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Milk of the Galapagos fur seal and sea lion, with a comparison of the milk of Eared seals (Otariidae)

FRITZ TRILLMICH* AND ERIKA LECHNER**

**Max-Planck-Institut für Verhaltensphysiologie, D-8131 Seewiesen, and **Südd. Versuchs- und Forschungsanstalt für Milchwirtschaft, Technische Universität München, Institut für Chemie und Physik, D-8050 Freising, West Germany*

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(With 1 figure in the text)

The milk of two tropical species of Eared seals (Otariidae) was analysed. In the Galapagos fur seal (*Arctocephalus galapagoensis*), milk fat content decreased and calcium content increased with age of the young (Table I), while protein content (12%) and potassium content (167 mg%) remained more or less constant. Fat content was 32% during the perinatal attendance period, later decreasing to 25%, while calcium increased from 57 to 70 mg%. The fewer samples of Galapagos sea lion (*Zalophus californianus wollebaeki*) milk contained on average 17% fat and 9% protein. Fat content in the milk of different otariid seal species correlates best with the average duration of maternal foraging trips and less with the weaning age of young (Fig. 1).

Contents

Introduction

No terrestrial mammal matches the high fat content of marine mammal milk (Jenness & Sloan, 1970). This high fat content appears to be an adaptation to the young's need to build up insulation against heat loss (in whales and many phocids) and/or to repeated episodes of fasting while the mother is away foraging (in otariids). The particularly high fat content of phocid milk aids mothers to conserve body water while they fast during lactation (Riedman & Ortiz, 1979).

Conservation of body water is also important for terrestrial mammals living in dry environments. Kangaroo rats living on dry seeds have unusually rich milk averaging about 23·5% fat (Kooyman, 1963). However, there are cases of terrestrial mammals living in humid environments, but nevertheless producing high fat-content milk. These are the Tree shrews (Tupaias; D'Sousa & Martin, 1974). Tupaia mothers, whose milk contains 26% fat, pay short

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visits every two days to their nests for suckling the young. The energy transferred during this time must sustain growth and maintenance metabolism of the young during the 48 h of the mother's absence. Thus short periods of nursing alternating with long maternal absences may also select for high fat contents of milk in terrestrial mammals (Jenness & Sloan, 1970).

Within the Otariidae, the Eared seals, females do not usually fast for more than one or two days, but pups must tolerate maternal absences that vary between one and seven days among different species (*Callorhinus ursinus*, *Arctocephalus gazella*, *A. pusillus*, *A. galapagoensis*, *Zalophus californianus wollebaeki*; Gentry & Holt, McCann, Doidge & Croxall, David & Rand, Trillmich *a* and *b*, all In press). One may ask if these differences in attendance schedules are reflected in the species' milk composition. Another markedly variable parameter in otariid ontogenies is the time to weaning. Subpolar species are weaned at about four months of age (Payne, 1979; Gentry, 1981), while in the Galapagos fur seal (*Arctocephalus galapagoensis*), young were regularly observed nursing until about two years old (Trillmich, 1984).

In this paper, we provide first data on the milk composition of two species of tropical otariids in which mothers spend only 1–4 days away from their pups (Trillmich, In press *a* and *b*), and nurse them for two years in the Galapagos fur seal, or about one year in the Galapagos sea lion (*Zalophus californianus wollebaeki*).

Material and methods

Collection of samples

Eight fur seal and 9 sea lion milk samples were obtained by stomach tubing pups shortly after the end of a sucking bout. Samples of 30–100 ml were drawn, an amount not very significant for pup nutrition compared to total milk intake. Fur seal pups were 2–36 days old; one sample was taken from a yearling. Sea lion pups were 2–50 days old.

A further 19 milk samples were obtained by milking female fur seals (with pups 1–30 days old and 1 with a yearling) and 1 by milking a female sea lion (with an approx. 60-day-old pup). To allow a more detailed analysis of changes in milk composition with pup age, 4 of these fur seal females were each milked 3 times, first on the day of their pup's birth, then when pups were 4–6 and finally when they were 12–15 days old. Females were restrained and given 20 international Units (i.U.) oxytocin intramuscularly (i.m.). Milk was extracted by massaging the area around the teat while applying suction. The milk was immediately mixed with sodium azide and stored at ambient temperature (*c.* 22 °C) until shipment to Germany.

Analytical methods

Milk composition was determined by using standard methods employed for cow milk analysis. Fat content was determined with the Röse-Gottlieb method (DIN 10312; Horwitz, 1965), total nitrogen (N) with the Kjeldahl procedure (DIN 10334; N × 6·38) and lactose enzymatically with the Boehringer test-kit. This lactose assay permits reliable and specific determination of lactose to a lower limit of 0·1%. Ca and K were determined by flame photometry with an Eppendorf photometer after wet digestion of the samples with conc. H_2SO_4 in a Büchi digestor 445. Non-protein N (NPN) was determined as the difference between total N and $ZnSO_4$-precipitated N.

Results

The fur seal

Galapagos fur seal females attend their young for the first seven days after parturition. Thereafter, they alternate between foraging trips of about two days and about one-day stays ashore. Mothers usually return from foraging in the morning (Trillmich, In press *a*). After the return of their mothers, the first several hundred ml of milk passed quite fast through the stomachs of pups. In the mornings, sampling milk from pups directly after a sucking bout only succeeded with pups $\leqslant$ five days old. These young pups had presumably been sucking during the previous night. Older pups were visibly swollen only in the evenings, and only then did we obtain fresh undigested milk in sufficient quantities.

Table I gives the results of the milk content analysis. Samples taken in different years (1979, 81, 83 and 84) were not significantly different. Fat, protein and calcium contents of milk obtained directly from the teat or from pup stomachs showed no significant differences. Potassium concentrations, however, were significantly reduced in the stomach samples (Mann-Whitney U test; $P = 0{\cdot}002$), indicating a higher rate of uptake for potassium than for calcium. Non-protein nitrogen concentrations were significantly lower in milked samples than in stomach samples (Table I; Mann-Whitney U test; $P = 0{\cdot}028$). Presumably, preservation of the samples with sodium azide without cooling allowed pup stomach enzymes to continue protein breakdown for a while.

Changes in milk composition with the age of the pup were analysed for milked samples over the first 30 days of pup life. Fat content decreased (%fat $= 32{\cdot}8 - 0{\cdot}38d$ (d = pup's age in days); $r = -0{\cdot}51$, $P < 0{\cdot}05$), and calcium content increased with age (Ca (mg%) $= 55{\cdot}0 + 0{\cdot}89d$; $r = 0{\cdot}67$, $P < 0{\cdot}01$). Potassium content showed a trend in the same direction as calcium (K (mg%) $= 158{\cdot}2 + 0{\cdot}99d$; $r = 0{\cdot}43$, $0{\cdot}1 > P > 0{\cdot}05$). Protein content did not correlate with age (%protein $= 12{\cdot}9 - 0{\cdot}05d$; $r = -0{\cdot}18$, P[illegible]0·1).

Lactose, if any was present, was below the analytical level (0·1%). Other sugars were not tested.

TABLE I

Milk composition (mean ± S.D.) of the Galapagos fur seal. Number of samples in brackets

Milk source	Female teat	Pup stomach
% fat	29·4 ± 5·9 (19)	23·8 ± 4·2 (8)
% fat on day 1–8	32·4 ± 5·3 (11)	25·5 ± 2·9 (3)
% fat on day ⩾ 12	25·1 ± 3·6 (8)	22·7 ± 4·8 (5)
% protein*	12·1 ± 2·9 (19)	10·9 ± 2·2 (8)
% non-protein nitrogen	0·11 ± 0·04 (3)	0·77 ± 0·16 (4)
calcium mg %	63 ± 10 (17)	64 ± 14 (8)
calcium (mg %) day 1–8	57 ± 7 (10)	64 ± 25 (3)
calcium (mg %) day ⩾ 9	70 ± 10 (7)	63 ± 7 (5)
potassium mg %	167 ± 18 (17)	98 ± 11 (8)

* Total nitrogen × 6·38

The sea lion

Sea lion mothers on Galapagos visit their pups almost every day. They usually return from foraging trips in the evening and leave the pup again next morning (Trillmich, In press *b*). Sea lion pups were stomach tubed in the morning at about the time their mothers left, when a 50 ml sample of apparently undigested milk was easily obtained.

Average fat and protein content in sea lion milk is given in Table II; neither parameter showed a significant change with pup age. Only pup stomach samples were analysed for non-protein

TABLE II

Milk composition (mean ± S.D.) of the Galapagos sea lion. Number of samples in brackets

Milk source	Female teat	Pup stomach
% fat	21·2 (1)	16·6 ± 4·8 (9)
% protein	7·3 (1)	9·0 ± 0·9 (9)
% non-protein nitrogen	—	0·49 ± 0·19 (5)
calcium mg %	—	58 ± 14 (5)
potassium mg %	—	150 ± 29 (5)

nitrogen and potassium. The values are likely to be misleading for the reasons given above. The average concentration of calcium ions was slightly but not significantly lower than in Galapagos fur seal milk (Mann-Whitney *U* test; $P > 0{\cdot}1$). Lactose was again below detectable levels.

Discussion

Fur seal samples from the perinatal period when mothers remain ashore, fasting for about seven days, differed from later samples when mothers regularly alternate between foraging at sea and nursing ashore. This suggests a physiological adaptation: fasting mothers produce high fat content milk (Table I) and thus save body water. They also save calcium (Table I), which at this stage must be mobilized from their own bone. At the same time, this fat-rich milk allows the relatively lean neonates to build up an insulating blubber layer which also serves as an energy store once the mother begins to leave for foraging at sea. The later increase in milk water and calcium content enhances the pup's ability to be active at the high environmental Galapagos temperatures and allows faster bone growth, while the mother draws this additional water and calcium from her food, presumably at low cost to herself.

The fat content measured in Galapagos sea lion milk from pup stomach samples may be somewhat low. In the Northern fur seal, milk fat content at the end of a mother's stay ashore is about 10% lower than when she arrives (Costa & Gentry, In press). The average given for sea lions in Table II of this paper may be biased towards low fat contents, as all samples from pup stomachs were taken at the end of a mother's stay. Thus, instead of the 17% fat content (Table II), a 10% higher value (*c.* 19% fat content), much closer to that from the one milked sample, might be a better estimate of average milk fat content.

The tropical otariids investigated in this report have low milk fat content for marine mammals (general compilation: Jenness & Sloan, 1970; phocid milks: Bryden, 1968; Riedman & Ortiz, 1979; Lavigne *et al.*, 1982; otariid milks (data used in the figure): Rand, 1956; Pilson & Kelly, 1962; Peaker & Goode, 1978; Fay, 1981; Schusterman, 1981; Costa & Gentry, In press). Gentry *et al.* (In press) hypothesize that milk fat content in otariids may be positively correlated with the length of the mothers' absence. This hypothesis can now be tested. For all otariid seals for which data are available, Fig. 1 shows the correlations between fat content of the milk and weaning age ($r = -0{\cdot}62$, N.S.), fat content and duration of the mother's absence ($r = 0{\cdot}88$, $P < 0{\cdot}01$) and weaning age and duration of absence ($r = -0{\cdot}83$, $P = 0{\cdot}02$). The closest correlation exists between fat content and the duration of the mothers' absences from their pups. This is the only significant partial correlation between the three measured variables ($P < 0{\cdot}05$, Fig. 1), suggesting that the fat

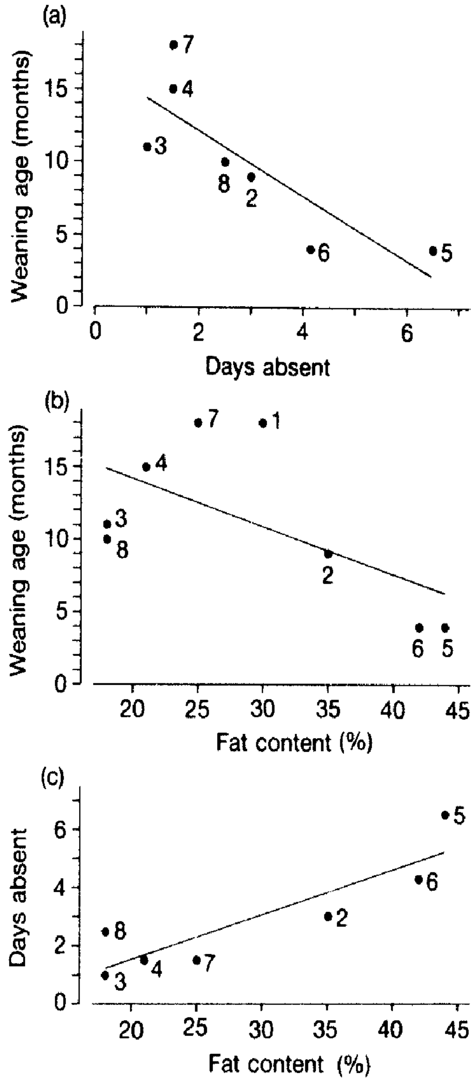

FIG. 1. The relations between (a) mothers' absence duration, (b) weaning age and (c) milk fat content in eight species of otariid seals. Lines are least squares regressions. Partial correlations between the variables are: $r_{ac.b} = 0{\cdot}835$, $P<0{\cdot}05$; $r_{ab.c} = -0{\cdot}763$, $P<0{\cdot}1$; $r_{bc.a} = 0{\cdot}417$, N.S. Numbers refer to species: 1 = *Odobenus rosmarus*; 2 = *Zalophus c. californianus*; 3 = *Z. c. wollebaeki*; 4 = *Eumetopias jubatus*; 5 = *Callorhinus ursinus*; 6 = *Arctocephalus gazella*; 7 = *A. galapagoensis*; 8 = *A. pusillus*.

content of otariid milk is adapted to satisfy the pups' need for sustaining normal activity during maternal absences (Arnold & Trillmich, 1985). The predictive regression equation for changes in maternal absences with changing fat content of the milk is $d = -1{\cdot}53 + 0{\cdot}153$ fat% (d = days absent). The best example for the close connection between these two variables is provided by the milks of the subspecies of the California sea lion: on Galapagos, where females visit their young almost daily, they have 17% fat in their milk, while in California, where they stay away for about three days, they have 35% milk fat (Fig. 1).

In contrast, protein content of all these milks does not correlate with weaning age, duration of absence or fat content. Protein contents of the milks of the above-mentioned otariid species vary between 8 and 14%, as even within one species, the Northern fur seal (Costa & Gentry, In press), average protein content varied between 11·7 and 15·5%. Depending on whether sampling was soon after birth or at the end of the perinatal attendance period, much of the variation between species may be due to differing sampling regimes. Protein content of the milk limits the growth of lean body mass. Despite the uncertainty about what percentage of a pup's body weight is lean body mass, it is clear that the much larger sea lion pups show faster absolute growth than the smaller fur seals (Gentry *et al.*, In press). If protein content of the milk is similar, milk volume must be larger to permit this growth. This additional variable (volume) has as yet not been taken into account, and may also partly explain differences in growth of dependent young between fur seal species.

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