Reproductive Energetics and Female Attendance Patterns of Cape Fur Seals (*Arctocephalus pusillus pusillus*) During Early Lactation

Author(s): CHRISTOPHER M. GAMEL, RANDALL W. DAVIS, JEREMY H. M. DAVID, MICHAEL A. MEŸER, and ELISIF BRANDON

Source: The American Midland Naturalist, 153(1):152-170.

Published By: University of Notre Dame

https://doi.org/10.1674/0003-0031(2005)153[0152:REAFAP]2.0.CO;2

URL: http://www.bioone.org/doi/full/10.1674/0003-0031%282005%29153%5B0152%3AREAFAP%5D2.0.CO%3B2

Am. Midl. Nat. 153:152–170

Reproductive Energetics and Female Attendance Patterns of Cape Fur Seals (Arctocephalus pusillus pusillus) During Early Lactation

CHRISTOPHER M. GAMEL[1] AND RANDALL W. DAVIS
Texas A&M University at Galveston, 5007 Ave. U., Texas A&M, Fort Crockett, Galveston 77551

JEREMY H. M. DAVID AND MICHAEL A. MEŸER
Marine and Coastal Management, Private Bag X2, Rogge Bay 8012, Cape Town, South Africa

AND

ELISIF BRANDON
97A Lowell Ave., Newtonville, Massachusetts 02160

Abstract.—The Cape fur seal (*Arctocephalus pusillus pusillus*) is a common pinniped species along the southern African coastline. While much information is available about this species, little is known concerning its reproductive energetics. With radio telemetry, we monitored attendance patterns for 1 to 4 mo from 1996–1999. Attendance of 29 nursing females averaged 1.86 ± 0.77 d on shore and 5.23 ± 2.87 d at sea. Mean cycle time was 7.09 ± 4.33 d, of which 29.6% was spent on shore and 70.4% at sea. A significant increase in length of time at sea was observed during the first 4 mo of lactation.

Reproductive condition was quantified using measures of body condition and milk composition. Milk ingestion and field metabolic rates established a baseline for the energetics of 1 mo old pups. Body composition averaged 11.05 ± 2.31% lipid and 19.15 ± 2.60% protein. Milk from 17 individuals was composed of 58.07 ± 6.79% water, 2.02 ± 0.58% ash, 10.76 ± 1.23% protein and 23.16 ± 8.24% lipid. Milk energy content averaged 11.02 ± 3.10 kJ ml^{-1}. Thirteen pups consumed milk at a rate of 136.58 ± 29.11 ml kg^{-1} d^{-1}. Mean energy intake was 1505.10 ± 320.80 kJ kg^{-1} d^{-1}, with 37.16 ± 8.04% going to body maintenance and 62.84 ± 8.04% to growth. Fat and protein tissue was deposited at a rate of 16.10 ± 34.93 g d^{-1} and 21.40 ± 59.20 g d^{-1}, respectively. Pup mass gain averaged 99.30 ± 3154.10 g d^{-1}. Male and female pups differed significantly in body mass and field metabolic rate.

Introduction

Lactation is the most energetically costly part of reproduction in mammals (Riedman and Ortiz, 1979; Oftedal, 1984; Gittleman and Thompson, 1988; Arnould *et al.*, 1995). Compared to lactation, the cost of producing a fetus is almost insignificant (Costa and Williams, 1999). This is particularly true in pinnipeds, which transfer large amounts of energy to their young in what are often prolonged lactation periods. Upon reaching sexual maturity, otariid females begin a pattern of almost continuous gestation and lactation (Boyd *et al.*, 1999). This is true for Cape fur seals (*Arctocephalus pusillus pusillus*), which wean their offspring at 8 to 11 mo postpartum, bearing the energetic costs of lactation for approximately 10 mo of every year for their entire reproductive life (Rand, 1949, 1955; David and Rand, 1986; David, 1987).

---

[1] Corresponding author: Current address: 2382 E. 2815 S., Salt Lake City, Utah 84109; e-mail: cgamel@comcast.net

Otariids separate foraging and reproduction spatially. Females give birth to a single pup, then alternate between periods of attendance on the colony and foraging trips to sea (Boyd, 1998; Boyd *et al.*, 1999). Otariid females lack the large blubber layer found in phocids requiring them to forage throughout lactation (Boyd *et al.*, 1999). Foraging trips range in duration from 1 d in Galapagos fur seals (*Arctocephalus galapagoensis*; Trillmich, 1986a) and Galapagos sea lions (*Zalophus californianus wollebaeki*; Trillmich, 1986b) to 10 d in subantarctic fur seals (*Arctocephalus tropicalis*; Georges and Guinet, 2000)) and 12 d in Juan Fernandez fur seals (*Arctocephalus philippii*; Francis *et al.*, 1998). During foraging trips, pups remain on the colony, supporting growth and metabolism with milk obtained during the female's last attendance period. This attendance cycle lasts from 4 mo to 1 y, occasionally extending up to 3 y in some species (Trillmich, 1986a; Gentry, 1998b).

The amount of energy pups receive depends on the composition and quantity of milk they consumed. The phocid maternal strategy relies on rapid weaning (Riedman and Ortiz, 1979; Oftedal *et al.*, 1988; Kovacs *et al.*, 1991), so pups receive large amounts of milk that is 25–60% lipid (Costa and Williams, 1999). Pups grow rapidly, with most of the gain in mass resulting from the formation of adipose tissue. Lean mass is gradually added after weaning (Lydersen and Kovacs, 1996; Costa and Williams, 1999). Otariids have a longer lactation period. Otariid milk contains less lipid, ranging from 17–45% by mass (Trillmich and Lechner, 1986; Riedman, 1990; Georges *et al.*, 2001). A lower concentration of milk lipid and longer lactation period lead to the gradual development of lean tissue prior to weaning, with only limited formation of adipose tissue (Oftedal *et al.*, 1987; Lydersen and Kovacs, 1996; Costa and Williams, 1999). Lower lipid levels and the use of milk nutrients to cover maintenance costs during extended fasting periods (a byproduct of female foraging trips during lactation) means otariid pups increase mass at a slower rate than phocid pups (Costa and Williams, 1999). However, weaning mass, as a percentage of maternal mass, is comparable in both groups (Costa and Williams, 1999).

Upon reaching sexual maturity, Cape fur seal females begin a yearly cycle of raising pups. A single pup is born to a female between early November and late December, with a median birth date around 1 December (David and Rand, 1986). Approximately 6 d after giving birth, a female copulates with a territorial or peripheral male. Following copulation, females begin an alternating pattern of foraging trips to sea and nursing their pup on the colony (Rand, 1955; David and Rand, 1986). Pups continue to nurse until they are weaned at 8–10 mo of age, except during periods of low food availability when pups may continue nursing until 2 or even 3 y of age (David and Rand, 1986). In these cases, newborn pups are usually lost as there is not enough milk to support both the yearling and the newborn (Reeves *et al.*, 1992). Similar weaning patterns have been observed in the South American fur seal (*Arctocephalus australis*; Trillmich *et al.*, 1986; Majluf, 1991), the Galapagos fur seal and the Galapagos sea lion (Trillmich and Dellinger, 1991).

In their overview of fur seal attendance behavior, Gentry and Kooyman (1986) identified two extremes of attendance patterns in fur seals; referred to as tropical and sub-polar patterns. Sub-polar species tend to have a short period of attendance, often with longer trips to sea and relatively rapid growth in pups. Evidence suggests this pattern is a response to the highly seasonal, but predictable, nature of the sub-polar environment (Gentry *et al.*, 1986). Species in this environment (*i.e.,* northern fur seals and Antarctic fur seals) have a small window of time in which to wean their offspring, often limited to 4 mo (Gentry and Holt, 1986; Gentry, 1998a). In contrast, tropical species (*i.e.,* Galapagos fur seal and Galapagos sea lion) live in a less seasonal, but more unpredictable, environment. In response, nursing females make shorter trips to sea, often returning daily to nurse the pup (Trillmich, 1986a, b). Weaning is slow (up to 12 mo) and often delayed (yearlings and 2 y old pups nursing on occasion; Trillmich, 1986b).

As a species living in a temperate environment, the Cape fur seal exhibits characteristics of both tropical and sub-polar species, falling somewhere between the two extremes. The length of the female's trips to sea progressively increases as the pup's energetic requirements increase. The first postpartum trips average 2.9 d, but increase to 4.0 d by the third month. Throughout the nursing period, the duration of visits to the colony average 2.4–2.8 d (David and Rand, 1986).

The attendance patterns of lactating fur seals are an index of reproductive effort. The energy and nutrients they obtain while foraging are used to produce milk and to support their own metabolic requirements. The distance traveled to foraging sites, prey availability and other physiological and environmental constraints influence foraging trip duration (Boyd *et al.*, 1991). Understanding how Cape fur seals balance the competing demands of nursing and foraging provides insight into the maternal strategies that have evolved in this and other species.

No data have been published regarding the reproductive energetics of the Cape fur seal. During this study we measured body composition as an index of body condition for lactating females at the beginning of lactation, determined milk composition, quantified milk ingestion and field metabolic rates in free ranging 1 mo old pups and measured attendance patterns. We were particularly interested in ascertaining: (1) current attendance patterns within the species compared to historic patterns, (2) Cape fur seal reproductive energetics compared to other species and (3) how the temperate Cape fur seal's maternal strategy fit into the tropical/sub-polar maternal strategy framework originally described in Gentry *et al.* (1986).

MATERIALS AND METHODS

STUDY SITE

Research was done at the Cape fur seal colony at Kleinsee (29°34′S, 17°00′E), 650 km north of Cape Town, South Africa on the Atlantic Coast. Fieldwork was done over 4 y (1996 to 1999), with data collection beginning at the start of each pupping season (November).

DATA COLLECTION

Female attendance.—Lactating Cape fur seals were captured with a hoop-net. Pregnant females were not captured due to concerns of harming the unborn pup and to reduce the possibility of attaching transmitters to females that might lose their pups in the first few hours following birth. Following capture, the female was physically restrained and weighed on an electronic platform balance (Rudd Weigh, Australia). From 1996 to 1998 females were sedated with an intramuscular injection (0.63 mg/kg) of Zoletil (Fort Dodge Laboratories, Fort Dodge, IW). In 1999 females were sedated with an intramuscular injection (0.5 mg/kg) of diazepam (Roche Products, Manati, Puerto Rica). Once sedated, females were branded with a unique letter-number combination for future identification (Rand, 1950). Females were captured within a 1-wk period during each of the 4 y of this study.

Female attendance patterns were monitored using radio telemetry. A total of 66 radio transmitters were deployed at Kleinsee between 1996 and 1999. Each adult female had a 164 or 165 MHz transmitter (120g; Advanced Telemetry Systems, Isanti, Minnesota) glued to the fur on its back. The transmitter was attached mid-dorsum and held in position with a quick setting epoxy (5-min; Devcon Inc., Danvers, Massachusetts). The transmitter was completely covered with 10-min epoxy (Ten-Set; Fibre Glass-Evercoat Co., Cincinnati, Ohio) and painted a unique color to facilitate location and identification of individuals on the colony. Radio tagged females were released in the same area where they were captured. When possible, a female's pup was captured and sex was recorded. The pup was then released with its mother.

The presence or absence of radio-instrumented animals was monitored with a radio receiver (R2100; Advanced Telemetry Systems, Isanti, Minnesota) and an omni-directional antenna. The colony was scanned at each frequency for 60 sec every 20 min. Individuals present on the colony were recorded on a D5041 Data Collection Computer (Advanced Telemetry Systems, Isanti, Minnesota) that was connected to the radio receiver. Suckling behavior was documented when observed as a record that a female's pup was alive. Attendance behavior of radio tagged females was recorded from 1 mo (1997 field season) to 6 mo (1999 field season). Three times daily (morning, midday and afternoon), the colony was scanned with binoculars to visually confirm the presence of individual animals.

Milk sample collection.—Seventeen nursing females (six in 1998 and eleven in 1999) in the early stages of attendance (pups approximately 2 wk of age) were captured with a hoop-net. Following capture, females were sedated and weighed. Five ml of oxytocin (Fujisawa USA, Inc., Deerfield, Illinois) were injected intramuscularly in the hip to facilitate milk collection. Milk samples were collected after 20 min with a plastic manual breast pump. Samples were stored at −70 C until analysis.

Body composition and pup milk intake.—Body composition was measured for adult females using the labeled water technique (Nagy and Costa, 1980; Costa, 1988). A 5 ml blood sample was taken from the hind flipper inter-digital vein for a background measurement of deuterium. Each female then received an intramuscular hip injection of 5 ml of sterile 96% enriched deuterium oxide (D_2O). After a 3 h equilibration period (Costa, 1988), a second 5 ml blood sample was taken.

One mo old pups were selected on the beach at random. Pups were collected from groups near the water during the day. By selecting these pups, we hoped to maximize the chance of pup survival as their access to the ocean reduced the chances of overheating. To reduce the possibility of a full stomach biasing our results (Oftedal and Iverson, 1987), we only performed energetic analysis on pups that did not have distended abdomens. During feeding bouts the pup's abdomen becomes visibly distended as a result of the large volume of milk being consumed. This bloated appearance can persist for several days following the female's departure. All pups were captured by hand and placed in an enclosure where they were sheltered from the sun.

Pups were treated similarly to adult females, with the exception that they received two 10 ml intramuscular injections of D_2O, one in each hip, for a total of 20 ml. The increased volume of D_2O permitted measurements to be made over a 7-d period. Each pup also received a 5 ml injection of 94.2% enriched O^{18} labeled water to measure field metabolic rate (FMR). A second blood sample was collected after a 3-h equilibration period and each pup was marked with a unique number for identification in the field. Pups were then released back onto the colony near the capture site. After 7 d, all pups were recaptured, weighed and another 5 ml blood sample was collected to determine body water turnover rate. If the pup's body mass changed by more than 10%, total body water (TBW) was assumed to have changed (Nagy and Costa, 1980; Costa 1987, 1988) and was remeasured by injecting another 3 ml of D_2O, allowing 3 h for equilibrium and taking a final 5 ml blood sample.

DATA ANALYSIS

Female attendance.—Of the 66 transmitters deployed, only 29 individuals provided data used in the analysis. Individual animals were excluded from the analysis because of: (1) poor transmitter reception, (2) loss or failure of the transmitter, (3) only one trip to sea recorded or (4) an individual was not observed nursing a pup or was observed nursing on only one or two occasions. It is possible that non-nursing females maintain different cycles than attending females.

Study animals were assumed to be on the colony if an uninterrupted signal was received for at least 1 h. This minimum requirement eliminated radio signals resulting from high background noise levels. Animals were assumed to be at sea if no radio signal was detected for at least 6 h. The time of 6 h was selected using a frequency distribution analysis as described in Boyd *et al.* (1991). For all individuals, trips to sea were routinely longer than 6 h.

Trips to sea initiated in response to human disturbance were eliminated from the analysis. In most cases, this included the initial trip to sea following capture as females often left the colony immediately after release. Individual fur seals differed in the total number of trips to sea and periods of attendance on the colony. As females are considered replicates for that year, mean values for time on shore, time at sea, total cycle time (start of one trip to sea to the start of the next trip to sea), percentage of the cycle time spent on the colony and percentage cycle time spent at sea were determined for each individual and used as the basis of comparison.

Milk analysis.—Samples were thawed and homogenized prior to analysis in duplicate for all components. The percentages of water and total solids in 5 ml aliquots of milk were determined gravimetrically after lyophilization for 48 h (Labconco Lyph-Lok 12) at −40 C and <5 microns Hg to a constant weight. Ash content was determined gravimetrically following incineration of lyophilized samples in a muffle furnace (Lindberg Moldatherm Box Furnace) programmed to ramp at 1.5 C per minute to 175 C, hold for 30 min, ramp to 550 C at 2 C per minute and hold for 24 h before cooling to room temperature.

Total nitrogen was determined colorimetrically with Nessler's reagent on a Beckman DU-64 spectrophotometer, following hydrogen peroxide/sulfuric acid digestion of 0.50 g liquid samples according to Hach Company (1990). We modified the technique by using an additional 10 ml hydrogen peroxide and increasing heating time by 2 min as described by Adams (2001). Modification was necessary due to high fat content of the milk compared to the dairy samples for which the procedure was developed. Protein was calculated as total nitrogen × 6.38 (Hach Company, 1990).

Total milk lipids were determined according to Folch *et al.* (1957) as modified by Iverson (1988). Energy content of milk was calculated assuming 39.3 kJ g^{-1} for lipid and 18.0 kJ g^{-1} for protein (Schmidt-Nielsen, 1990). Carbohydrates were not analyzed since their contribution to the total solids in otariid milk is considered negligible (Oftedal, 1984).

Body composition and pup milk intake.—Blood samples were collected in 10 ml vacutainers containing serum separators and centrifuged for 10 min. The serum was placed in 5 ml cryotubes and stored in a freezer. Serum samples were sent to Metabolic Solutions, Inc. (Nashua, New Hampshire) for analysis of deuterium and O^{18} isotopes.

Initial total body water (TBW_1) for females and pups was calculated as:

$$TBW_1 = \frac{\frac{[(^2H_{dilution})-(^2H_{H2O})]}{[(H^*{}_2-H^*{}_1)]} \times \frac{[(gH_2O)\times(g\ \text{isotope given})]}{[g\ \text{stock used}\times 18.02]}}{1.04}, \tag{1}$$

where $^2H_{diultion}$ is the deuterium enrichment, $^2H_{H2O}$ is the background enrichment of deuterium and $H^*{}_1$ and $H^*{}_2$ are the initial and final specific activities of the isotope in body water, respectively (Nagy and Costa, 1980; Costa, 1988; Metabolic Solutions, Inc., 1999). Isotope given (g) refers to the amount of isotope injected in the field. Stock used (g) is the amount of isotope used during laboratory analysis to determine actual enrichment of the dose (Metabolic Solutions, Inc., 1999). TBW was assumed to increase in constant proportion to body mass over the measurement period. TBW at recapture (TBW_2) for pups was calculated as:

$$TBW_2 = M_2 \times (TBW_1/M_1), \tag{2}$$

where M is body mass (kg) and subscripts 1 and 2 signify initial and recapture values, respectively. Total water efflux (TWE) for pups was calculated as:

$$\mathrm{TWE} = \frac{2000(\mathrm{TBW}_2 - \mathrm{TBW}_1) \times \ln(\mathrm{H}^* 1\mathrm{TBW}1/\mathrm{H}^* 2\mathrm{TBW}2)}{(\mathrm{M}_1 + \mathrm{M}_2) \ln(\mathrm{TBW}_2/\mathrm{TBW}_1)\mathrm{t}}, \tag{3}$$

where TBW_2 is body water volume (ml) at recapture and TBW_1 is body water volume at the time on initial injection (ml), $\mathrm{H}^*{}_1$ and $\mathrm{H}^*{}_2$ are the initial and final specific activities of the isotope in body water, respectively, M is body mass (g) and t is the time between initial injection and final sample collection (Nagy and Costa, 1980). Embedded within the formula is the conversion of mass from g to kg. Total water intake (TWI) was calculated as:

$$\mathrm{TWI} = \mathrm{TWE} + [2000(\mathrm{TBW}_2 - \mathrm{TBW}_1)/(\mathrm{t} \times (\mathrm{M}_1 + \mathrm{M}_2))] \tag{4}$$

We calculated mass specific milk intake (MI) as:

$$\mathrm{MI} = (100 \times \mathrm{TWI})/(\%\mathrm{W}_\mathrm{M} + 1.07\%\mathrm{F}_\mathrm{M}) \tag{5}$$

where $\%\mathrm{W}_\mathrm{M}$ and $\%\mathrm{F}_\mathrm{M}$ are the average proportions of water and fat in the milk (Oftedal *et al.*, 1987).

The percentage of mass that was lipid for both adult females and pups was calculated as:

$$\mathrm{TBL}_1(\%) = 66.562 - 0.845 \times \mathrm{TBW}_1(\%) \tag{6}$$

where TBL_1 is the total body lipid at initial capture. The percentage of TBL at recapture (TBL_2) was calculated using TBW_2 in place of TBW_1. The percentage of mass that was lean tissue was calculated as:

$$\mathrm{TBP}_1(\mathrm{kg}) = 0.267 \times \mathrm{M}_1(\mathrm{kg}) - 0.130 \times \mathrm{TBW}_1(\mathrm{kg}) + 0.087 \tag{7}$$

where TBP is total body protein at initial capture. The lean body mass at recapture (TBP_2) was calculated substituting in M_2 and TBW_2. Equations 6–7 are taken from Arnould *et al.* (1996). From the values for TBL_1 and TBL_2, the daily rate of fat deposition (F_D) was calculated as:

$$\mathrm{F}_\mathrm{D} = \{[(\mathrm{TBL}_2(\%) \times \mathrm{M}_2)/100] - [(\mathrm{TBL}_1(\%) \times \mathrm{M}_1)/100]\}/\mathrm{t} \tag{8}$$

The daily rate of protein deposition (P_D) was calculated as:

$$\mathrm{P}_\mathrm{D} = (\mathrm{TBP}_2(\mathrm{kg}) - \mathrm{TBP}_1(\mathrm{kg}))/\mathrm{t} \tag{9}$$

Statistical analysis followed the methods described in Zar (1984). Data were tested for normality using the Kolmogorov-Smirnov test and an F-test was used to confirm homogeneity of variances. Unless otherwise stated, data are presented as means ± SD. Statistical results were considered significant for $P \leq 0.05$. Where no significant difference was found between years or sexes, data were combined. Statistical analysis was done using SPSS computer software (SPSS Inc., Chicago, Illinois).

RESULTS

Female attendance.—Twenty-nine females were used in the analysis of attendance patterns: 10 in 1996, four in 1997, eight in 1998 and seven in 1999 (Table 1). Two hundred seventy one periods on shore and 290 trips to sea were recorded. During the first 4 mo of lactation, time on shore had an average duration of 1.86 ± 0.77 d (range: 0.1 to 6.8 d). Trips to sea had an average duration of 5.23 ± 2.69 d (range: 0.3 to 25.9 d). There were no significant differences among years for time on shore ($F = 0.917$, $P = 0.447$) or trip duration ($F = 2.766$, $P = 0.063$). Over the 4-y study period, lactating females spent an average of 29.62% of their

TABLE 1.—Summary of annual attendance patterns. This table shows mean time on shore, time at sea, total attendance cycle, percentage of time on shore and percentage of time at sea for each year (mean ± standard deviation)

Year	n	Time on shore (days)	Time at sea (days)	Total cycle time (days)	% of Cycle time on shore	% of Cycle time at sea
1996	10	2.15 ± 0.69	5.93 ± 2.44	8.08 ± 5.26	28.6 ± 11.18	71.4 ± 11.18
1997	4	1.71 ± 0.55	2.02 ± 1.62	3.73 ± 2.75	50.6 ± 13.46	49.4 ± 13.46
1998	8	1.85 ± 0.62	5.96 ± 3.25	7.81 ± 3.54	27.2 ± 10.97	72.7 ± 10.97
1999	7	1.55 ± 1.07	5.21 ± 1.66	6.76 ± 2.88	21.9 ± 11.10	78.1 ± 11.10
All Years	29	1.86 ± 0.77	5.23 ± 2.69	7.09 ± 4.32	29.62 ± 13.99	70.37 ± 13.99
ANOVA; $P \leq 0.05$		P = 0.447	P = 0.063	P = 0.094	P = 0.004 1997 > 1996, 1998, 1999	P = 0.004 1996, 1998, 1999 > 1997

time on shore and 70.37% at sea. Individual attendance cycles (period of time between one arrival on shore and the next) averaged 7.09 ± 4.33 d (range: 1.8 to 21.8 d) (Table 1). There were no significant differences in attendance cycle among years (F = 2.381, P = 0.094).

Attendance patterns were analyzed for interannual variation over the 4 y of this study (Table 2). No significant interannual differences were found among years for time on shore (F = 0.135; 0.286; 0.243; and 0.002, $P > 0.05$, respectively) or foraging trip duration (F = 1.683; 0.205; 1.392; and 0.440, $P > 0.05$) during each of the first 4 mo of lactation.

Intra-annual variation in attendance patterns among months (November to February) was also examined (Table 2). A comparison of each of the first four months of attendance showed no significant differences in the time spent on shore among months (F = 2.001, P = 0.122). By contrast, trips to sea differed significantly among months (F = 4.456, P = 0.006), with trips to sea during the second and fourth months being significantly longer than trips

TABLE 2.—Summary of monthly attendance patterns. Shows mean monthly attendance for time on shore and trips to sea for the first four months of attendance. Sample size and mean (±SD) values are reported for each year. Reported values are in days

Year	n	Month 1 (Nov. 20–Dec. 19)	n	Month 2 (Dec. 20–Jan. 19)	n	Month 3 (Jan. 20–Feb. 19)	n	Month 4 (Feb. 20–Mar. 19)
Mean Time on Shore								
1996	9	1.88 ± 0.60	7	2.78 ± 1.02	3	1.64 ± 1.11	0	—
1997	4	1.71 ± 0.48	0	—	0	—	0	—
1998	8	1.86 ± 0.91	6	2.24 ± 1.28	8	1.66 ± 0.84	4	2.23 ± 2.10
1999	7	2.05 ± 1.23	6	2.13 ± 1.65	5	1.16 ± 1.24	3	2.07 ± 1.83
All Years	28	1.89 ± 0.84	19	2.40 ± 1.28	16	1.50 ± 0.98	7	2.16 ± 1.83
ANOVA; $P \leq 0.05$				P = 0.122				
Mean time at sea								
1996	9	3.34 ± 1.51	7	8.44 ± 4.66	7	8.88 ± 4.88	0	—
1997	4	2.02 ± 1.62	0	—	0	—	0	—
1998	8	3.96 ± 2.19	6	7.21 ± 5.88	6	6.09 ± 5.40	6	10.29 ± 7.42
1999	7	4.80 ± 2.66	7	6.51 ± 3.34	5	3.21 ± 2.66	3	4.21 ± 1.56
All Years	28	3.69 ± 2.14	20	7.40 ± 4.36	18	6.37 ± 4.92	9	8.26 ± 6.65
ANOVA; $P \leq 0.05$				P = 0.006; Mon. 1 < Mon. 2, 4				

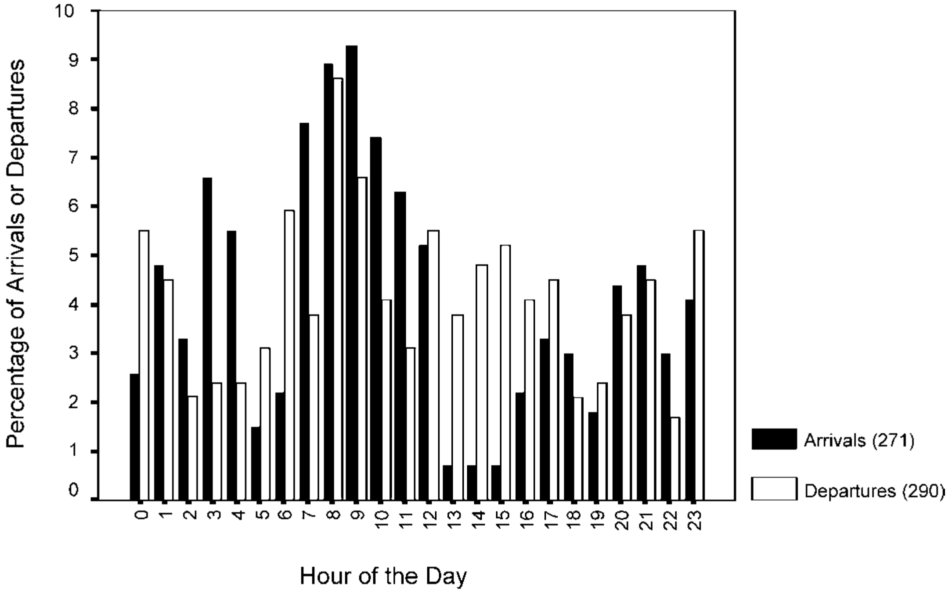

FIG. 1.—Percentage of arrivals and departures by time of day. Shows all arrivals and departures on the rookery from 1996 to 1999 occurring in each hour of the day (29 females)

to sea during the first month (mean differences = 3.71 and 4.57 d; P = 0.018 and 0.029, respectively).

Attending females moved on and off the colony throughout the day (Fig. 1). A value of 33.3% of arrivals on the colony occurred between 07:00 and 10:00, with smaller peaks between 03:00 and 04:00 (12.1%) and 20:00 and 21:00 (9.2%). The majority of trips to sea began between 06:00 and 09:00 (24.9%), with the largest number departing at 08:00 (8.6%).

Body composition.—Morphometric data were collected from 35 adult lactating females (Table 3). In 1998 the 24 females examined had an average mass of 62.71 ± 13.21 kg (range: 43.0–81.5 kg), a standard length of 136.44 ± 8.31 cm (range: 120.0–148.0 cm) and an axillary girth of 99.65 ± 8.48 cm (range: 84.0–115.0 cm). Eleven females were examined in 1999, with a mean mass of 58.64 ± 11.04 kg (range: 40.5–73.5 kg), a standard length of 137.91 ± 9.14 cm (range: 122.0–149.5 cm) and an axillary girth of 95.64 ± 7.34 cm (range: 86.0–105.0 cm).

TBL and TBP were measured for 19 adult lactating females, eight in 1998 and 11 in 1999 (Table 3). No significant difference was found between years for either TBL ($t = 0.152$,

TABLE 3.—Summary of Adult female morphometrics and body composition showing mean (± standard deviation) values for female mass, standard length, axillary girth, total body lipids and total body protein. Values are reported for 1998, 1999, and both years combined. No significant difference was found between years at $P \leq 0.05$

Year captured	Mass (kg)	Standard length (cm)	Axillary girth (cm)	Total body lipids (%)	Total body protein (%)
1998	62.71 ± 13.21	136.44 ± 8.31	99.65 ± 8.48	11.32 ± 3.02	19.28 ± 2.80
	(n = 24)	(n = 24)	(n = 24)	(n = 8)	(n = 8)
1999	58.64 ± 11.04	137.91 ± 9.14	95.64 ± 7.34	10.85 ± 1.76	19.06 ± 2.58
	(n = 11)	(n =11)	(n = 11)	(n = 11)	(n = 11)
All Years	61.43 ± 12.56	136.90 ± 8.47	98.39 ± 8.25	11.05 ± 2.31	19.15 ± 2.60

TABLE 4.—Pup body composition summary showing sex, initial body mass, recapture body mass, % total body lipids at initial capture, % total body lipids at recapture, % total body proteins at initial capture and % total body protein at recapture for Cape fur seal pups. Pups were recaptured 7 d following initial capture. Statistical analysis compares data for male and female pups. Where no significant difference was found between the sexes, data were combined into a single mean value

Seal pup id	Sex	Initial mass (kg)	Recapture mass (kg)	Initial total body lipid (%)	Recapture total body lipid (%)	Initial total body protein (%)	Recapture total body protein (%)
P1	M	8.9	9.4	8.7	11.7	18.8	19.2
P2	M	7.7	8.8	10.6	9.9	19.2	19.0
P3	M	7.1	8.8	8.3	10.9	19.0	19.1
P4	F	5.7	5.6	4.3	3.2	18.7	18.5
P5	F	5.8	5.2	8.3	1.6	19.2	18.4
P6	M	7.5	6.4	8.0	9.8	18.9	19.3
P7	M	6.0	6.4	7.4	11.1	19.1	19.5
P8	M	7.9	8.5	9.9	13.9	19.1	19.6
P9	F	7.0	7.4	8.6	11.8	19.0	19.4
P10	M	7.9	6.7	7.7	8.6	18.8	19.1
P11	F	6.4	6.8	8.5	11.9	19.1	19.6
P12	F	5.6	4.9	9.2	7.9	19.4	19.5
P13	F	6.2	6.1	6.6	5.6	18.9	18.8
Mean (± SD)	7M	7.57 ± 0.89	7.86 ± 1.30	8.15 ± 1.55	9.06 ± 3.63	19.00 ± 0.22	19.15 ± 0.41
	6F	6.12 ± 0.53	6.00 ± 1.96				
t-test, $P \leq 0.05$		$P = 0.006$	$P = 0.015$	NS	NS	NS	NS

$P = 0.881$) or TBP ($t = -0.466$, $P = 0.647$). Mean values for TBL (11.05 ± 2.31%) and TBP (19.15 ± 2.60%) are a combination of both years.

During the 1999 field season, 13 1 mo old pups (seven males and six females) were captured and their body composition was measured (Table 4). Male pups had a mean TBL of 8.64 ± 1.17% (range: 7.4–10.6%) and a mean TBP of 18.95 ± 0.17% (range: 18.8–19.2%). Female pups had a mean TBL of 7.58 ± 1.83% (range: 4.3–9.2%) and a mean TBP of 19.06 ± 0.27% (range: 18.7–19.4%). No significant differences were observed in TBL ($t = -1.259$, $P = 0.234$) or TBP ($t = 1.259$, $P = 0.234$) between the sexes. When data for all pups were combined, mean TBL was 8.15 ± 1.55% (range: 4.3–10.6%) and TBP was 19.00 ± 0.22% (range: 18.7–19.4%).

Milk composition.—Milk was collected from 17 lactating females during the second week of attendance, six in 1998 and eleven in 1999 (Table 5). Mean proximate composition was as follows: water 58.07 ± 6.79% (range: 47.5–68.0%), lipid 23.16 ± 8.24% (range: 7.9–35.3%), protein 10.76 ± 1.23% (range: 9.1–13.1%;) and ash 2.02 ± 0.58% (range: 1.2–2.8%). Milk

TABLE 5.—Milk composition (percentage of water, ash, protein and lipid) and energy content is shown. Data from 1998 ($n = 6$) and 1999 ($n = 11$) is combined. No significant difference was found between years at $P \leq 0.05$

	n	Water (%)	Ash (%)	Protein (%)	Lipid (%)	Energy (kJ ml^{-1})
Mean (± SD)	17	58.07 ± 6.79	2.02 ± 0.58	10.76 ± 1.23	23.16 ± 8.24	11.02 ± 3.10
Range		(47.5–68.0)	(1.2–2.8)	(9.1–13.1)	(7.9–35.3)	(5.5–15.6)

TABLE 6.—Pup energetic summary showing field metabolic rate, energy intake, percentage of energy going to maintenance, percentage of energy going to growth, milk intake rate, energy intake rate, amount of milk fat taken in, amount of milk protein taken in, body fat deposited, body protein deposited and daily mass gain for Cape fur seal pups. Statistical analysis compares data for male and female pups. Where no significant difference was found between the sexes, data were combined into a single mean value

	n	Mean ± SD	Range	*t*-test, $P \leq 0.05$
Field Metabolic Rate ($kJ\ kg^{-1}\ d^{-1}$)	7M	504.08 ± 30.53	(463.1–538.3)	$P < 0.001$
	6F	578.02 ± 19.48	(557.3–600.5)	
Energy Intake ($kJ\ kg^{-1}\ d^{-1}$)	13	1505.14 ± 320.80	(1093.3–2181.8)	NS
Energy to maintenance (%)	13	37.16 ± 8.04	(25.8–51.2)	NS
Energy to Growth (%)	13	62.84 ± 8.04	(48.8–74.2)	NS
Milk Intake ($ml\ kg^{-1}\ d^{-1}$)	13	136.58 ± 29.11	(99.2–198.0)	NS
Milk Fat Intake ($g\ d^{-1}$)	13	220.32 ± 46.59	(172.8–256.4)	NS
Milk Protein Intake ($g\ d^{-1}$)	13	102.35 ± 21.63	(77.0–142.9)	NS
Fat Deposition ($g\ d^{-1}$)	13	16.10 ± 34.93	(−58.1–54.0)	NS
Protein Deposition ($g\ d^{-1}$)	13	21.40 ± 59.20	(−125.3–78.2)	NS
Daily Mass Gain ($g\ d^{-1}$)	13	99.30 ± 3154.10	(−4240.8–5935.2)	NS

energy content averaged 11.02 ± 3.10 $kJ\ ml^{-1}$ (range: 5.5–15.6 $kJ\ ml^{-1}$). Reported values are a combination of the 2 y.

Pup energetics.—The FMR of 13 pups (7 males, 6 females) was measured in 1999 with labeled water methods (Table 6). FMR averaged 538.21 ± 45.78 $kJ\ kg^{-1}\ d^{-1}$ (male pups: 504.08 ± 30.53 $kJ\ kg^{-1}\ d^{-1}$; female pups: 578.02 ± 19.48 $kJ\ kg^{-1}\ d^{-1}$). Pups' milk intake averaged 136.58 ± 29.11 $ml\ kg^{-1}\ d^{-1}$ (range: 99.2–198.0 $ml\ kg^{-1}\ d^{-1}$). Mean energy intake was 1505.14 ± 320.80 $kJ\ kg^{-1}\ d^{-1}$ (range: 1093.3–2181.8 $kJ\ kg^{-1}\ d^{-1}$), of which 37.16 ± 8.04% went to body maintenance and 62.84 ± 8.04% went to growth. Milk fat and protein intake averaged 220.32 ± 46.59 $g\ d^{-1}$ (range: 172.8–256.4 $g\ d^{-1}$) and 102.35 ± 21.63 $g\ d^{-1}$ (range: 77.0–142.90 $g\ d^{-1}$), respectively. Fat was deposited at a rate of 16.10 ± 34.93 $g\ d^{-1}$ (range: –58.1–54.0 $g\ d^{-1}$) and protein at a rate of 21.40 ± 59.20 $g\ d^{-1}$ (range: –125.3–78.2 $g\ d^{-1}$). Daily mass gain averaged 99.30 ± 3154.10 $g\ d^{-1}$ (range: –4240.8–5935.2 $g\ d^{-1}$). No significant difference was found between males and females in terms of energy intake ($t = 0.719$, $P = 0.487$), energy spent on growth ($t = –0.516$, $P = 0.616$), energy used for body maintenance ($t = –0.326$, $P = 0.751$), milk intake ($t = –0.939$, $P = 0.368$), milk lipid intake ($t = 1.276$, $P = 0.228$), milk protein intake ($t = 1.276$, $P = 0.228$), lipid deposition ($t = 2.134$, $P = 0.056$), protein deposition ($t = 1.655$, $P = 0.126$) or daily mass gain ($t = 1.105$, $P = 0.293$). Male pups were significantly larger than female pups at both initial capture ($t = 3.401$, $P = 0.006$) and recapture ($t = 2.880$, $P = 0.015$). However, females had significantly greater field metabolic rates (7.3%) than males ($t = –5.093$, $P < 0.001$).

DISCUSSION

Female attendance.—Time on shore was fairly consistent among individuals within years and between years. The duration of time on shore observed in this study was similar to that for other fur seals, including the Australian fur seal (*Arctocephalus pusillus doriferus*; Arnould and Hindell, 2001), northern fur seal (*Callorhinus ursinus*; Gentry and Holt, 1986; Gentry, 1998a), subantarctic fur seal (Georges and Guinet, 2000) and Antarctic fur seal (*Arctocephalus gazella*; Doidge *et al.*, 1986; Boyd *et al.*, 1991; Boyd, 1999). It has been suggested that time on shore is regulated in response to environmental factors and physiological limitations (Costa and Gentry, 1986; Kovacs and Lavigne, 1992).

Gentry (1998b) found that northern fur seals were not limited in their time on shore by the female's ability to fast. Time spent on shore with the pup was consistent in duration, but the total time on shore was flexible enough to accommodate the time needed for a female to find her pup and begin nursing. As Cape fur seals on average are larger than northern fur seals, we would expect to see a similar ability to extend the time on shore as needed to locate and nurse a pup. Up to a point, a female's ability to fast should not be the limiting factor for time on shore.

Among otariids, duration of trips to sea is highly variable. Documented mean trip lengths during the summer range from 0.5 d for the Galapagos sea lion (Trillmich, 1986a) to 12.3 d for the Juan Fernández fur seal (Francis *et al.*, 1998), with many species such as northern fur seals, Antarctic fur seals, subantarctic fur seals and South American fur seals (*Arctocephalus australis*) showing a mean trip duration falling between four to ten days (Doidge *et al.*, 1986; Gentry and Holt, 1986; Trillmich *et al.*, 1986; Boyd *et al.*, 1991; Gentry, 1998b; Georges and Guinet, 2000).

Rand (1949) reported extended trips to sea at the Sinclair Island colony (27°40′S, 15°31′E) between 1947 and 1949, with 7–9 d absences from the colony being the average. These findings differ from those of David and Rand (1986). Attendance data from the Sinclair Island colony (1947 and 1948) and the Van Reenen Bay colony (27°25′S, 15°19′E; 1977 to 1982) show a mean time on shore of 2.4 d, interrupted by trips to sea lasting 2.9 d (David and Rand, 1986). A mean time on shore of 1.86 d was observed in the current study. Time spent on shore differed significantly between the different studies ($t = -3.777$, $P = 0.001$). We observed a mean time at sea of 5.23 d (125.52 ± 64.488 h) that was significantly greater than the 2.9 d trips recorded by David and Rand (1986; $t = 4.663$, $P \leq 0.001$). However, the mean trip duration in our study was significantly shorter than Rand's earlier observations (1949; $t = -5.5580$ $P \leq 0.001$).

Rand's (1949) reported findings of 7–9 d trips to sea from the Sinclair Island colony are greater than the 5.23 d trips observed at Kleinsee. David and Rand (1986), on the other hand, observed a mean time at sea from both the Sinclair Island and Van Reenen Bay rookeries to be 2.3 d less than at Kleinsee and a time on shore that was 0.5 days longer. The variation observed both at different times and in different locations suggests that the attendance patterns of Cape fur seals are plastic enough to be modified in response to environmental factors. Little variation was observed in the time on shore at different locations. This supports the idea that time on shore is a balance between providing the pup with enough nutrition while the mother remains within her fasting limits (Gentry *et al.*, 1986).

While time on shore did not differ by month, mean time at sea increased over the first 4 mo of lactation. Similar behavioral patterns have been reported for northern fur seals (Gentry and Holt, 1986), California sea lions (*Zalophus californianus californianus*; Peterson and Bartholomew, 1967), subantarctic fur seals (Georges and Guinet, 2000), Steller sea lions (*Eumetopias jubatus*; Gentry, 1970) and Galapagos sea lions (Trillmich, 1986a). The increase has previously been documented in the Cape fur seal (David and Rand, 1986) and its closest relative the Australian fur seal (Arnould and Hindell, 2001). Field observations showed that pups do not nurse continuously while their mothers are on shore. By increasing the percentage of time spent nursing or ingesting milk with increased lipid content, it is possible for the pup to increase its nutrient intake without the mother increasing her time on shore. The increase in length of trips to sea is a predictable response to the increased energetic demands placed on the nursing female by her growing pup. As the energetic needs of the pup increase, the female must spend greater periods of time foraging to meet both her own and the pup's needs. Assuming the same foraging sites are used, increased time at sea permits the female to increase her total foraging effort on each trip, without an increase in transit time.

Arrival and departure times from the colony were consistent with daily movement patterns on the colony. The pupping season occurs in the summer months of the southern hemisphere. As a result, daytime temperatures are often high on Cape fur seal rookeries. To avoid the heat, adult fur seals move to the water's edge as the daytime temperature increases. Actual movement times vary with temperature; a mass movement of animals is usually observed between 08:00 and 10:00. Seals move away from the waters edge and back onto the inland portion of the colony between 17:00 and 20:00. During the first month of life, pups remain near the natal site, usually sheltered from the sun by rock outcrops. Month old pups, which are mobile, follow the same mass movement patterns seen in adults.

With 24.9% of departures from the colony occurring between 06:00 and 09:00, many lactating females time their departures from the colony to coincide with the daily movement to the water's edge. Still, many departures occurred at all hours, with the minimum of 1.7% of departures occurring at 22:00.

Arrivals also showed a relationship with daily movement patterns on the colony. One-third (33.3%) of all arrivals took place between 07:00 and 10:00. This coincides with the mass movement to the water. It is not known if arriving females remained at the water's edge until daytime temperatures decreased or if they immediately made efforts to locate and nurse their pup. Smaller peaks in arrival times coincided with periods of cooler temperatures on the colony. Few arrivals occurred between 13:00 and 15:00, suggesting that females either arrive in the morning, or wait until temperatures on the colony drop before returning.

Milk composition.—Milk composition values in this study (milk lipid 23.16%, protein 10.76%) were similar to those observed by Rand (1955), who found values of 18.6% and 10.0% for lipid and protein, respectively. These lipid and protein levels are similar to those of other otariids. Milk lipid levels in otariids range from 17 to 45%, with rare cases reaching 57% (Trillmich and Lechner, 1986; Riedman, 1990; Boyd *et al.*, 1999; Georges *et al.*, 2001). Species that undergo brief lactation periods coupled with long foraging trips provide their young with milk containing higher lipid levels than species with more extended lactation periods and short foraging trips (Trillmich and Lechner, 1986). Cape fur seals fall between these two extremes.

Both the Galapagos sea lion and the Steller sea lion have lower milk lipid levels at 17% and 20%, respectively (Poulter *et al.*, 1965; Trillmich and Lechner, 1986). In contrast, California sea lions, subantarctic fur seals, northern fur seals, Galapagos fur seals, South American fur seals and Antarctic fur seals all produce milk containing lipid levels ranging from 36% to 57%, more than double that observed in Cape fur seals (Costa and Gentry, 1986; Trillmich and Lechner, 1986; Vaz-Ferreira and Ponce de Leon, 1987; Oftedal and Gittleman, 1989; Arnould and Boyd, 1995).

The Juan Fernandez fur seal, which also lives in a temperate environment and makes foraging trips lasting more than 12 d produces milk with a lipid content averaging 41% during the summer (Francis *et al.*, 1998; Ochoa-Acuña *et al.*, 1999). Similarly, the subantarctic fur seals found on Amsterdam Island, a temperate environment, are away from the colony for 10 d and produce milk with one of the highest lipid contents of any otariid (Georges and Guinet, 2000; Georges *et al.*, 2001). Australian fur seals produces milk composed of 40–42% lipid while foraging for 3–6 d (Arnould and Hindell, 1999; Arnould and Hindell, 2001). In contrast to these other temperate species, the Cape fur seal goes on foraging trips of moderate length (5.23 d) and produce milk with a comparatively low lipid content (23.16%).

Trillmich and Lechner (1986) proposed a general pattern according to which fat content correlates with the average duration of maternal foraging trips. This pattern is consistent with the maternal strategies of the Australian fur seal, subantarctic fur seal and the Juan Fernandez fur seal (Francis *et al.* 1998; Arnould and Hindell, 1999; Ochoa-Acuña *et al.*, 1999; Georges and Guinet, 2000; Arnould and Hindell, 2001; Georges *et al.*, 2001). The Cape fur seal does not follow the predicted pattern. Based on foraging trip duration, Cape fur seals are expected to produce milk with a lipid content of 32%. Instead, we recorded a lipid content of 23.16%, similar to levels previously reported by Rand (1955).

One possible explanation for the Cape fur seal not following the same patterns exhibited by other otariids is geographic location. Of the four temperate fur seal species for which data is available, the Cape fur seal is the only one that is found in a high quality tropic environment. The Benguela upwelling system off the coast of southern Africa is a nutrient rich environment (Rand, 1967; Chapman and Shannon, 1987; Estrada and Marrasé, 1987; Shannon, 1989; Ware, 1992). Australian fur seals, subantarctic fur seals and Juan Fernandez fur seals, on the other hand, all occur in nutrient poor environments or must travel significant distances to obtain the nutrients they need (Francis *et al.*, 1998; Georges and Guinet, 2000; Georges and Guinet, 2001; Arnould and Hindell, 2002). Tropic conditions are an important component of maternal investment and can have a significant impact on the maternal strategy of a species (Georges and Guinet, 2001).

Pup energetics.—In a comparative review of milk composition and energy consumption at peak lactation in 15 species of terrestrial mammals, energy intake of suckling young was found to scale to body mass (kg) to the 0.83 power, compared to the body mass to the 0.75 power for adults (Oftedal, 1984). Using this scaling factor, young terrestrial mammals ingest 941.4 kJ $kg^{-0.83}$ d^{-1} at the peak of lactation (Oftedal, 1984). While the appropriate scaling factor for otariid pups is not known, energy intake (kJ d^{-1}) was expressed in relation to mass to the power of 0.83 for interspecies comparisons. Energy intake values for northern fur seal pups (1556.5 kJ $kg^{-0.83}$ d^{-1}; Costa and Gentry, 1986), California sea lion pups (1510.4 kJ $kg^{-0.83}$ d^{-1}; Oftedal *et al.*, 1987) and Steller sea lion pups (1364.0 kJ $kg^{-0.83}$ d^{-1}; Adams, 2001) indicate that these species maintained energy intake levels 45–65% higher than those observed in terrestrial mammals. In our study, energy intake of Cape fur seal pups averaged 2082.00 ± 418.70 kJ $kg^{-0.83}$ d^{-1}, which was 121% higher than predicted for terrestrial mammals and 34–53% higher than other otariid pups. Australian fur seal pups average an energy intake level of only 720 kJ kg^{-1} d^{-1} (Arnould and Hindell, 2002), slightly less then half of the 1505.14 kJ kg^{-1} d^{-1} energy intake values documented in this study.

Australian fur seal pups increase mass at an average rate of 53–62 g d^{-1} (Arnould and Hindell, 2002). These values compare to those seen in Galapagos fur seal pups with males gaining 43–71 g d^{-1} and females 40–61 g d^{-1} (Trillmich, 1996). Daily mass gain was significantly higher in the Cape fur seal (99.30 g d^{-1}) then in other temperate and tropical species and is more in line with daily gains observed in sub-polar species like the Antarctic and northern fur seals (82–125 g d^{-1}; Goldsworthy, 1992; Kovacs and Lavigne, 1992; Lunn *et al.*, 1993). David (1987) observed an average daily mass gain of 84 g d^{-1} in Cape fur seal pups, only 15% lower then the values reported in this study.

Of the energy taken in from milk, Cape fur seal pups used 62.84 ± 8.04% on growth and only 37.16 ± 8.04% on maintenance. This appears to differ from the recorded pattern of otariid growth (Costa and Williams, 1999). Antarctic fur seal pups used approximately 80% of their total energy on general maintenance and only 15% on growth (Doidge *et al.*, 1984).

Costa and Williams (1999) identified an inverse relationship between ambient temperature and maternal metabolism in adult females while on shore. Both northern and Antarctic fur seals, which are found in environments with low ambient temperatures, maintain metabolic rates 3.4 times greater than the predicted basal metabolic rate (Costa and Trillmich, 1988). In contrast, Galapagos fur seal females maintain metabolic rates only 1.1 times the predicted basal metabolic rate (Costa and Trillmich, 1988). These variations are a result of decreased on shore activity and lower thermoregulatory costs in warmer environments (Costa *et al.*, 1986; Costa and Trillmich, 1988; Costa and Williams, 1999). Pups at the Kleinsee colony are more likely to be subjected to extreme heat than cold. Rather than expending energy to stay warm, Cape fur seal pups find shelter from the sun and keep activity levels to a minimum. As pups become mobile, they spend the hot part of the day at the water's edge, using the physical environment to maintain a comfortable body temperature with minimum energetic costs (Costa and Trillmich, 1988). Accordingly, we would expect to observe lower metabolic rates in Cape fur seal pups when compared to sub-polar species, which would permit the allocation of a greater proportion of energy towards growth.

In this study male pups were significantly larger than females. Larger pups ingest greater amounts of milk and subsequently receive more lipid, protein and total energy (Doidge *et al.*, 1984). However, there was no difference between the sexes in ingestion of these components once a correction for mass was applied. Recent studies on otariid energetics have suggested that male and female pups employ different growth strategies, with males increasing lean mass and females accumulating greater adipose tissue stores (Guinet *et al.*, 2000; Georges and Guinet, 2001; Arnould and Hindell, 2002; Beauplet *et al.*, 2003).

Female pups maintained higher field metabolic rates than did males. This was to be expected as larger organisms maintain lower metabolic rates per unit volume than smaller organisms (Schmidt-Nielsen, 1990). However, no increase in milk intake to compensate for the elevated metabolic rate was recorded.

An underlying assumption of the labeled water method used to estimate milk intake is that the organism only ingests known quantities of water in milk. Ingestion of additional water will inflate estimates of milk intake. Gentry (1981) documented mariposia (ingestion of seawater) in a number of otariid species, including California sea lions, northern fur seals and New Zealand fur seals (*Arctocephalus forsteri*) and indicated that this behaviour is more common in species residing in warm environments as a way to counter high ambient temperatures. Lea *et al.* (2002) reported numerous examples of mariposia in Antarctic fur seal pups and showed how water consumption has implications for the estimation of milk intake. Cape fur seal pups cannot swim until about six weeks old, but younger pups form groups near the water's edge in order to stay cool and some splash about in shallow water. While pups were never observed drinking water during this study and have not previously been documented, it is possible that some seawater was consumed. If water was consumed, our calculations of metabolic water production would be overestimated.

Milk samples were collected from nursing females with 2 wk old pups. Samples collected were therefore not collected during the perinatal period. We could not be certain about the timing of the previous foraging trip or suckling bout prior to initiating measurements for a pup. Milk lipid content can be affected by the amount of time that has passed since the last foraging trip or nursing bout. Costa and Gentry (1986) found milk lipid content to be 6% lower in northern fur seals just before departing on a foraging trip. Similarly, milk volume and composition can change following a nursing bout (Arnould and Boyd, 1995). These factors were beyond our control and might have had some impact on our analysis of milk content.

It must be kept in mind that this study only examined attendance and energetics of the Cape fur seal during early lactation. It has been demonstrated in several long-term studies of otariid maternal strategies (Gentry, 1970; Gentry and Holt, 1986; Trillmich, 1986a; Arnould and Hindell, 1999; Georges *et al.*, 2001; Arnould and Hindell, 2002) that foraging trip length and milk content change throughout the lactation period. Our study represents the first complete attempt to document the maternal strategy of the Cape fur seal, but conclusions drawn from these data must be considered in the context of early lactation and not as a complete picture of the entire lactation period.

CONCLUSIONS

As a species found in temperate latitudes, the Cape fur seal does not clearly follow either the tropical or sub-polar maternal strategies. Instead, the Cape fur seal falls between these two extremes, exhibiting aspects of both strategies and number of unique characteristics. Lactating females demonstrated a high level of flexibility in attendance patterns with trips to sea falling in between the lengths commonly observed in tropical and sub-polar species (Gentry *et al.*, 1986). Trips to sea were significantly shorter than has been documented in any other temperate latitude otraiid species (Francis *et al.*, 1998; Georges and Guinet, 2000; Arnould and Hindell, 2001). Weaning does not usually occur within this species until the pup is approximately 10 mo old (Rand, 1967; David and Rand, 1986), although weaning is rarely delayed beyond the birth of a new pup (Rand, 1947).

Milk lipid content is only 72% of that predicted by Trillmich and Lechner (1986) and in line with tropical species (Poulter *et al.*, 1965; Trillmich and Lechner, 1986). Daily growth rate, on the other hand, is similar to sub-polar species like the Antarctic and northern fur seals (Goldsworthy, 1992; Kovacs and Lavigne, 1992; Lunn *et al.*, 1993). This is explained by the tremendous amount of energy Cape fur seal pups intake on a daily basis (1505.14 kJ kg^{-1} d^{-1}) and their ability to use most of that energy for growth (62.84%) rather then maintenance (37.16%). The environmental conditions off the coasts of South Africa and Namibia have resulted in the evolution of a maternal strategy that is flexible enough to respond to environmental fluctuations while maintaining a consistent annual cycle.

Ongoing research of the Cape fur seal will continue to improve our understanding of this species' behavior and biology. This study has revealed several interesting differences between this species and temperate latitude otariids. The Cape fur seal population continues to increase at a rate of 2.2% per year (Anonymous, 1991) and is rapidly becoming a serious management concern of the South African government. Only an understanding of the biological parameters influencing the Cape fur seal population will allow the proper regulation and management of this species.

Acknowledgments.—Field assistance was provided by K. Booley, S. Berry, D. Du Toit, S. Glass, Z. Isaacs, S. Karpel, D. Kotze, D. Reynolds and S. Swanson. The Marine and Coastal Management branch of the South African Department of Environmental Affairs and Tourism provided additional support through the entire project. We gratefully acknowledge Dr. N. Gamel, Dr. J. M. Packard, Dr. G. T. Rowe and Dr. B. Würsig for their suggestions on project design and early drafts of the manuscript. We also thank the De Beers Mining Company for providing access to the Kleinsee colony and their support throughout the project. Funds to help defray costs of conducting research were provided by Texas A&M University and Texas A&M University at Galveston, which are gratefully acknowledged. All captures and handling of marine mammals were done under National Marine Fisheries Service Permit #1021, Amendment No. 1 and in accordance with animal use protocols for Texas A&M University.

LITERATURE CITED

ADAMS, T. C. 2001. Indices of maternal investment and dietary preferences in adult female Alaskan Steller sea lions (*Eumetopias jubatus*). Ph.D. Thesis, Texas A&M University, College Station, Texas.

ANONYMOUS. 1991. Report on the Benguela Ecology Programme workshop on seal fishery biological interactions. *Report of the Benguela Ecol. Program S. Afr.,* **22**:1–65.

ARNOULD, J. P. Y. AND I. L. BOYD. 1995. Inter- and intra-annual variation in milk composition in Antarctic fur seals (*Arctocephalus gazella*). *Physiol. Zool.,* **68**:1164–1180.

———, ——— AND A. CLARKE. 1995. A simplified method for determining the gross chemical composition of pinniped milk samples. *Can. J. Zool.,* **73**:404–410.

———, ——— AND J. R. SPEAKMAN. 1996. Measuring the body composition of Antarctic fur seals (*Arctocephalus gazella*): validation of hydrogen isotope dilution. *Physiol. Zool.,* **69**:93–116.

——— AND M. A. HINDELL. 1999. The composition of Australian fur seal (*Arctocephalus pusillus doriferus*) milk throughout lactation. *Physiol. Biochem. Zool.,* **72**:605–612.

——— AND ———. 2001. Dive behaviour, foraging locations and maternal-attendance patterns of Australian fur seals (*Arctocephalus pusillus doriferus*). *Can. J. Zool.,* **79**:35–48.

——— AND ———. 2002. Milk consumption, body composition and pre-weaning growth rates of Australian fur seal (*Arctocephalus pusillus doriferus*) pups. *J. Zool. Lond.,* **256**:351–359.

BEAUPLET, G., C. GUINET AND J. P. Y. ARNOULD. 2003. Body composition changes, metabolic fuel use and energy expenditure during extended fasting in subantarctic fur seal (*Arctocephalus tropicalis*) pups at Amsterdam Island. *Physiol. Biochem. Zool.,* **76**:262–270.

BOYD, I. L. 1998. Time and energy constraints in pinniped lactation. *Am. Nat.,* **152**:717–728.

———. 1999. Foraging and provisioning in Antarctic fur seals: interannual variability in time energy budgets. *Behav. Ecol.,* **10**:198–208.

———, C. LOCKYER AND H. D. MARSH. 1999. Reproduction of marine mammals, p. 218–286. *In:* J. E. Reynolds and S. A. Rommel (eds.). Biology of marine mammals. Smithsonian Institution Press, Washington, DC.

———, N. J. LUNN AND T. BARTON. 1991. Time budgets and foraging characteristics of lactating Antarctic fur seals. *J. Anim. Ecol.,* **60**:577–592.

CHAPMAN, P. AND L. V. SHANNON. 1987. Seasonality in the oxygen minimum layers at the extremities of the Benguela system. *S. Afr. J. Mar. Sci.,* **5**:85–94.

COSTA, D. P. 1987. Isotopic methods for quantifying material and energy intake of free-ranging marine mammals, p. 43–66. *In:* A. C. Huntley, D. P. Costa, G. A. J. Worthy and M. A. Castellini (eds.). Approaches to marine mammal energetics. Allen Press, Lawrence, Kansas.

———. 1988. Methods for studying the energetics of freely diving animals. *Can. J. Zool.,* **66**:45–52.

——— AND R. L. GENTRY. 1986. Free-ranging energetics of northern fur seals, p. 79–101. *In:* R. L. Gentry and G. L. Kooyman (eds.). Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, New Jersey.

———, B. J. LE BOEUF, C. I. ORTIZ AND C. A. HUNTLEY. 1986. Energetics of lactation in the northern elephant seal, *Mirounga angustirostris. J. Zool.,* **209**:21–33.

——— AND F. TRILLMICH. 1988. Mass changes and metabolism during the perinatal fast: a comparison between Antarctic (*Arctocephalus gazella*) and Galapagos fur seals (*Arctocephalus galapagoensis*). *Physiol. Zool.,* **61**:160–169.

——— AND T. M. WILLIAMS. 1999. Marine mammal energetics, p. 176–217. *In:* J. E. Reynolds and S. A. Rommel (eds.). Biology of marine mammals. Smithsonian Institution Press, Washington, DC.

DAVID, J. H. M. 1987. Status, biology and Ecology of fur seal. NOAA Tech. Rep., NMFS 51.

——— AND R. W. RAND. 1986. Attendance behavior of South African fur seals, p. 126–141. *In:* R. L. Gentry and G. L. Kooyman (eds.). Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, New Jersey.

DOIDGE, D. W., J. P. CROXALL AND C. RICKETTS. 1984. Growth rates of Antarctic fur seal *Arctocephalus gazella* pups at South Georgia. *J. Zool. Lond.,* **203**:87–93.

———, T. S. MCCANN AND J. P. CROXALL. 1986. Attendance behavior of Antarctic fur seals, p. 102–114. *In:* R. L. Gentry and G. L. Kooyman (eds.). Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, New Jersey.

ESTRADA, M. AND C. MARRASÉ. 1987. Phytoplankton biomass and productivity off the Namibian coast. *S. Afr. J. Mar. Sci.,* **5**:347–356.

FOLCH, J., M. LEES AND G. H. SLOANE-STANLY. 1957. A simple method for the isolation and purification of total lipid from animal tissues. *J. Biol. Chem.,* **226**:497–509.

FRANCIS, J., D. BONESS AND H. OCHOA-ACUÑA. 1998. A protracted foraging and attendance cycle in female Juan Fernández fur seals. *Mar. Mamm. Sci.,* **14**:552–574.

GENTRY, R. L. 1970. Social behavior of the Steller sea lion. Ph.D. Thesis, University of California, Santa Cruz.

———. 1981. Seawater drinking in eared seals. *Comp. Biochem. Physiol.,* **68A**:81–86.

———. 1998a. Behavior and ecology of the northern fur seal. Princeton University Press, Princeton, New Jersey.

———. 1998b. Female attendance behavior, p. 219–231. *In:* R. L. Gentry (ed.). Behavior and ecology of the northern fur seal. Princeton University Press, Princeton, New Jersey.

———, 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, p. 220–264. *In:* R. L. Gentry and G. L. Kooyman (eds.). Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, New Jersey.

——— AND J. R. HOLT. 1986. Attendance behavior of northern fur seals, p. 61–78. *In:* R. L. Gentry and G. L. Kooyman (eds.). Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, New Jersey.

——— AND G. L. KOOYMAN (eds.). 1986. Maternal strategies on land and at sea. Princeton University Press, Princeton, New Jersey.

GEORGES, J.-Y., R. GROSCOLAS, C. GUINET AND J.-P. ROBIN. 2001. Milking strategy in subantarctic fur seals *Arctocephalus tropicalis* breeding on Amsterdam Island: evidence from changes in milk composition. *Physiol. Biochem. Zool.,* **74**:548–559.

——— AND C. GUINET. 2000. Maternal care in the subantarctic fur seals on Amsterdam Island. *Ecology,* **81**:295–308.

——— AND ———. 2001. Prenatal investment in the subantarctic fur seal, *Arctocephalus tropicalis. Can. J. Zool.,* **79**:601–609.

GITTLEMAN, J. L. AND S. D. THOMPSON. 1988. Energy allocation in mammalian reproduction. *Am. Zool.,* **28**:863–875.

GOLDSWORTHY, S. D. 1992. Maternal care in three species of southern fur seals (*Arctpcephalus spp.*) Ph.D. Thesis, Monash University, Melbourne, Australia.

GUINET, C., M.-A. LEA AND S. D. GOLDSWORTHY. 2000. Mass change in Antarctic fur seal (*Arctocephalus gazella*) pups in relation to maternal characteristics at the Kerguélen Islands. *Can. J. Zool.,* **78**:476–483.

HACH COMPANY. 1990. Procedures manual: systems for food, feed and beverage analysis. Loveland, Connecticut.

IVERSON, S. J. 1988. Composition, intake and gastric digestion of milk lipids in pinnipeds. Ph.D. Thesis, University of Maryland, College Park, Maryland.

KOVACS, K. M. AND D. M. LAVIGNE. 1992. Maternal investment in otariid seals and walruses. *Can. J. Zool.,* **70**:1953–1964.

———, ——— AND S. INNES. 1991. Mass transfer efficiency between harp seal (*Phoca groenlandica*) mothers and their pups during lactation. *J. Zool. Lond.,* **223**:213–221.

——— AND ———. 1992. Maternal investment in otariid seals and walruses. *Can. J. Zool.,* **70**:1953–1964.

LEA, M.-A., F. BONADONNA, M. A. HINDELL, C. GUINET AND S. D. GOLDSWORTHY. 2002. Drinking behaviours and water turnover rates of Antarctic fur seal pups: implications for the estimation of milk intake by isotopic dilution. *Comp. Biochem. Physiol. A,* **132**:321–331.

LUNN, N. J., I. L. BOYD, T. BARTON AND J. P. CROXALL. 1993. Factors affecting the growth rate and weaning mass of Antarctic fur seal pups at Bird Island, South Georgia. *J. Mammal.,* **74**:908–919.

LYDERSEN, C. AND K. M. KOVACS. 1996. Energetics of lactation in harp seals (*Phoca groenlandica*) from the Gulf of St. Lawrence, Canada. *J. Comp. Physiol. B,* **166**:295–304.

MAJLUF, P. 1991. El Niño effects on pinnipeds in Peru, p. 55–65. *In:* F. Trillmich and K. A. Ono (eds.). Pinnipeds and El Niño: responses to environmental stress. Springer-Verlag, New York, New York.

METABOLIC SOLUTIONS, INC. 1999. Measurement of body composition using deuterium oxide. Tech Paper 913, Nashua, New Hampshire.

NAGY, K. A. AND D. P. COSTA. 1980. Water flux in animals: analysis of potential errors in the tritiated water method. *Am. J. Physiol.,* **238**:R454–R465.

OCHOA-ACUÑA, H., J. M. FRANCIS AND O. T. OFTEDAL. 1999. Influence of long intersuckling interval on composition of milk in the Juan Fernandez fur seal, *Arctocephalus philippii. J. Mamm.,* **80**:758–767.

OFTEDAL, O. T. 1984. Milk composition, milk yield and energy output at peak lactation: a comparative review. *Symp. Zool. Soc. Lond.,* **51**:33–85.

———, D. J. BONESS AND W. D. BOWEN. 1988. The composition of hooded seal (*Cystophora cristata*) milk: an adaptation for postnatal fattening. *Can. J. Zool.,* **66**:318–322.

———, ——— AND R. A. TEDMAN. 1987. The behaviour, physiology and anatomy of lactation in the pinnipedia. *Curr. Mammal.,* **1**:175–245.

——— AND J. L. GITTLEMAN. 1989. Patterns of energy output during reproduction in carnivores, p. 355–378. *In:* J. L. Gittleman (ed.). Carnivore behaviour, ecology and evolution. Cornell University Press. New York.

——— AND S. J. IVERSON. 1987. Hydrogen isotope methodology for measurement of milk intake and energetics of growth in suckling young, p. 67–96. *In:* A. C. Huntly, D. P. Costa, A. J. Worthy and M. A. Castellini (eds.). Approaches to marine mammal emergetics. Society for Marine Mammalogy, Lawrence.

PETERSON, R. S. AND G. A. BARTHOLOMEW. 1967. The natural history and behavior of the California sea lion. *Am. Soc. Mammal. Sp. Publ.,* **1**:1–79.

POULTER, T. C., T. C. PINNEY, R. JENNINGS AND R. C. HUBBARD. 1965. The rearing of Steller seal lion, *Eumetopias jubata. J. of Auditory Research,* **6**:165–173.

RAND, R. W. 1947. Attendance at the colony. Union of South Africa, Department of Agriculture: Government Guano Islands Administration, progress report no 2:1–19.

———. 1949. The Cape fur seal. 2. Attendance at the colony. Unpublished progress report, Government Guano Islands Administration, Department of Agriculture, Union of South Africa.

———. 1950. Branding in field-work on seals. *J. Wildl. Manage.,* **14**:128–132.

———. 1955. Reproduction in the female Cape fur seal, *Arctocephalus pusillus. Proc. Zool. Soc. Lond.,* **124**:717–740.

———. 1967. The Cape fur seal (*Arctocephalus pusillus*). 3. General behavior on land and at sea. Republic of South Africa, Dept of Commerce and Industries, Division of Sea Fisheries, Investigation, Rep No 60.

REEVES, R. R., B. S. STEWART AND S. LEATHERWOOD. 1992. The Sierra Club handbook of seals and sirenians. Sierra Club Books, San Francisco, California.

RIEDMAN, M. L. 1990. The pinnipeds: seals, sea lions and walruses. University of California Press, Berkeley, California.

——— AND C. L. ORTIZ. 1979. Changes in milk composition during lactation in the northern elephant seal. *Physiol. Zool.,* **52**:240–249.

SCHMIDT-NIELSEN, K. 1990. Animal physiology: adaptation and environment, 4th ed. Cambridge University Press, Cambridge.

SHANNON, L. V. 1989. The physical environment, p. 12–27. *In:* A. I. L. Payne and R. J. M. Crawford (eds.). Oceans of life. Vlaeberg Publishers, Johannesburg, South Africa.

TRILLMICH, F. 1986a. Attendance behavior of Galapagos sea lions, p. 196–208. *In:* R. L. Gentry and G. L. Kooyman (eds.). Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, New Jersey.

———. 1986b. Attendance behavior of Galapagos fur seals, p. 168–185. *In:* R. L. Gentry and G. L. Kooyman (eds.). Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, New Jersey.

———. 1996. Parental investment in pinnipeds. *Adv. Study Behav.,* **25**:533–577.

——— AND T. DELLINGER. 1991. The effects of El Niño on Galapagos pinnipeds, p. 66–74. *In:* F. Trillmich and K. A. Ono (eds.). Pinnipeds and El Niño: responses to environmental stress. Springer-Verlag, New York, New York.

———, G. L. KOOYMAN, P. MAJLUF AND M. SANCHEZ-GRINAN. 1986. Attendance and diving behavior of South American fur seals during El Niño in 1983, p. 153–167. *In:* R. L. Gentry and G. L.

Kooyman (eds.). Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, New Jersey.

——— AND E. LECHNER. 1986. Milk of the Galapagos fur seal and sea lion, with a comparison of the milk of eared seals (Otariidae). *J. Zool. Lond.,* **209**:271–277.

VAZ-FERREIRA, R. AND A. PONCE DE LEON. 1987. South American fur seal, *Arctocephalus australis,* in Uruguay. *In:* J. T. L. Croxall and Gentry (eds.). Status, biology and ecology of fur seals. Proceedings of an International Symposium and Workshop, Cambridge, England (1984). NOAA Technical Report NMFS, 51:29–32.

WARE, D. M. 1992. Production characteristics of upwelling systems and the trophodynamic role of hake. *S. Afr. J. Mar. Sci.,* **12**:501–513.

ZAR, J. H. 1984. Biostatistical analysis. Prentice Hall, Englewood Cliffs, New Jersey.

SUBMITTED 22 DECEMBER 2003 ACCEPTED 22 JUNE 2004