breeding on Amsterdam Island is consistent (i) with the relatively long time lactating females spend at sea, due to the relatively poor local trophic conditions near the colony that necessitate that they travel long distances to reach the foraging grounds, and (ii) with the consequently short time mothers spend with their pups ashore. Milk composition changed according to the time mothers were fasting ashore: milk produced during the first 2 d spent ashore, when more than 80% of milk transfer occurred, had higher levels of lipids, proteins, and gross energy than milk produced later during the visit ashore, suggesting that the pups were fed with two types of milk during a suckling period. Throughout the year, mothers in good condition produced milk of higher lipid content than others, suggesting that individual foraging skills contribute to enhance milk quality. Milk lipid and gross energy content varied with pup age, according to quadratic relationships, increasing during the earlier stages of lactation before reaching asymptotic values when pups were 180 d old. The stage of lactation appears to be a better predictor of milk lipid content than the duration of the preceding foraging trip, suggesting that either changes in the nutritional requirements of the pup and/or seasonal changes in trophic conditions act on milk composition. These changes in milk quality may also be related to changes in maternal care; lactating subantarctic fur seals apparently reallocate their body reserves toward gestation rather than lactation at the end of the pup-rearing period.

Introduction

In mammals, lactation is the way that mothers provide nutrients and energy to their offspring until they are capable of feeding themselves. Lactation is energetically the most expensive period in a mammal's life cycle (Pond 1977), while milk composition and energy content vary among species according to life history (Oftedal et al. 1987). For example, marine mammals have been reported to produce extremely lipid-rich, energy-dense milk (Bonner 1984; Oftedal et al. 1987) as an adaptation to the young's need to built up insulation against heat loss (in cetaceans and phocids; Hindell and Slip 1997) and/or to repeated fasting periods when the mother is away foraging (e.g., in otariids; Trillmich and Lechner 1986). This latter fundamental constraint leads to several adaptations in foraging and reproductive strategies that make pinnipeds interesting animals on which to test life history theories.

In otariids (fur seals and sea lions), maternal care consists of lactation during a long pup-rearing period (4 mo–3 yr) that alternately includes foraging trips at sea and fasting visits ashore to nurse the pup (Gentry and Kooyman 1986). Interspecific differences in the duration of the pup-rearing period and of the foraging trips have been shown to induce differences in milk lipid content, with species that have short lactation and long foraging trips producing fatter milk than others (Trillmich and Lechner 1986). In addition, due to the general pattern that most otariid species with short lactation periods tend to have

longer foraging trip durations than those with long lactation periods, species with short lactation periods have a shorter interval to deliver milk energy to their pups than do species with long lactation periods and, thus, are expected to have higher milk fat. Consistently, Costa (1991a) found a strong negative relationship between milk fat content and the amount of time lactating pinnipeds spend ashore with their pups for both phocids and otariids. Other studies showed that the relationship between milk fat and trip duration applies within species: in the northern *Callorhinus ursinus*, Antarctic *Arctocephalus gazella*, and Galápagos *Arctocephalus galapagoensis* fur seals, mothers spending a long time foraging at sea come back ashore with fatter milk than those spending less time at sea (Costa and Gentry 1986; Arnould and Boyd 1995b; Trillmich 1996).

In the few otariid species where milk composition has been monitored throughout the pup-rearing period, lipid content has been reported to increase during lactation (South American fur seal *Arctocephalus australis* [Ponce de Leon 1984]; California sea lions *Zalophus californianus* [Oftedal et al. 1987]; Antarctic fur seals [Arnould and Boyd 1995a]; Australian sea lions *Neophoca cinerea* [Gales et al. 1996]; Australian fur seals *Arctocephalus pusillus doriferus* [Arnould and Hindell 1999]). Such an increase in milk lipid content throughout lactation may be due to the seasonal increase in the foraging trip duration, as previously reported in these species (Boness et al. 1985; Boyd et al. 1991; Higgins and Gass 1993; Lunn et al. 1994). However, it is unclear whether changes in milk composition are primarily determined by the stage of lactation (i.e., the age of the pup) or by the length of time mothers spend foraging at sea.

In otariids, pup growth and survival mainly depend on the three major components of maternal care: the pattern of pup provisioning, the amount of milk transferred to the pup, and the quality of the milk. On Amsterdam Island, the subantarctic fur seals *Arctocephalus tropicalis* show a unique life history pattern for an otariid, nursing pups during a long, 10-mo rearing period (Tollu 1974; Georges et al. 1999) while performing one of the longest foraging trips ever reported for otariids (spending, on average, from 10.8 to 22.7 d at sea in summer and winter, respectively, while remaining ashore about 3.8 d, suckling their pups; Georges and Guinet 2000b). Lactating subantarctic fur seals appear to compensate for the long fasting periods of their pups by transferring large amounts of their body reserves to the pups via lactation (Georges and Guinet 2000b; Guinet and Georges 2000). According to the aforementioned relationship (Costa 1991a), and taking into consideration the seals' very long absences and the relatively short time they spend ashore suckling their pups, lactating subantarctic fur seals breeding on Amsterdam Island are expected to produce lipid-rich milk.

Furthermore, lactating subantarctic fur seals in good physical condition have been shown to promote milk transfer to their pups and, ultimately, to promote pup growth rate by transferring a larger amount of their own body reserves than others seals do (Georges and Guinet 2000a, 2000b). One may expect that they also do so by transferring milk of higher energy density, but, to date, this hypothesis has never been investigated.

In this study, we measured the milk composition in subantarctic fur seals breeding on Amsterdam Island throughout the long lactation period, relative to pup age, maternal attendance pattern, and maternal characteristics, in order to (i) assess seasonal changes, (ii) determine if these changes were primarily due to the stage of lactation or to the seasonal changes in foraging trip duration previously reported in this species, and (iii) investigate individual effects on milk composition. Furthermore, we considered the unique life history pattern of these fur seals to test Costa's (1991a) aforementioned prediction.

Material and Methods

Animals and Milk Sampling

The study was carried out on Amsterdam Island (37°55′S, 77°30′E), in the Indian Ocean, during the entire 1995–1996 reproductive season and during the 1996–1997 perinatal period. The study period was divided into four seasons, according to pup age: the perinatal period (birth to 20 d old), summer (20–90 d old), fall (91–180 d old), and winter (more than 180 d old). Study mothers were known to be lactating because they were observed giving birth to pups that were identified and marked just after birth (Georges and Guinet 2000a) and suckling their pups normally; both mothers and pups were double-tagged (Rototag, Dalton, Nettlbed, U.K.) as described in Georges and Guinet (2000a). Thus, pup age (i.e., the stage of lactation) was known for all individuals used in this study. Maternal attendance pattern (the alternation of mother's presence and absence) was determined directly by observing tagged mothers and indirectly by monitoring daily changes in body mass of tagged pups (Salter spring scale, ±0.1 kg): when mothers were not observed directly, they were considered to be at sea when their pups were losing mass and ashore when their pups were gaining mass (see details in Georges and Guinet 2000b). Thanks to this daily monitoring, pup mass gain was investigated according to the time mothers spent ashore with their pups in summer; tagged lactating mothers were captured during their visits ashore (as described in Gentry and Holt 1982), and the time lag between mother's arrival ashore and milk sampling was known. Mothers were physically restrained on a wooden board to be weighed (±1 kg) and measured (standard body length, from nose to tail, ±1 cm) in order to assess body condition by calculating the individual residual value of the linear regression between body mass and body length (see Georges and Guinet 2000b). Milk samples were obtained by manual manipulation of a single teat. Collection was facilitated by an intramuscular injection of oxytocin (1 mL, 10 IU/mL) injected 5 min before sampling. Samples were frozen

at −20°C within a few minutes of collection and were not thawed until immediately before analysis.

Milk samples were collected on 290 occasions from 98 tagged individuals captured randomly during their visit ashore (14, 75, 49, and 25 seals during the perinatal period, in summer, fall, and winter, respectively), allowing us to determine changes in milk composition both through the seasons and during suckling bouts ashore. Samples were analyzed in duplicate, and all components were measured independently.

Sample Analyses

Before analysis, the frozen milk samples were thawed at room temperature and mixed thoroughly with a glass rod. Lipid content was determined gravimetrically after extraction, according to the Dole and Meinertz procedure (1960), after validation (see below). This method allowed us to save time when a large number of samples were to be analyzed. One gram of milk was weighed to the nearest 0.1 mg in a 20-mL glass tube containing 7.5 mL of a propanol-2 : heptane : H_2SO_4 N mixture in a 4 : 1 : 0.1 proportion (v/v/v). The tube was capped with a Teflon-lined screw stopper and vigorously agitated. The mixture was kept at room temperature for 1 h, and 4.5 mL of heptane and 3 mL of distilled water were added to it. Following agitation, it was decanted for 30 min and centrifuged for 5 min at 2,000 rpm. The volume of the upper heptane phase, which contained lipids, was measured to the nearest 0.05 mL. It averaged 6.80 mL. A 5-mL aliquot was transferred into a preweighed glass vial and heated at 60°C in a ventilated oven until the solvent completely evaporated and the weight remained constant. A 20-h heating duration was found adequate and was used routinely. Heating any longer should be avoided because it induces an increase in the weight of the lipid extract, by up to 5% after 3 d, probably as a consequence of the oxidation of unsaturated fatty acids.

The Dole and Meinertz (1960) procedure was originally designated to quantitatively extract neutral lipids, such as free fatty acids and triglycerides, but not phospholipids when they are abundant. We checked its validity to extract total milk lipids by comparing the Folch et al. (1957) reference method. Milk from six individuals was pooled and extracted in quadruplicate according to both procedures. For the Folch et al. (1957) procedure, a double extraction was performed, and the lipid content was determined gravimetrically after evaporation of the solvent under vacuum at 37°C. The two procedures gave nonsignificantly different results: the CV for the Dole and Meinertz (1960) procedure was 1.0% ± 0.1% ($n = 4$) versus 1.8% ± 0.6% for the Folch et al. (1957) procedure. Moreover, we checked that the proportion of the different lipid classes, as determined by separation by thin-layer chromatography on silica gel G and quantification by gas-liquid chromatography (Groscolas and Herzberg 1997) was identical in both types of lipid extracts. Total milk lipids were mostly triglycerides

(97.3%), and the remainder was equally distributed into free fatty acids, diglycerides, and phospholipids (0.9% each).

Total nitrogen was assessed in 0.5 g of milk by a Kjeldahl procedure and was converted to protein by multiplying by 6.38 (Oftedal and Iverson 1995). Milk water content was determined by lyophilization of 1 g of milk until a constant weight was reached. Carbohydrate mass was not measured, as it generally represents less than 1% of total mass in pinniped milk (Oftedal et al. 1987). Gross energy content of milk was assessed by using an adiabatic calorimetric bomb (Parr) after partial dehydration in four milk samples of variable lipid content (26%–61.5%, i.e., the lipid content range observed in analysis). To improve representativity, samples were made by mixing equal portions of milk from two different individuals. Measurement of gross energy was made in triplicate, and the lipid and protein content of the four samples were determined in duplicate. The energy content of milk lipids and proteins was similarly determined in triplicate on a dry lipid extract and on a dry protein extract, respectively, obtained after delipidation and repeated washing with solvent, alcohol, and water to totally eliminate lipids, water, and water-soluble compounds (e.g., carbohydrates). The lipid and protein extracts were obtained after pooling 80 and 12 representative milk samples, respectively, that were collected during the whole sampling period.

During the 1-yr study, most of the females were sampled several times. To avoid pseudoreplication, data of gross milk composition were calculated and averaged for each individual. Thus, data used in the global analyses are the means of repeated measures of individuals. However, for several analyses in which the studied variables were related to initial characteristics of the mother-pup pairs (e.g., pup age, maternal body condition), we employed a random-sampling procedure to consider one visit ashore per mother-pup pair per season, so that some individuals were considered several times but for different seasons. Because of changes in milk composition during maternal fast (see "Results"), only samples obtained at day 0 and day 1 after arrival ashore (referred to hereafter as "days [0–1]") were used to investigate seasonal changes in milk composition and the effects of the duration of the preceding foraging trip. Data are presented as means ± SD, and analyses were run according to Sokal and Rolf (1981) using the Systat statistical package (Systat 6.0 Statistics, SPSS). Statistical significance was determined at $P < 0.05$.

Results

Proximate Composition

Actual gross energy measured by calorimetric bomb in four samples was significantly correlated to the gross energy estimated using lipid and protein contents of the duplicates of these four samples (gross energy measured = −0.199 + 1.023 × gross energy estimated; $r^2 = 0.999$, $n = 4$). Since the slope and the y-intercept were close from 1 and 0, respectively,

this indicated that gross energy content can be validly calculated by multiplying the derived chemical composition by energy density of milk lipid and protein over the entire range of milk composition (see "Material and Methods"). Energy density of lipids and proteins in subantarctic fur seal milk averaged 40.6 ± 0.2 kJ/g and 23.3 ± 0.3 kJ/g, respectively.

A summary of the milk composition over the whole study period is given in Table 1. On average, the sum of measured protein, lipid, and water accounted for $98.1\% \pm 0.9\%$ ($n = 83$) of the milk mass. Water and lipid contents each accounted for 43% of the milk mass, while lipids contributed to about 85% of the gross total energy in the milk. There were negative relationships (Fig. 1) between water content and lipid content (lipid [%] = $66.59 - 0.56 \times$ water [%]; $r^2 = 0.571$, $n = 83$, $P < 0.001$), protein content (protein [%] = $14.54 - 0.058 \times$ water [%]; $r^2 = 0.08$, $n = 83$, $P = 0.009$), and gross energy (gross energy [kJ/g] = $37.02 - 0.389 \times$ water [%]; $r^2 = 0.976$, $n = 83$, $P < 0.001$).

In order to assess the possible sources of variation in milk composition throughout the study period, we conducted a multiple linear regression analysis on milk lipid content (the milk component for which we have the greatest sample size) as the dependent variable; duration of the preceding foraging trip at sea, duration of maternal fast ashore before sampling occurred, maternal body length, and maternal body condition as independent variables; and the sex of the pup and season as factors. This analysis was performed with the data for one randomly sampled individual ($n = 80$), so that initial conditions were taken into account while pseudoreplication was avoided. Maternal body length ($P = 0.897$), the duration of the preceding foraging trip ($P = 0.227$), and the sex of the pup ($P = 0.112$) had no significant effect on milk lipid content. A stepwise backward analysis indicated that the milk lipid content (i) was related to the duration of maternal fast ashore before sampling occurred ($F_{1,75} = 26.65$, $P < 0.001$) and (ii) varied between seasons ($F_{2,75} = 17.16$, $P < 0.001$) and, to a lesser extent, varied with maternal body condition ($F_{1,75} = 3.656$, $P = 0.06$; final model $r^2 = 0.587$, $n = 80$, $P < 0.001$). According to these re-
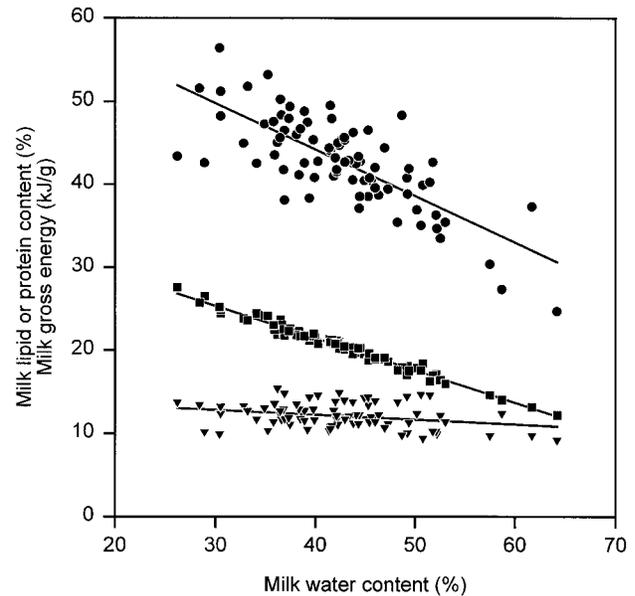
Table 1: Mean gross chemical composition of milk in subantarctic fur seals on Amsterdam Island, collected during the entire pup-rearing period

	Mean	SD	n	Range
Lipid (%)	42.8	5.7	98	24.7–56.4
Protein (%)	12.1	1.5	83	9.2–15.4
Water (%)	42.6	7.3	83	26.2–64.2
Total mass (%)	98.1	.9	83	95.5–99.9
Gross energy (kJ/g)	20.4	2.9	83	12.2–27.6

Note. Mean values are means of individual average values, regardless of the time mothers spent fasting ashore before sampling occurred (see "Material and Methods").

Figure 1. Relationships between water (%) and lipid (%; *circle*), protein (%; *triangle*), and gross energy (kJ/g; *square*) in subantarctic fur seal milk at Amsterdam Island.

sults, we investigated separately the effects of each of these parameters on milk composition.

Effect of the Duration of Maternal Fast Ashore before Sampling Occurred

Because of the significant effect of the seasons, analyses were performed by season. During the perinatal period, we did not find any significant changes in milk composition according to the time mothers were fasting ashore before sampling occurred (Table 2). In summer, milk samples were obtained from 0 to 6 d after mother's arrival ashore. Throughout the maternal fast period ashore, there were significant changes in the content in lipids, protein, water, and gross energy (Table 2). Bonferroni post hoc tests indicated that samples collected during the first 2 d of presence ashore (days [0–1] after mother's arrival ashore) had more lipid, more protein, more energy, and less water than milk sampled later in the visit ashore ($P < 0.05$; Table 2). In fall and winter, similar changes in lipid content were found between milk sampled at days [0–1] after mother's arrival ashore and days later (fall: days [0–1]: $52.2\% \pm 4.8\%$, $n = 27$; days [2+]: $45.3\% \pm 8.1\%$, $n = 22$; $t = 3.505$, $P = 0.001$; winter: days [0–1]: $52.0\% \pm 5.8\%$, $n = 11$; days [2+]: $45.4\% \pm 8.0\%$, $n = 14$; $t = 2.404$, $P = 0.025$), indicating that this pattern occurred during most of the pup-rearing period. Analyses were not performed for protein and water content in fall and winter due to small sample sizes.

During 4-d visits ashore in summer (the average duration

Table 2: Changes in milk composition in subantarctic fur seals at Amsterdam Island according to the duration of maternal fast ashore before sampling occurred, during the perinatal period and in summer

	Perinatal Period				Summer			
	Days 0–1 $n = 3$	Days 2–3 $n = 4$	Days 4+ $n = 6$	U, P Values	Days 0–1 $n = 32$	Days 2–3 $n = 15$	Days 4+ $n = 8$	U, P Values
Lipid (%)	37.1 ± 2.6	36.8 ± 11.8	36.1 ± 5.9	.01, .99	44.9 ± 4.5[A]	32.5 ± 7.6[B]	34.4 ± 7.5[B]	33.48, <.001
Protein (%)	10.6 ± 1.6	10.7 ± 2.1	10.8 ± 1.1	.25, .88	13.4 ± 1.6[A]	11.1 ± 1.9[B]	10.7 ± 1.8[B]	18.30, <.001
Water (%)	51.1 ± 1.0	51.1 ± 10.0	51.0 ± 6.0	.02, .99	40.6 ± 4.7[A]	55.4 ± 9.1[B]	54.1 ± 7.9[B]	25.95, <.001
Gross energy (kJ/g)	17.5 ± 1.0	17.4 ± 4.4	17.2 ± 2.4	.01, .99	20.9 ± 1.7[A]	15.5 ± 3.4[B]	15.7 ± 3.2[B]	25.75, <.001

Note. Sample size for lipid content during the perinatal period on days 4+ is $n = 7$; during the summer period, days 0–1: $n = 44$, days 2–3: $n = 20$, days 4+: $n = 10$. Analyses were performed using data for a random sample of one individual per season to avoid pseudoreplication. Values are means ± SD. For summer, different superscript letters indicate significant differences between days (Bonferroni tests, $P < 0.05$).

in summer; Georges and Guinet 2000b), pups did not gain body mass regularly, as they gained 42% ± 23%, 82% ± 15%, and 91% ± 12% of the total body mass gain during the first, second, and third days, respectively, of mother's visit ashore. According to the observed changes in milk composition during the visit ashore, the next analyses investigating changes in milk composition were only performed with milk collected during days [0–1] after mother's arrival ashore.

Effect of the Stage of Lactation

In further results, the perinatal period was excluded from the analyses because only three milks were sampled at days [0–1] after mother's arrival ashore for this season. All major components measured in milk sampled during days [0–1] after mother's arrival ashore were related to pup age according to quadratic relationships that provided a better fit than linear models, except for protein content (Fig. 2). Milk lipid and gross energy increased during the first stages of lactation, reached their maximum value when pups were about 180 d old, and tended to decrease during the later stage, whereas water content varied according to the inverse pattern, which fits better with a linear model (Fig. 2). Consistently, milk composition at days [0–1] after mother's arrival ashore differed significantly in summer compared to fall and winter (Table 3). Thus, fall and winter data were pooled and randomly sampled to avoid pseudoreplication while promoting sample size for late lactation for the next analyses.

All major components measured in milk sampled during days [0–1] after mother's arrival ashore varied with the duration of the preceding trip according to linear relationships (Fig. 3), with lipid content and gross energy increasing and protein and water contents decreasing with longer trip duration. The trends of the relationships between milk components and trip duration were similar to those observed with pup age (Figs. 2, 3), because pup age and trip duration were dependent variables when considering the entire pup-rearing period (trip duration [d] =

5.8 + 0.10 × pup age [d]; $n = 73$, $r^2 = 0.613$, $P < 0.001$). However, when considering summer, trip duration was not related to pup age ($r^2 = 0.034$, $P = 0.137$, $n = 67$) though it was in fall–winter ($r^2 = 0.394$, $P < 0.001$, $n = 33$). In order to assess if changes in lipid content in milk sampled during days [0–1] after mother's arrival ashore were principally determined by pup age or by the duration of the preceding foraging trip in summer, we conducted a multiple linear regression analysis with milk lipid content as dependent variable; maternal body length, maternal body condition, pup age, and duration of the preceding trip as independent variables; and the sex of the pup as factor. According to the general model, the duration of the preceding trip ($P = 0.25$) and the sex of the pup ($P = 0.169$) had no significant effect on milk lipid content in summer that was positively related (i) to the age of the pup ($F_{1,66} = 30.38$, $P < 0.001$) and (ii) to maternal body condition ($F_{1,66} = 16.64$, $P < 0.001$) and, to a lesser extent, to maternal body length ($F_{1,66} = 4.23$, $P = 0.044$). Stepwise backward analysis removed the later variable at the 5% level, resulting in the following equation for lipid content in milk sampled at days [0–1] after mother's arrival ashore in summer: lipids (%) = 35.23 + 0.144 × pup age (d) + 0.549 × maternal condition ($r^2 = 0.44$, $P < 0.001$, $n = 70$). Similar analysis considering gross energy in milk sampled at days [0–1] in summer gave similar results: gross energy (kJ/g) = 17.98 + 0.050 × pup age (d) + 0.163 × maternal condition ($r^2 = 0.274$, $P < 0.001$, $n = 48$). In fall–winter, when trip duration and pup age were dependent variables, we conducted simple linear regression analyses using each independent variable separately: milk lipid content was related to maternal body condition ($r^2 = 0.137$, $P = 0.019$, $n = 41$) but not to pup age ($P = 0.215$), duration of the preceding trip ($P = 0.112$), or maternal body length ($P = 0.464$), and it did not differ between pup sexes ($P = 0.93$).

Discussion

Subantarctic fur seals breeding at Amsterdam Island produce energy-dense (21–24 kJ/g) milk over the entire pup-rearing

period, corresponding to one of the richest milks ever reported in otariids, of similar lipid content (45%–52%) as that reported in phocid seals (see Costa 1991*b*). Milk lipid and water contents were negatively related, and gross energy was the parameter best related to water content (Fig. 1), indicating that measuring water content can provide a reasonable estimate of gross energy content, as previously reported in Antarctic and Australian fur seals (Arnould and Boyd 1995*a*; Arnould and Hindell 1999). This is particularly interesting because water content is the simplest parameter to measure in milk samples.

Milk composition changed significantly as mothers were fasting ashore. During the first 2 d spent ashore, milk composition remained roughly constant, but showed a sharp decline in lipid and protein contents, associated with a significant increase in water content (Table 2), after that period. Milk produced after the second day spent ashore consistently was less energy rich than that produced earlier. We showed that during 4-d visits ashore (the average duration of visits in subantarctic fur seals on Amsterdam Island; Georges and Guinet 2000*b*), 80% of the total body mass gained by the pups was gained during the first 2 d mothers spent ashore. As pup mass gain only depends on milk ingestion, these results suggest that lactating subantarctic fur seals appear to maximize their maternal input to their pups during the two first days spent ashore by increasing both the quality and the quantity of milk transferred to their pups in the beginning of their visit ashore. In doing so, lactating subantarctic fur seals probably compensate for the pups' relatively long fasting periods, which are a result of long foraging trips performed by their mothers (Georges and Guinet 2000*b*). The observed decrease in milk quantity transferred to the pups during the remaining days spent ashore may result from pup satiety (particularly in summer; see Georges and Guinet 2000*b*), whereas the decrease in milk quality may be due to a decrease in maternal body reserves (see below). In northern and Antarctic fur seals, milk fat has been reported to decline as mother's time ashore increases (Costa and Gentry 1986; Arnould and Boyd 1995*a*), whereas it remains constant over fasting periods in Australian sea lions (Gales et al. 1994). In southern elephant seals *Mirounga leonina*, a species in which mothers fast 3 wk while suckling their pups to weaning, fat content increases by more than twice between parturition and pup weaning (Hindell et al. 1994). Such differences between phocids and otariids illustrate differences in growth strategies between these two groups: in phocids pup growth consists in the accumulation of adipose tissues stored as blubber with little growth in lean tissues (Costa et al. 1986), whereas otariids mainly grow by lean tissue deposition. In subantarctic fur seals, the significant change in milk composition and gross energy after 2 d ashore suggests that two types of milk are fed to the pup, depending on the time during the visit ashore. This is supported by analyses of fatty acid composition, suggesting, first, that milk is produced directly from prey components and, second, that it is produced from maternal stores when the mother is fasting
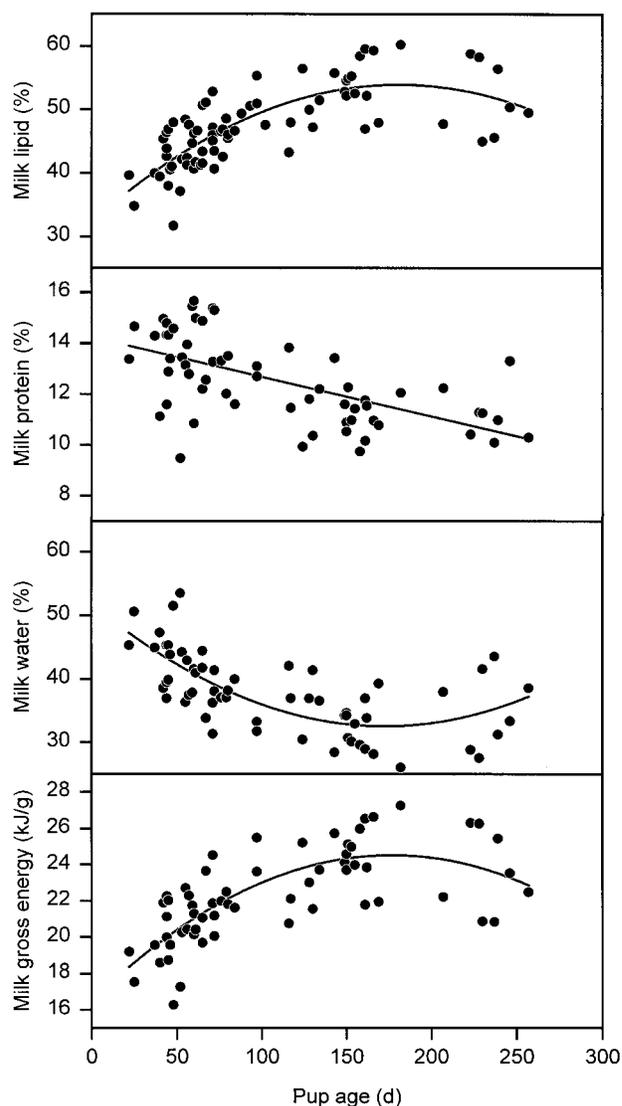

Figure 2. Changes in the levels of the m ajor milk components in relation to pup age (in days) in subantarctic fur seals on Amsterdam Island, considering milk samples obtained at days [0–1] after mother's arrival ashore. Lipid (%) = $32.1 + 0.24 \times$ pup age $- 0.00066 \times$ pup age^2; $r^2 = 0.582$, $n = 78$, $P < 0.001$. Protein (%) = $14.2 - 0.0156 \times$ pup age; $r^2 = 0.359$, $n = 63$, $P < 0.001$. Water (%) = $52.0 - 0.228 \times$ pup age $+ 0.00067 \times$ pup age^2; $r^2 = 0.496$, $n = 63$, $P < 0.001$. Gross energy (kJ/g) = $16.4 + 0.091 \times$ pup age $- 0.00026 \times$ pup age^2; $r^2 = 0.538$, $n = 63$, $P < 0.001$.

ashore (R. Groscolas, J.-Y. Georges, E. Mioskowski, and C. Guinet, unpublished data).

We did not find significant changes in milk composition during the perinatal period, when lactating fur seals fast for an unusually long period. Northern fur seals show a reduction in milk lipid content during the 7-d perinatal period and the subsequent 2-d visit ashore (Costa and Gentry 1986). In Ant-
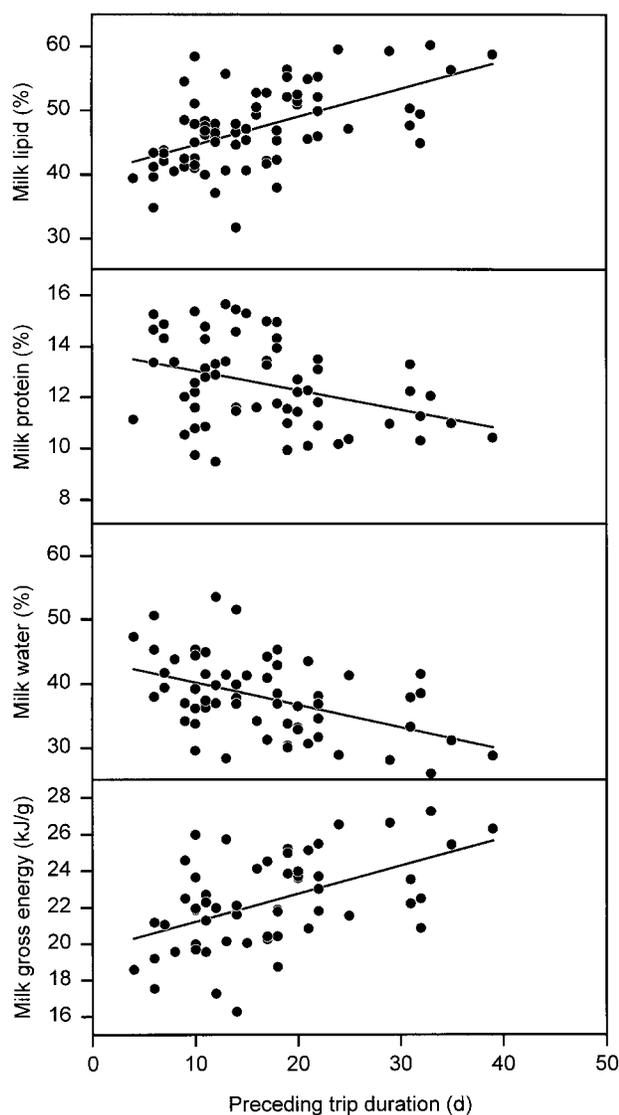
Figure 3. Relationships between the levels of the major milk components and the duration of the preceding foraging trip (days) in subantarctic fur seals on Amsterdam Island, considering milk sampled at days [0–1] after mother's arrival ashore. Lipid (%) = 40.2 + 0.443 × trip duration; r^2 = 0.312, n = 74, $P < 0.001$. Protein (%) = 13.8 − 0.076 × trip duration; r^2 = 0.132, n = 61, P = 0.003. Water (%) = 43.6 − 0.347 × trip duration; r^2 = 0.213, n = 61, $P < 0.001$. Gross energy (kJ/g) = 19.7 + 0.153 × trip duration; r^2 = 0.257, n = 56, $P < 0.001$.

arctic fur seals, lipid content and gross energy have been shown to decrease during the perinatal period, between the day of parturition and the day of departure for the first foraging trip (Arnould and Boyd 1995a). On Amsterdam Island, pregnant subantarctic fur seals spend 1–2 d ashore without feeding before giving birth and spend about 8 d ashore suckling their newborn

(Georges and Guinet 2000a). Milk composition was similar during the perinatal period (after parturition occurred) and after 2 d spent fasting ashore during the remaining pup-rearing period. This suggests a common process for milk synthesis in these two distinct fasting situations, with milk components originating from the mobilization of maternal body stores. The lack of a significant change in milk composition during the perinatal period may also be due to small sample sizes for this season in this study.

Previous studies have shown that lipid content increases both with pup age and the duration of the preceding trip and concluded that the increase in milk lipid content throughout lactation was related to the seasonal increase in foraging-trip duration (California and Australian sea lions—Boness et al. 1985, Oftedal et al. 1987, Higgins and Gass 1993, Gales et al. 1996; northern fur seals—Costa and Gentry 1986; Antarctic fur seals—Arnould and Boyd 1995a, 1995b; Australian fur seals—Arnould and Hindell 1999). Thus, it is not clear whether pup age or trip duration is the primary determinant of milk composition. In subantarctic fur seals, trip duration increases as the pups become older (Georges and Guinet 2000b; Guinet and Georges 2000). In this study, we investigated whether lipid content increased during the study period because pups aged or because their mothers spent more time feeding at sea. A multiple linear model performed in summer—when the duration of the trips was independent of the age of the pup—showed that milk lipid content increased as the pups became older, regardless of the duration of the preceding trip. The increase in milk lipid content through the summer may result from mothers recovering the body condition they had at parturition, which they lost during the long perinatal period (Georges and Guinet 2000a) and recovered during the consecutive foraging trips, as reported for Galápagos fur seals (Trillmich 1986). This is supported by the significant effect of maternal body condition on milk lipid content observed in this study. Increasing milk lipid content in summer may also result from maternal response to the increasing requirements in the growing pups. Furthermore, the lack of a relationship between milk lipid content and the duration of the preceding foraging trip in summer also suggest that during this season subantarctic fur seals compensate for the longer fast of their pups by transferring more milk, as previously reported (Georges and Guinet 2000b; Guinet and Georges 2000), rather than by transferring high-quality milk in summer.

In subantarctic fur seals, lipid and energy content increased during the first 6 mo of lactation and remained constant (Fig. 2). An increase in lipid and energy content during the first months of lactation has been previously reported in South American (Ponce de Leon 1984), northern (Costa and Gentry 1986), Antarctic (Arnould and Boyd 1995a), and Australian fur seals (Arnould and Hindell 1999) and California sea lions (Boness et al. 1985), whereas lipid levels decrease with pup age in Galápagos fur seals (Trillmich and Lechner 1986). In Aus-

Table 3: Seasonal changes in mean milk composition in subantarctic fur seals on Amsterdam Island, considering milk sampled at days [0–1] after mother's arrival ashore (except during the perinatal period, where all data were used but were excluded for comparisons)

	Perinatal Period $n = 13$	Summer $n = 49$	Fall $n = 25$	Winter $n = 14$	U, P Values
Lipid (%)	36.6 ± 7.0	45.0 ± 3.7^A	51.9 ± 4.9^B	52.3 ± 6.0^B	44.51, <.001
Protein (%)	10.8 ± 1.4	13.4 ± 1.4^A	11.6 ± 1.3^B	11.5 ± 1.2^B	27.24, <.001
Water (%)	51.0 ± 6.3	40.7 ± 4.5^A	33.3 ± 4.0^B	33.3 ± 4.9^B	36.69, <.001
Gross energy (kJ/g)	17.4 ± 2.7	21.0 ± 1.7^A	24.3 ± 1.7^B	24.3 ± 2.0^B	43.20, <.001

Note. Values are means ± SD. Sample sizes are $n = 14$, $n = 71$, $n = 32$, and $n = 15$ for lipid contents during the perinatal period, in summer, fall, and winter, respectively. Different superscript letters indicate significant differences between seasons, excluding the perinatal period (Bonferroni tests, $P < 0.05$).

tralian sea lions, where lactation lasts 18 mo, milk lipid content has been reported to increase during the first 13 mo of lactation (Gales et al. 1996). Examination of Figure 2 (this study) suggests that milk lipid content tends to decrease during the last months of lactation, as was recently found in Australian fur seals, which lactate for 11 mo (Arnould and Hindell 1999). Similarly, the examination of the data of Gales et al. (1996) suggests a similar pattern in the later stage of lactation in Australian sea lions. Despite the several differences in life history traits between otariids and phocids, it is interesting to note that lipid content reaches an asymptotic value in the last days of lactation in grey seals *Halichoerus grypus* (Iverson et al. 1993), while it decreases during the same period in southern elephant seals (Carlini et al. 1994). A previous study showed that on Amsterdam Island, lactating subantarctic fur seals transfer their body reserves at a higher rate in both summer and fall (pups gain ∼270 g/d mothers spent at sea) than in winter (∼170 g/d mothers spent at sea; Georges and Guinet 2000b), while milk energy content is the highest in fall (this study). These results indicate that in subantarctic fur seals, the amount of energy delivered to the pup per unit of time is maximum in fall, when pups are about 180 d old (Fig. 2), intermediate in summer, and low in winter. Similarly, Arnould and Hindell (1999) showed that the highest amount of energy delivered to the Australian fur seal pups occurred at 220 d. In subantarctic fur seals, the observed threshold in milk lipid content in fall and winter and the decrease in the rate of mass transfer to the pups (Georges and Guinet 2000b) may contribute to a decrease in maternal input toward the pup of the year in the later stages of lactation, either in association with the weaning process and/or with competitive use of maternal resources toward both lactation and gestation during late lactation. Consistently, it has been suggested that, on Amsterdam Island, lactating subantarctic fur seals would be able to reallocate their body reserves toward gestation rather than lactation at the end of the pup-rearing period (Georges and Guinet 2000b).

In subantarctic fur seals, milk protein content decreased linearly as the pups became older (Fig. 2). In Antarctic fur seals, protein levels decrease with pup age during years of low food availability but increase during years of normal food availability (Arnould and Boyd 1995a). In Australian fur seals, protein content increases slightly during the 11-mo lactation (Arnould and Hindell 1999). These observations suggest that interspecific differences in the seasonal changes in milk protein content may not be related to differences in the duration of pup dependence: in Antarctic fur seals, the pup-rearing period is short (4 mo), and it has been proposed that increasing milk protein content may facilitate the rapid transfer of nutrients to the growing pups (Arnould and Boyd 1995a). In subantarctic fur seals, who nurse their pups for 10 mo (Tollu 1974; Georges et al. 1999), proteins may be transferred by lactation at a lower yield than in Antarctic fur seal pups. The decrease in protein content observed in this study also indicates that lactating subantarctic fur seals breeding on Amsterdam Island cope with relatively poor trophic conditions. This suggestion is supported by the protracted attendance pattern (Georges and Guinet 2000b) due to the wide foraging range (Georges et al. 2000) and resulting in the relatively low rate of pup growth observed in subantarctic fur seals on Amsterdam Island compared with other species (38 g/d; Georges and Guinet 2000b). In contrast, subantarctic fur seals breeding at Macquarie Island forage at sea, close to the colony, for 0.4 to 3.8 d, and produce milk with 16.1% protein content, resulting in a pup growth rate of 55–80 g/d (Goldsworthy 1999; Goldsworthy and Crowley 1999). Since subantarctic fur seals on Amsterdam Island produce fatter milk than do seals on Macquarie Island (42.8% vs. 38.6%, respectively), this contributes to lower milk protein contents that may act as a limiting factor in pup growth on Amsterdam Island, because pup growth in otariids mainly consists of lean tissue deposition (i.e., protein) rather than adipose tissue stores.

When considering interspecific comparisons in milk composition relative to the duration of the foraging trips, Juan Fernandez fur seals *Arctocephalus philippii* wean their pups within 11 mo, perform long foraging trips (about 10 d in summer; Francis et al. 1998), and produce milk as lipid rich (41% in summer; Francis et al. 1998, Ochoa-Acuña et al. 1999) as

that found in subantarctic fur seals at Amsterdam Island (45%; see also Fig. 4). In both species, lactating females leave the poorly productive insular system to forage in oceanic grounds several hundred kilometers away from the breeding site. High milk lipid levels in Juan Fernandez and subantarctic fur seals may be related to the protracted maternal absence observed in these species and seems to be a way by which both species accommodate poor local insular ecological environments. These results on milk composition in different fur seal species agree with Trillmich and Lechner (1986), who proposed a general pattern according to which fat content in the milk of different otariid species correlates with the average duration of maternal foraging trips. Figure 4 shows that an asymptote is reached between milk fat and trip duration, whereas previous studies reported a positive linear relationship between these two parameters (Trillmich and Lechner 1986; Costa 1991*a*). Furthermore, despite the relatively long pup-rearing period, lactating subantarctic fur seals breeding on Amsterdam Island only spend about 64 d ashore with their pups because of the protracted foraging trips. Thus, in this study, the high level of lipids associated with the short time mothers spend with their pups ashore is consistent with Costa's (1991*a*) predictions. However, similar calculations indicate that at Macquarie Island, lactating subantarctic fur seals spend 60% more time ashore with their pups (106 d; Goldsworthy 1992) but produce milk only 10% less lipid rich than on Amsterdam Island (38.6%; Goldsworthy and Crowley 1999). One may conclude that other factors, such as trophic conditions (prey availability/accessibility and energy density), also act on the lipid concentrations of otariid milks. However, precise interspecific comparisons of milk composition between pinniped species are difficult because the quality of the overall data is poor: (i) sample sizes are usually small and often cover only the early phase of lactation and (ii) samples are frequently done randomly, regardless of the time previously spent feeding at sea and/or fasting ashore and of the individual characteristics (e.g., Goldsworthy and Crowley 1999), whereas this study clearly shows that these parameters have to be taken into account.

Maternal individual characteristics contributed to the changes in lipid content observed in the milk of subantarctic fur seals, as mothers in good condition produced fatter/richer milk than those in poorer condition throughout the year. In Antarctic and Australian fur seals, heavier mothers produced fatter/richer milk than lighter ones (Arnould and Boyd 1995*b*; Arnould and Hindell 1999). In subantarctic fur seals, we did not find relationships between milk lipid content and maternal body length, as also previously reported in Australian sea lions (Kretzmann et al. 1991) and Australian fur seals (Arnould and Hindell 1999). In fur seals, body length increases throughout life, and longer individuals are likely to be older (Lunn et al. 1994; Trites and Bigg 1996). This study suggests that, in subantarctic fur seals, the quality of the milk seems to be more determined by individual maternal foraging skills and conse-
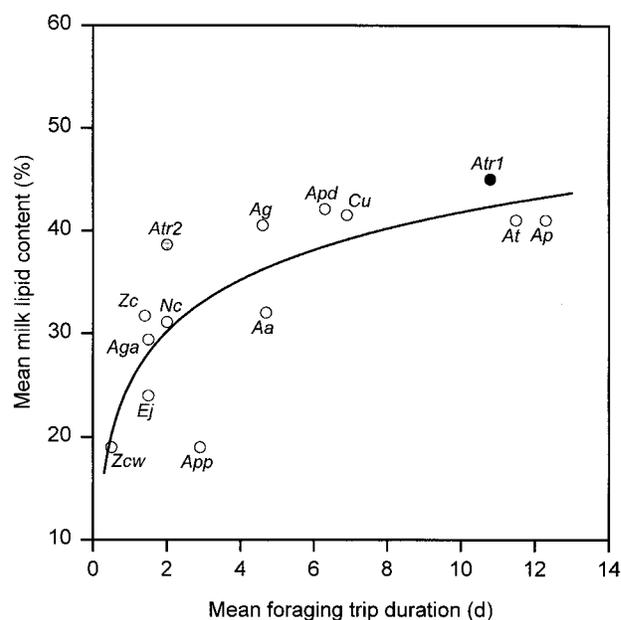

Figure 4. Relationship between mean foraging trip duration (days) and mean milk lipid content (%) in 13 species of otariid seals during the early stage of lactation. Lipid (%) = 25.2 + 7.21 × ln (trip duration); $r^2 = 0.625$, $n = 14$, $P < 0.001$. *Atr1*: subantarctic fur seal *Arctocephalus tropicalis* at Amsterdam Island (this study) and *Atr2* at Macquarie Island (Goldsworthy and Crowley 1999); *Cu*: northern fur seal *Callorhinus ursinus* (Costa and Gentry 1986; Gentry and Holt 1986); *At*: Guadalupe fur seal *Arctocephalus townsendi* (Figueroa 1994); *Ap*: Juan Fernandez fur seal *Arctocephalus philippii* (Francis et al. 1998; Ochoa-Acuña et al. 1999); *Aga*: Galápagos fur seal *Arctocephalus galapagoensis* (Gentry et al. 1986; Trillmich and Lechner 1986); *Aa*: South American fur seal *Arctocephalus australis* (Ponce de Leon 1984; Trillmich et al. 1986); *App*: Cape fur seal *Arctocephalus pusillus pusillus* (Gentry et al. 1986); *Apd*: Australian fur seal *A. pusillus doriferus* (Arnould and Hindell 1999); *Ag*: Antarctic fur seal *Arctocephalus gazella* (Arnould and Boyd 1995*a*, 1995*b*); *Ej*: Steller sea lion *Eumetopias jubatus* (Higgins et al. 1988); *Zc*: California sea lion *Zalophus californianus* (Oftedal et al. 1987); *Zcw*: Galápagos sea lion *Z. californianus wollebaeki* (Gentry et al. 1986); *Nc*: Australian sea lion *Neophoca cinerea* (Gales and Costa 1997).

quent body condition than by maternal age. In domestic mammals such as cows and goats, maternal body condition also determines milk lipid content by affecting mobilization of body reserves (Journet and Chilliard 1985; Chilliard 1992; Chilliard et al. 1998). Finally, in late lactation, lactating subantarctic fur seals in good condition produced fatter milk than others, suggesting that they were able to maintain their maternal input successfully despite the previously proposed resource competition between lactation and gestation (Georges and Guinet 2000*b*).

In short, the high level of milk lipid content associated with low protein content can be related to the unusual life history pattern observed in subantarctic fur seals breeding on Am-

sterdam Island: pups fast for unusually long periods, for which mothers compensate by transferring large quantities of high-quality milk whose energy density is dependent on maternal body condition (Georges and Guinet 2000*b*; this study). Subantarctic fur seals breeding at Amsterdam Island have been reported to be larger in body size than in other locations where they breed (Bester and Van Jaarsveld 1994, 1997), suggesting that they are able to store more maternal body reserves compared with individuals of other populations. Large body size is one obvious characteristic of pinnipeds, particularly in phocids, which have to store large amounts of blubber to be transferred to the offspring during reproduction (Costa 1991*b*). These characteristics suggest that subantarctic fur seals breeding on Amsterdam Island adopt a phocidlike strategy, resulting in the relatively high transfer of adipose tissue rather than lean tissue to the pups and, ultimately, in a relative low growth rate.

Acknowledgments

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