

Evidence of a maternal foraging cycle resembling that of otariid seals in a small phocid, the harbor seal

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Received: 26 March 1993 / Accepted after revision: 2 November 1993

Summary. Lactation strategies in the two largest families of seals have been characterized as a phylogenetic dichotomy, with sea lions and fur seals (Otariidae) exhibiting foraging cycles and true seals (Phocidae) a strategy of fasting. We show that a lactating phocid, the harbor seal, *Phoca vitulina*, has a foraging cycle similar to that of otariids. Time-depth recorders attached to lactating harbor seal mothers revealed that 9 of 11 females began bouts of diving, averaging 12–40 m, by mid-lactation (12 days). During the remainder of lactation, females made an average of seven diving trips, lasting about 7 h. They returned to the rookery during the interval between successive bouts to nurse their pups. Diving was more frequent during daylight than at night and diving bouts increased in duration as lactation progressed. The diving behavior of females that had weaned their pups and previously collected data from stomach lavage, suggest that the bouts of diving represent successful foraging. We propose that the lactation strategy of the harbor seal is intermediate to that of the otariids and other phocids studied. The harbor seal has a foraging cycle like the otariids, but typically resembles other phocids in length of lactation, rate of mass gain in pups, and in milk fat content. As harbor seals are among the smallest phocids, and only slightly larger than most otariids, it seems likely that maternal size constrains the amount of stored energy harbor seal females can bring to the rookery, forcing them to start feeding during the lactation period.

Key words: Maternal strategy – Lactation – Foraging – Pinnipeds

Introduction

In polygynous mammals, males maximize their reproductive success by monopolizing females. In contrast, females, as the primary care-givers, maximize their success

by selecting good mates and by ensuring survival of their young to nutritional independence (Trivers 1972; Clutton-Brock 1991). The suite of characteristics associated with successful maternal care (commonly referred to as the maternal or lactation strategy) should reflect phylogenetic constraints and ecological pressures (Robbins and Robbins 1979; Loudon and Kay 1984; White and Luick 1984).

A major ecological and physiological constraint that faces all pinnipeds (true seals, sea lions, fur seals and walrus) and plays a major part in shaping their maternal strategies is the duality of their marine food supplies and the terrestrial (or ice-based) sites where parturition and maternal care occur (Bartholomew 1970; Stirling 1975). Maternal strategies in the Order Pinnipedia have been categorized as dichotomous, with the two major families exhibiting different patterns. These patterns have been referred to as the “fasting strategy” and the “foraging cycle strategy.” The fasting pattern is typical of the Phocidae (true seals) and the foraging cycle appears to be characteristic of the Otariidae (fur seals and sea lions) (reviewed in Bonner 1984; Gentry and Kooyman 1986; Oftedal et al. 1987; Costa 1991).

The major features of these strategies are presented in the reviews cited above. The fasting strategy of the phocids is characterized by: (1) maternal arrival at the breeding site with large energy stores in the form of blubber to support maintenance and lactation costs; (2) a short lactation period (4–50 days); (3) extremely high-fat milk in mid to late lactation (40–60% fat); and (4) rapid fattening of pups. In contrast, the foraging cycle strategy of otariids is characterized by: (1) moderate maternal energy stores used to sustain a short perinatal fast, followed by feeding trips at sea alternating with visits to land in order to nurse pups; (2) a long lactation period (4 months–2 years); (3) milk that is generally lower in fat (19–50%); and (4) slow rates of mass gain in pups.

Although most of the available evidence supports this hypothesized phylogenetic dichotomy, the only phocids that have been studied to date are of larger body size, especially in relation to the otariids. Little is known

about the smaller phocids in which maternal mass at parturition is comparable to that of many otariids. In fact, in several of these small species, as well as two larger ones (the harp seal, *Phoca groenlandica* and Weddell seal, *Leptonychotes weddellii*) there is evidence of feeding by lactating females (reviewed in Oftedal et al. 1987, Table IV; Testa et al. 1989; Bowen et al. 1989; Smith et al. 1991). It has been suggested for the larger species that feeding is only opportunistic and not an important component of their lactation strategy (Testa et al. 1989). However, this may not be the case for the small phocids (Costa 1991; Bowen et al. 1992).

In a recent study of the energetics of lactation in a small phocid, the harbor seal, *Phoca vitulina*, we found food in the stomachs of about 20% of the lactating females intubated (Bowen et al. 1989). Further, during the first 80% of lactation, harbor seal females showed a greater depletion (80%) of body fat than has been reported for other female phocids (Bowen et al. 1992). These findings suggested that harbor seal mothers may not be able to rely solely on body stores to support the energetic cost of lactation. Thus, we hypothesized that harbor seal females exhibit a foraging strategy like that of otariids. To test this idea, we fitted time-depth recorders (TDRs) to lactating females to investigate their diving behavior, and by inference, their feeding behavior.

Methods

The study was conducted from 20 May to 10 June 1989 and from 20 May to 14 June 1990 on Sable Island (43°55'N; 60°00'W), located 160 km east of Nova Scotia, Canada. About 600 harbor seal females gave birth on Sable during each year of the study.

Mother-pup pairs were captured as described by Bowen et al. (1992). Fourteen lactating females were fitted with a Mk3+ TDR (Wildlife Computers, Woodinville, WA) containing 256 Kbytes of memory, and with a VHF transmitter (164 MHz, Advanced Telemetry Systems, Isanti, MN) to assist in the relocation of females on the beach. To attach the TDR without unduly stressing the seals, they were sedated by injection of 0.5–0.7 mg/kg of diazepam into the extradural vein. The TDR (15 cm long × 2.5 cm in diameter) was secured by two hose clamps to an epoxy mount with a transmitter embedded. The entire unit weighed 350 g, about 0.4% of the initial body mass of females. A piece of nylon mesh (24 cm long × 15 cm wide), that had been embedded in the base of the mount was glued to the fur of the animal, using a 5-min epoxy.

TDRs were programmed to record depth every 7 s once a salinity switch was activated by seawater. When the salinity switch was dry, the number of 7-s periods was counted and recorded at the next activation of the switch by seawater.

We used the "dry counts" to quantify time on land, but from detailed observations of females with TDRs on land, we know that the salinity switch did not consistently distinguish between wetness due to rain, fog, wet sand or seawater. Thus, time on land will be somewhat underestimated, depending on weather conditions.

Generally, we held mothers and their pups for 30–40 min during fitting and removal of the TDR. However, some pairs were held for

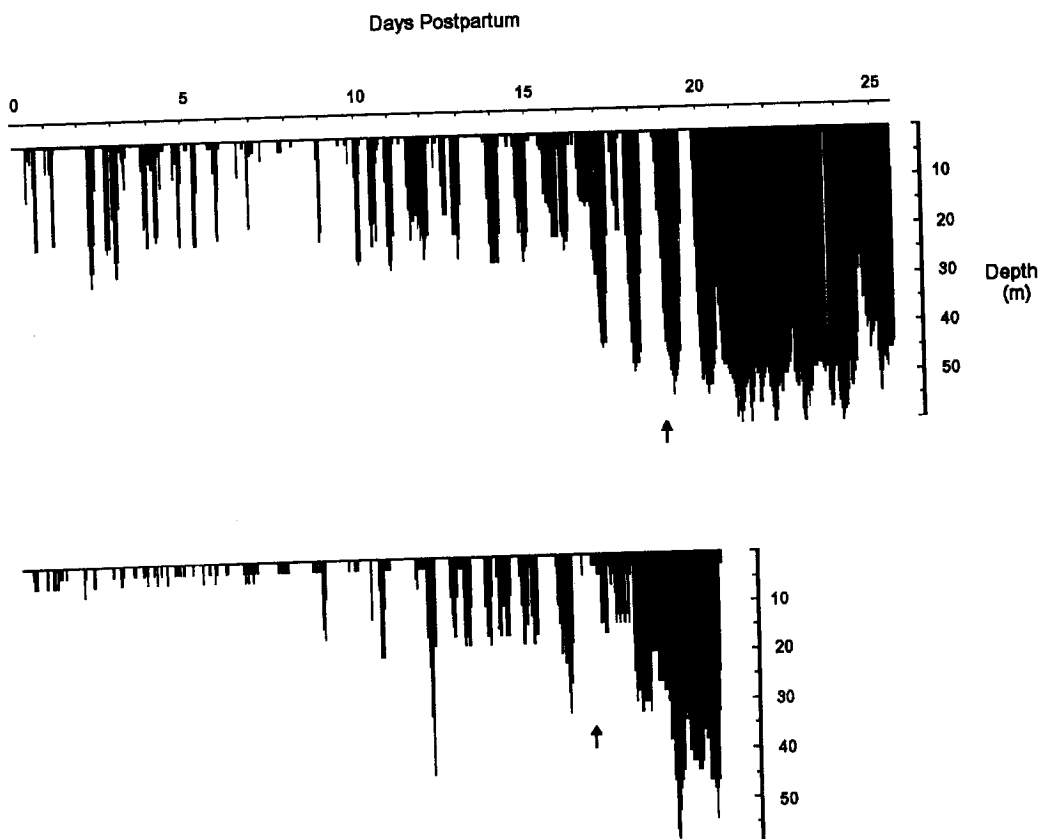


Fig. 1. Sample dive records produced by Strip Chart Program (Wildlife Computers) for two harbor seal females for which records continued beyond weaning. Note the bouts of diving during lactation and that diving activity changed after weaning (arrow)

up to 4 h to permit the equilibration of deuterium oxide for water turnover studies which will be reported elsewhere. These same females and pups were recaptured after 7–10 days and held for 10 min while pups were weighed and blood was taken from mothers.

Each day all newborn pups were tagged (Roto-tag, Dalton, England) in the hind flipper to provide accurate information on age and also the lactation stage of females. Identical marks were painted on mothers and their pups using a fast-drying fluorescent paint so they could be identified rapidly at a distance.

Dive analysis. The data from each TDR were processed using specialized software from the manufacturer (Wildlife Computers). Data were transferred into a hexadecimal file on a personal computer via a RS232 connection. Hexadecimal files were initially examined graphically (Strip Chart program) to obtain an overall picture of the diving behavior of each mother (Fig. 1). These files were then prepared for analysis by correcting for potential changes in the calibration of the pressure transducer of the TDR (ZOC program), which may have occurred over the period of data collection. The processed files were analyzed (Dive Analysis program) to provide estimates of several parameters for each dive in the TDR record. The parameters defined below were based on the default definitions in the Dive Analysis program with the exception of bottom time.

- Dive duration: the period between surface readings immediately preceding and following the dive, minus one sample interval
- Surface time since last dive: elapsed time that the animal in the water was at or less than the depth resolution of the TDR (2 m in 1989 and 1 m in 1990)
- Rate of descent and ascent: descent is the average rate from the start of the dive to the beginning of bottom time; ascent is the average rate from the end of bottom time to the end of the dive
- Bottom time: the time spent within 2 m of the maximum depth

Based on an inspection of the overall patterns, we operationally defined two major classes of diving behavior: shallow or “surface” dives (<6 m) and dives of 6 m or more. Shallow dives are not dealt with in this paper for several reasons. First, it is only feasible to correct for transducer drift in blocks of dives. Thus instrument “noise” may be recorded as shallow dives. Second, normal swimming behavior near the surface and social interactions include shallow diving, and these are outside the primary interest of this study.

Thus, for the remainder of the paper our focus is on dives of at least 6 m. Furthermore, since diving occurred in clusters or bouts (Fig. 1), to characterize the temporal aspects of bouts of diving we operationally defined the onset of a dive bout as a minimum of four consecutive dives of at least 6 m followed by deeper dives. Dive bouts were considered to end when at least four consecutive dives of <6 m occurred, or when an animal remained at the surface for >30 min.

Using this operational definition, nearly a quarter of dive bouts are less than 1 h. These short bouts are shallower in depth, shorter in duration, occur primarily early in lactation, and are often followed by extremely long inter-bout intervals, leading us to believe that the short bouts may not actually represent serious foraging activity. Thus, in describing the characteristics of diving bouts we present values for all bouts and separately for bouts >1 h in duration.

To examine diving behavior with respect to day and night, local standard time of sunrise (0520 hours) and sunset (2035 hours) at the midpoint of the study (31 May) was used. To examine differences between early and late lactation, the mean lactation length for females in Table 1 (22 days) was divided into two equal periods.

Statistical analyses were performed using SAS PC Version 4.1. Unless otherwise stated the probability level accepted for a significant difference was $\alpha=0.05$. Standard errors are given as the measure of variance about the mean. Statistical analyses were not performed on average changes over the course of lactation because of the lack of independence of measures for consecutive days and because the small sample of animals and variable length of dive records precluded a repeated measures analysis.

Results

TDRs were deployed and some data recovered from all 14 lactating harbor seals. However, TDR records covered only a small part of lactation for 3 females, precluding their use in some analyses. Among females outfitted with TDRs, the range in mass at parturition (Table 1) is similar to that recorded for parturient harbor seals on

Table 1. Aspects of lactation and diving records for 14 harbor seal females with time-depth recorders (TDRs)

ID	Initial maternal mass (kg)	Record duration (dpp) ^a	Lactation length (d)	Percent lactation	Number of dive bouts	Number of dives	Dive effort (min/h) ^e
Dot89	77.0 ^b	1–19	>25	—	3	11	0.10
Bar89	84.1 ^b	2–22	23	91	14	1470	6.40
Four89	85.6	0–18	19	100	3	850	2.24
Nine89	85.1 ^b	1–19	20	95	6	1099	5.60
Dbl89	86.4	0–20	>24	—	5	524	1.65
Plus89	85.3	0–18	>23	—	5	468	2.01
D1590	79.5	0–16	17	100	11	1268	3.70
D590	85.9	0–20 ^c	24	88	0	0	0
D290	94.1	0–20	24	88	19	1803	6.40
D790	94.4	0–19	27	70	3	51	0.20
D190	105.3	0–21	28	78	0	0	0
D1190 ^d	71.5	0–8	—	—	3	326	—
D1290	81.2	0–6	27	22	3	74	—
D1490 ^d	72.0	0–12	—	—	4	378	—

^a Days postpartum

^b Estimated using average daily mass loss of 1.9 kg (Bowen et al. 1992)

^c Record interrupted from 3 to 6 days postpartum

^d Pup lost during a storm

^e Number of minutes of diving ≥ 6 m per hour of TDR record

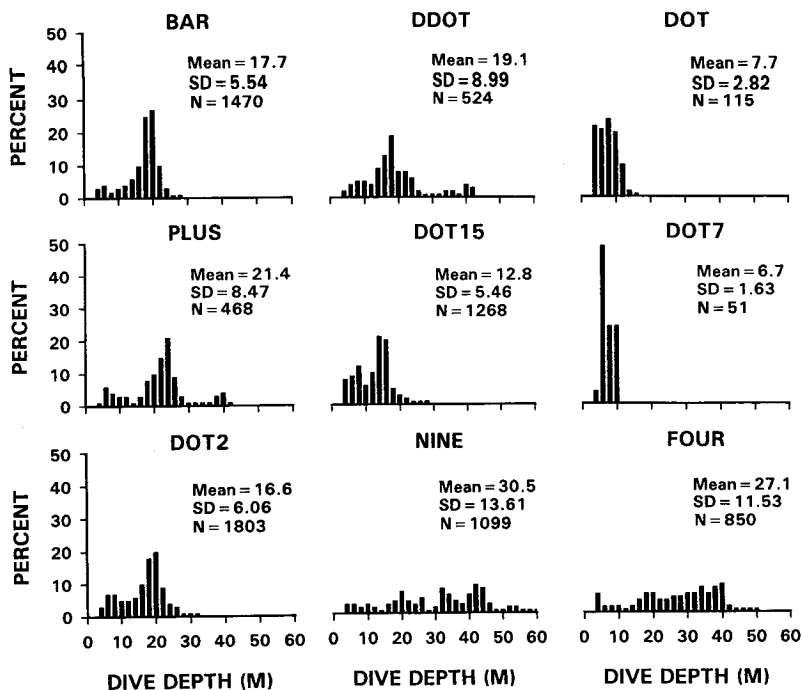


Fig. 2. Distribution of dive depths for nine lactating harbor seal females

Sable Island (61–113 kg; unpubl. obs.). Diving occurred in 12 of the 14 females, with 2 showing no diving during the part of lactation we were able to monitor (78% and 88% respectively). Among the nine females which did dive and for which TDR records covered most (80% or more) of lactation, neither the number of dive bouts nor diving effort (Table 1) significantly correlated with either the percentage of lactation or the number of days sampled by TDR (Spearman correlation; number of bouts $r = -0.31$, $P = 0.58$ and $r = 0.34$, $P = 0.41$, respectively; dive effort $r = -0.34$, $P = 0.31$ and $r = 0.40$, $P = 0.32$, respectively).

Characteristics of individual dives

The distribution of dive depths within bouts was variable among females (Fig. 2). Most females showed a clear modal depth, although this was not true of females Four and Nine. Several females showed a bimodal distribution in depth. The modal depth ranged from 6 to 42 m among

Table 2. Characteristics of dives of nine lactating harbor seal females (see Table 1 for duration of records)

	Mean \pm SE	Range	CV
Depth (m)	17.7 \pm 2.53	6.7–30.6	42.9
Duration (min)	1.6 \pm 0.18	0.4–2.3	33.7
Bottom time (min) ^a	1.0 \pm 0.14	0.1–1.4	42.0
(% of dive)	61.3 \pm 3.75	36–71	18.4
Descent rate (m/s)	1.0 \pm 0.11	0.5–1.8	33.0
Ascent rate (m/s)	1.0 \pm 0.16	0.4–2.2	48.0
Interval between repeated dives (min)	0.8 \pm 0.05	0.6–0.9	18.8

^a Continuous time within 2 m of maximum depth

the nine mothers. Those with modal dives less than 10 m (Dot and Dot7) dived little compared to the other females. The maximum depth to which any female dived was 60 m.

Average dive characteristics for the nine females are shown in Table 2. Variation among females in these characteristics is greatest for depth, bottom time and rate of ascent, with coefficients of variation (CV) of 40–45%. Mean dive depth was about 18 m and individual means ranged from about 7 to 31 m. The duration of dives was short, lasting 1.6 min on average, with a CV of about 35%. The maximum duration of an individual dive recorded for any female was 5.8 min. Dives tended to be “flat-bottomed” and symmetrical, with comparable rates of descent and ascent on average. Mean time at the bottom of a dive was 1 min, accounting for about 60% of the dive. The interval at the surface between successive dives averaged less than 1 min. Both relative bottom time and surface interval showed little variability among females (CV = 18.4% and 18.8%, respectively). The duration of dives increased with dive depth, ranging from 6-m dives lasting an average of 0.5 min to 60-m dives averaging 3.5 min. Bottom time showed parallel changes with depth.

The characteristics of dives changed during lactation (Fig. 3). The changes tended to be especially pronounced around 10–12 days postpartum. The mean number of dives per day increased by a factor of 7 from early to late lactation. Dive duration was about 50% greater later in lactation than in the first 11 days. The depth to which females dived early in lactation generally averaged less than 10 m, but increased to approximately 20 m in late lactation. The small sample sizes early in lactation (Fig. 3) reflect the fact that many females did not dive then.

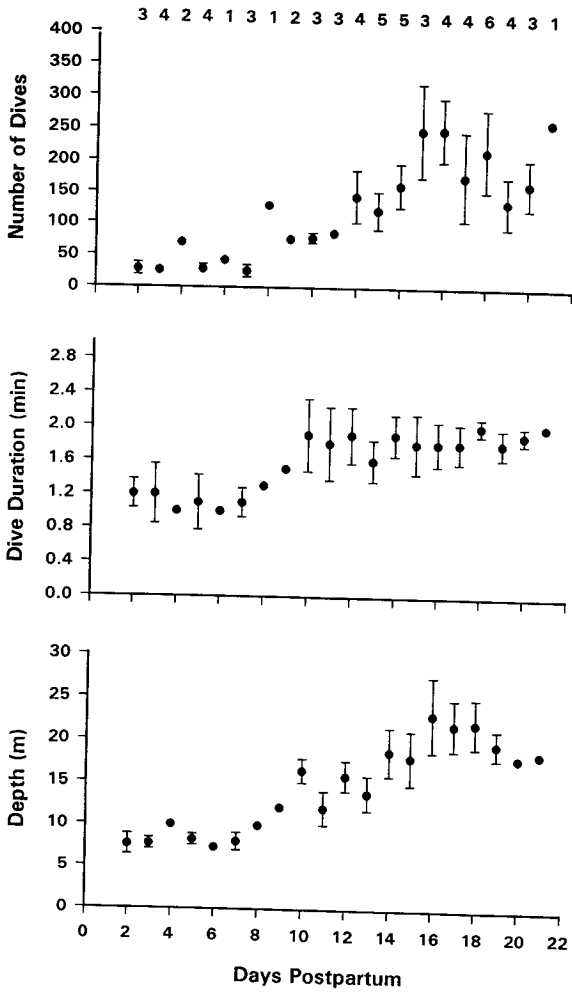


Fig. 3. Changes in mean duration, depth and number of dives of harbor seals during lactation. The numbers at the top of the figure indicate the number of females represented at each day postpartum vertical bars represent \pm one standard error

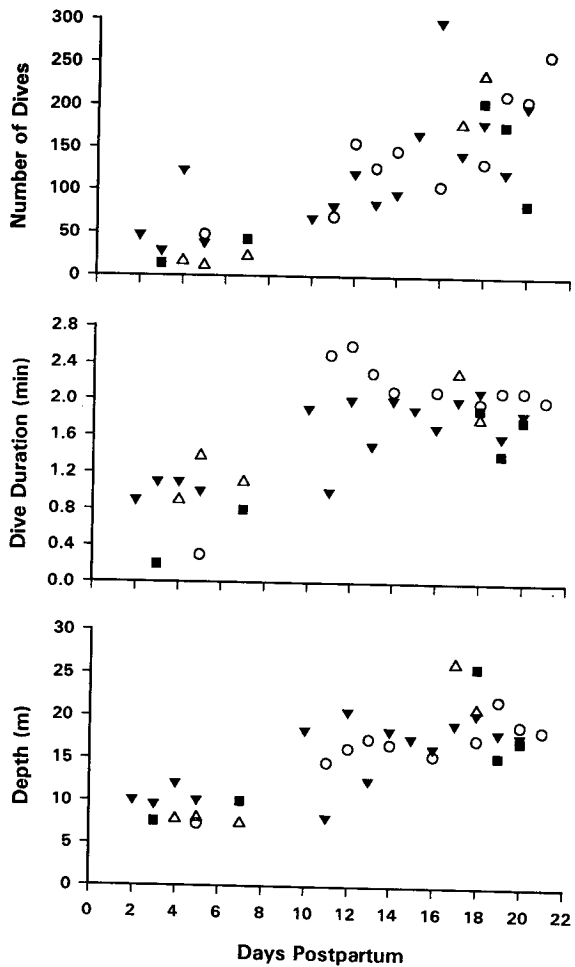


Fig. 4. Changes in mean duration, depth and number of dives for four harbor seal females with dive bouts during both early and late lactation. Each symbol represents a different female

As all females did not dive during both early and late lactation, it is possible that the trends shown in Fig. 3 result from variation in the diving behavior of individuals rather than systematic changes of individuals over lactation. To examine this, we plotted and statistically analyzed the dive characteristics of four females that dived both early and late (Fig. 4). We found similar trends, i.e. a significant increase from early to late lactation in all three measures (paired t -test: number of dives $t=6.00$, $P=0.009$; dive duration $t=6.97$, $P=0.006$; dive depth $t=4.62$, $P=0.02$).

To assess whether there was a diel pattern in diving activity, as has been reported in lactating otariid seals (see Gentry and Kooyman 1986), the hours of daylight were divided into two 7-h blocks and the hours of darkness into two 5-h blocks (Fig. 5). A repeated-measures ANOVA was performed for each dependent variable (mean percent of total dives, mean depth of dives and mean dive duration) on the within-individual ranks over the four hour-blocks. Diving occurred more frequently during daylight than during darkness, tending to be

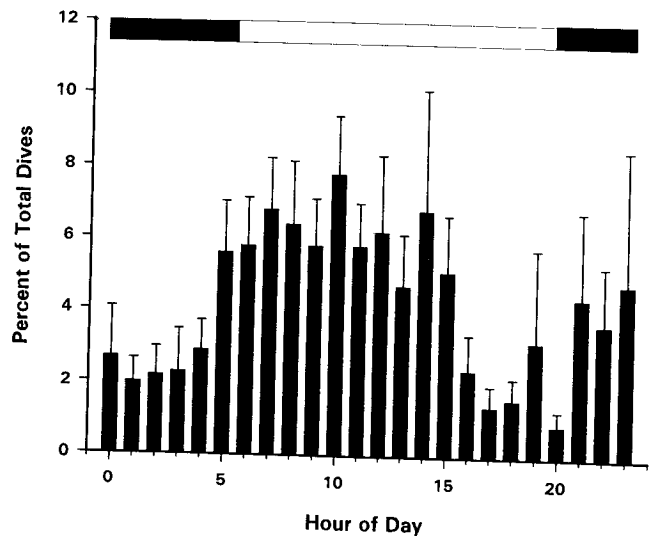


Fig. 5. The mean percentage of total dives of 12 lactating harbor seal females as a function of time of day. The dark bars at the top represent darkness and the open bar represents daylight. Error bars indicate the standard error

Table 3. Characteristics of dive bouts of nine lactating harbour seal females (see Table 1 for duration of records)

	All dive bouts			Dive bouts > 1 h		
	Mean ± SE	Range	CV	Mean ± SE	Range	CV
Days postpartum at onset	6.1 ± 1.57	2–14	77	11.3 ± 2.09	2–18	56
Number of bouts	7.6 ± 1.91	2–18	75	6.9 ± 2.21	1–18	96
Duration (h)	4.8 ± 1.19	0.6–11.5	74	7.1 ± 1.54	1.3–13.9	65
Inter-bout interval (h)	30.5 ± 9.64	7.3–84.7	95	17.5 ± 2.00	12.6–27.2	34
% Of time spent in dive bouts	12.5 ± 5.69	0.4–15.6	137	11.1 ± 3.70	0.4–15.6	100

greatest from early morning to early afternoon ($F = 4.22$, $P = 0.01$) (Fig. 5). Daytime dives were only slightly deeper than nighttime dives ($F = 3.77$, $P = 0.04$), but there was no significant difference in dive duration.

Characteristics of diving bouts

Dive records from TDRs (e.g. Fig. 1) indicated that individual dives clustered into bouts comparable to those described as evidence of foraging cycles in otariid seals (Gentry and Kooyman 1986; Boyd and Croxall 1992). Nearly a quarter of our harbor seal dive bouts were less than 1 h long. As these short bouts may represent little or no foraging (see Methods), bout characteristics are given for all dive bouts and for the subset of dive bouts that were > 1 h in duration (Table 3). When the short bouts were eliminated, the average number of dive bouts per female only decreased by about 1, but the average onset of diving was delayed nearly twofold, from 6 to 11 days postpartum. When short bouts are excluded, the mean inter-bout interval was only about half that calculated on the basis of all dive bouts (Table 3). On the basis of dive bouts > 1 h, the average harbor seal mother on Sable Island began making trips to sea to dive at about 11 days postpartum. These bouts of diving lasted 7.1 h and were separated by 17.5 h (Table 3). However, there was considerable variation among females in the frequency and temporal characteristics of dive bouts, as indicated by the coefficients of variation in Table 3.

Females usually returned to land following bouts of diving. Eliminating inter-bout intervals with no land time recorded (see explanation of failure of saltwater switch in Methods), the average time spent on land between diving bouts was 4.5 ± 1.24 h. This amounted to an average of 31% of the inter-bout interval. From observations of TDR females at the rookery, we know that females nursed their young during these visits and that mothers and their pups periodically entered the water together to swim in the shallow inter-tidal region.

Dive bouts > 1 h changed during lactation (Fig. 6). Bout duration in the first half of lactation was short, averaging about 1 h. In the second half, the mean duration increased as lactation progressed. The apparent decrease in mean duration at 19–21 days postpartum may be due to sampling error. Dive bout interval did not change systematically over the course of lactation. The mean percentage of time spent in dive bouts increased

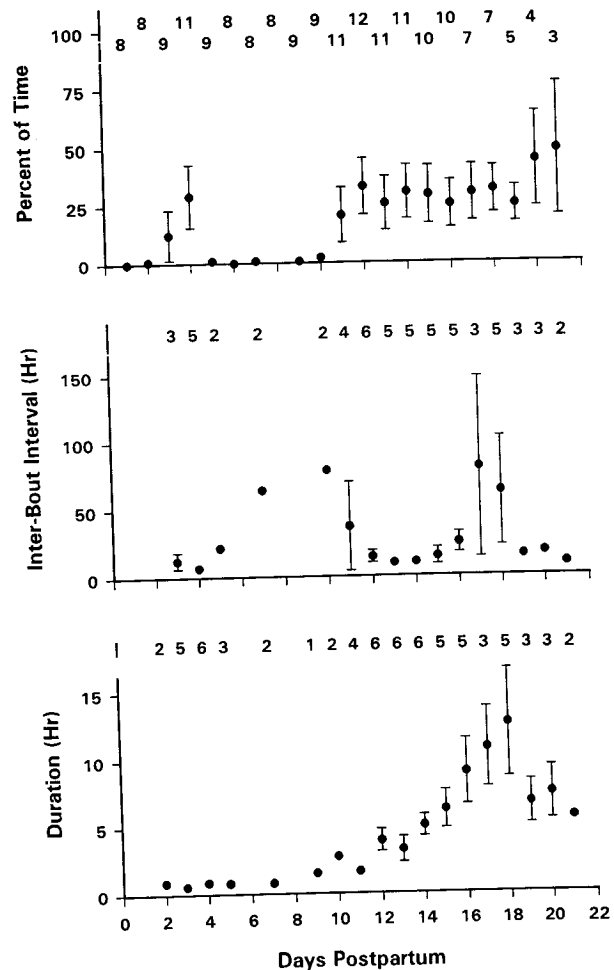


Fig. 6. Changes in mean duration, inter-bout interval and percent of time spent in dive bouts for harbor seals during lactation. The numbers above each graph indicate the number of females represented at each day postpartum. Vertical bars represent \pm one standard error

from almost nil in the first half of lactation to about 25% during the second half, with a tendency toward an increased amount of diving late in lactation.

Post-weaning diving

We would expect diving activity to increase once females have weaned their pups because females lose more than 80% of body fat during lactation (Bowen et al. 1992) and

must replenish lost stores. We tested this expectation using data for three females whose TDR records continued beyond the end of lactation (for 3, 7 and 14 days, respectively). Dive bouts averaged 17.3 ± 6.4 h after weaning (cf. Table 3) and sometimes lasted several days (Fig. 1). The mean number of post-weaning dives per day was 357 ± 58.2 compared to 206 ± 28.5 in late lactation and 26 ± 25.8 in early lactation. The three females spent an average of $82 \pm 12.4\%$ of their time diving after weaning compared to $66 \pm 18.0\%$ during late lactation and only $20 \pm 20.0\%$ during early lactation.

Maternal mass and diving activity

Insofar as maternal mass at parturition reflects maternal energy stores, then small females might begin to dive earlier in lactation and dive more often than large females because small females must subsidize more of lactation. To test this, a simple regression analysis was performed on several characteristics of diving behavior (days postpartum at onset, percent of time spent deep diving, and dive effort) against maternal mass at parturition (see Table 1). Maternal mass was not significantly correlated to any of the diving characteristics, although there was a tendency for smaller mothers to begin dive bouts > 1 h in duration earlier in lactation than larger mothers ($F = 4.62$, $P < 0.060$).

Discussion

Although there are occasional reports of food in the stomachs of lactating females for some phocids (see Oftedal et al. 1987; Testa et al. 1989; Smith et al. 1991), there have been no studies focusing specifically on maternal foraging. Further, foraging has not been considered a major or necessary component of the maternal strategy for this group. Rather, the phocids have been characterized as fasting during lactation, in contrast to the otariids, which alternate foraging trips to sea with periods of nursing young on land (Bonner 1984; Gentry and Kooyman 1986; Oftedal et al. 1987; Costa 1991). However, we have not only found food in the stomachs of lactating harbor seals (Bowen et al. 1989), but have also determined that lactating harbor seals make cyclical trips to sea to dive. These findings suggest that foraging is an important component of the maternal strategy of harbor seals that breed on Sable Island.

At Sable Island, lactating harbor seals spent a considerable amount of time in the water, as do harbor seals at other breeding colonies (Venables and Venables 1955; Renouf et al. 1983; Eliason 1986; Miller 1988; Thompson et al. 1989). During this time they engaged in diving that was deeper and more prolonged than the shallow activity that has been observed in social interactions between females and pups near rookeries (Bishop 1967; Wilson 1974; Renouf et al. 1983). The onset of diving bouts occurred at about the time at which food regularly can be found in the stomachs of lactating females by gastric lavage (Bowen et al. 1989). In 160 females whose stom-

achs were checked, none of the 26 in the first quartile of lactation (0–6 days) had food remains, whereas about 20% of the females checked during each of the subsequent three quartiles had food remains in their stomachs.

The interpretation that these diving bouts represent foraging activity is supported by the fact that diving activity increased dramatically after pups were weaned (Fig. 1). A similar post-weaning diving pattern has been shown to represent foraging, in both the northern and southern elephant seals, *Mirounga angustirostris* and *M. leonina*, respectively (Le Boeuf et al. 1989; Boyd and Arnborn 1991; Hindell et al. 1992). In these species, lactating females fast for 23–27 days (Carrick et al. 1962; Reiter et al. 1978; McCann 1982) and lose about a third of their body mass before pups are weaned (Costa et al. 1986; McCann et al. 1989).

Data on the loss of body fat and energy by lactating harbor seals indicate that lactation is particularly demanding. The average female loses 80% of her stored fat over the first 19 days of the 24-day lactation and clearly could not afford to continue the same net rate of fat loss for the remainder of lactation (Bowen et al. 1992). Thus, feeding may become necessary as stored reserves diminish. For example, it has been estimated that lactating grey seals, northern elephant seals, and hooded seals use about 84%, 58% and 33% of stored fat, respectively over their entire lactation periods, during which they unequivocally fast (Fedak and Anderson 1982; Costa et al. 1986; Bowen et al. 1987). The females of all of these species are substantially heavier (170–500 kg) than harbor seal mothers (ca. 85 kg), suggesting that they may have larger fat and energy stores per unit metabolic mass and thus may be more capable of sustaining lactation in the absence of food consumption (see Oftedal 1993).

It is likely that lactating harbor seals make foraging trips at other rookeries apart from at Sable Island, but because mothers are not easily captured at most rookeries few detailed studies have been conducted. From a combination of behavioral observations and automated radio-telemetry of 15 lactating females, Miller (1988) reported that mothers did not leave Drakes Estero, where her study site was located in California, for the first 2 weeks of lactation, but subsequently they departed for an increasing number of hours during the night. In another study, by triangulation of lactating females with radio-transmitters attached, Thompson et al. (in press) monitored movements away from haulout sites in Scotland. Early in lactation females restricted the range of their movements, but as lactation progressed their range of movements increased to encompass distances comparable to those traveled prior to parturition (about 45 km from shore). Females frequented the same areas they had used prior to the breeding period, which were presumed to be feeding sites.

The foraging cycle we describe here is on average about a day in length. This short cycle contrasts with that seen in most otariids. The only otariid that alternates foraging trips and rookery visits daily is the Galapagos sea lion, *Zalophus californianus wollabaeki* (Trillmich 1986). In most species, mothers go to sea for 2–6 days, staying with their pups for 1–2 days between foraging

trips (reviewed in Gentry et al. 1986; Oftedal et al. 1987). Recent studies in the Juan Fernandez fur seal, *Arctocephalus philippii*, reveal even longer foraging trips, lasting 9–12 days on average (J.M. Francis, D.J. Boness & H. Ochoa, unpubl. obs.). Despite foraging trips of several days, diving bouts are not continuous over the period of absence (see Fig. 15.3 in Gentry et al. 1986). In most otariid species there is a diel cycle, with most diving occurring at night, between 2000 and 0400 hours. Hence, substantial portions of the time at sea may not involve actual foraging.

Many studies of the foraging cycle in otariids are based on behavioral observations of presence or absence at the rookery (e.g. Bartholomew and Hoel 1953; Peterson 1968; Stirling 1971; see several chapters in Gentry and Kooyman 1986; Heath et al. 1991), and thus implicitly equate the duration of foraging activity to the duration of absence. The accuracy of the estimated duration of absence is influenced by the amount of observation effort, which may vary considerably from study to study. Two recent studies comparing results from both radio-telemetry and behavioral observation reveal that significant differences in estimated foraging trip duration can occur as a function of the method used to assess it (Boyd et al. 1991; Goldsworthy 1992). Furthermore, the more detailed information on diving behavior acquired from TDRs allows one to distinguish different types of dives that may represent activities other than foraging (e.g. Le Boeuf et al. 1992), or to detect surface intervals that may reflect resting rather than foraging.

Given the short duration of foraging trips by harbor seals on Sable Island, it is likely that they are feeding close to the island. Bathymetric maps of the region indicate that water depths of the magnitude recorded on the TDRs occur within a few nautical miles of Sable. Although it is generally assumed that the duration of foraging trips in lactating otariids is related to how far females must travel to reach their food supplies (Gentry et al. 1986), few studies have directly determined foraging location. However, location data obtained for the northern fur seal, *Callorhinus ursinus*, and the Juan Fernandez fur seal are consistent with this hypothesis. The northern fur seal, which averages about 6 days at sea, travels round-trip distances of 400–750 km from the rookery (Loughlin et al. 1987). The Juan Fernandez fur seal spends an average of 9 days at sea, traveling up to 450 km away from the rookery (J.M. Francis, D.J. Boness and H. Ochoa, unpubl. obs.).

Body size has been shown to be an important constraint on the evolution of behavior and life history patterns of animals (Blueweiss et al. 1978; Robbins and Robbins 1979; Clutton-Brock and Harvey 1983; Bekoff et al. 1981). Costa (1991) has argued that the dichotomy in maternal strategies between otariids and phocids relates to the ability to store energy at parturition, which is partially a consequence of maternal body size. We suggest that the small body size of harbor seals is an important factor in the evolution of their maternal strategy also. Females of all but two otariid species weigh less than 100 kg (Fig. 7), and all exhibit maternal foraging and have a long lactation period. The harbor seal, with a

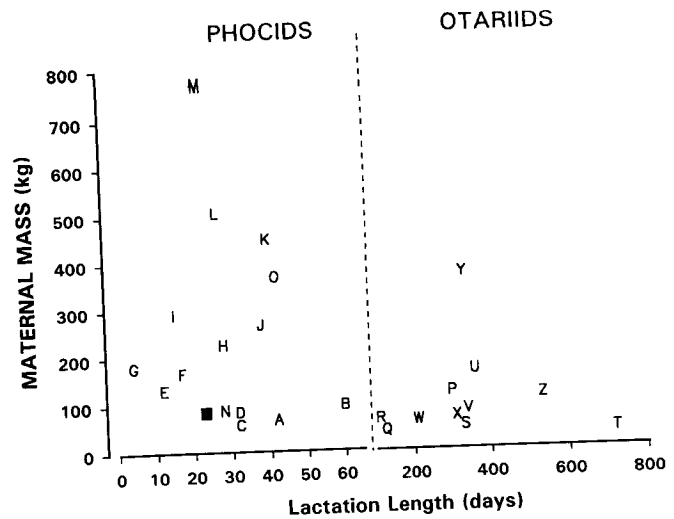


Fig. 7. The relationship between maternal mass and lactation length for otariids and phocids, indicating that harbor seals are among the smallest phocids and similar in size to otariids. For the phocids: A, *Phoca hispida*; B, *P. siberica*; C, *P. caspica*; D, *P. fasciata*; E, *P. groenlandica*; G, *Cystophora cristata*; F, *Halichoerus grypus*; H, *Lobodon carcinophagus*; I, *Erignathus barbatus*; J, *Monachus schauinslandi*; K, *Leptonychotes weddellii*; L, *Mirounga angustirostris*; M, *Mirounga leonina*; N, *Phoca largha*; O, *Hydrurga leptonyx*; ■, *Phoca vitulina*. For the otariids: P, *Zalophus californianus*; Q, *Callorhinus ursinus*; R, *Arctocephalus gazella*; S, *A. forsteri*; T, *A. galapagoensis*; U, *Otaria byronia*; V, *A. pusillus*; W, *A. philippii*; X, *A. tropicalis*; Y, *Eumetopias jubatus*; Z, *Neophoca cinerea*. Data for the phocids were taken from Kovacs and Lavigne (1986) and for the otariids from Costa (1991), with the exception of *A. philippii*, which are unpublished data from J.M. Francis

maternal body mass of about 85 kg (Bowen et al. 1992) is only slightly larger in body mass than most otariids, and it is small for a phocid (Fig. 7).

Differences in foraging behavior might be expected among females differing in maternal size within a colony. Thompson et al. (in press) found that the onset of an increase in range of movement away from haulout sites was positively correlated with maternal body length among lactating harbor seals in Scotland. Interestingly, the onset of diving activity among harbor seals on Sable Island showed a similar positive correlation with maternal body mass, although it was not significant ($P < 0.06$). As body size *per se* is only an approximate measure of maternal energy stores, further studies examining individual differences in maternal foraging behavior should employ indirect measures of maternal body fat, such as can be obtained by isotope methods (Costa 1987; Oftedal and Iverson 1987).

Evidence relating foraging to maternal mass in otariids is also equivocal. In one study of the Antarctic fur seal, *Arctocephalus gazella*, there was no relationship between maternal mass and either temporal parameters of foraging activity or individual dive characteristics (Boyd et al. 1991; Boyd and Croxall 1992). In another study of this species, foraging trip duration was negatively related to the mass of mothers of female pups, but unrelated to the mass of mothers of male pups (Goldsworthy 1992). The range of maternal body mass in the former study was small and might account for the lack of a relationship

between body mass and foraging, but the variances in maternal mass in the two studies do not differ.

As with the otariids, quantitative variation in the details of the foraging behavior of harbor seals may exist from colony to colony as a function of local food distribution. We might also expect inter-annual variation at a given colony because environmental conditions, which may vary from year to year, can affect food resources and maternal behavior (e.g. Trillmich 1986; Ono et al. 1987; Heath et al. 1991).

In summary, the suggested dichotomy in maternal strategies between otariid and phocid seals is overly simplistic. At least one small phocid, the harbor seal, exhibits a maternal foraging cycle similar to that of otariids. However, the harbor seal does have the short lactation characteristic of phocids. Their lactation strategy should thus be viewed as intermediate to that of the foraging otariids and the fasting phocids. This intermediate strategy appears to be necessitated by the small body mass (and hence restricted energy stores) of lactating harbor seals. We predict that the five phocid species (i.e. baikal seal *Phoca siberica*, Caspian seal *Phoca caspica*, largha seal *Phoca largha*, ribbon seal *Phoca fasciata* and ringed seal *Phoca hispida*; see Fig. 7) that are similar or smaller in body size and that have comparable or longer lactation periods as the harbor seal also forage extensively during lactation.

Acknowledgements. We would like to thank John Francis for introducing us to TDR technology and B. Beck, D. Benoit, S. Iverson and P. Ross for assistance in the field. G. Forbes and the staff of the Canadian Atmospheric and Environmental Service provided valuable logistical support on Sable Island. Several people provided helpful comments on drafts of the manuscript, including P. Duignan, M. Muelbert, A. Rosenberger, and F. Trillmich. The work was funded by the Department of Fisheries and Oceans (Canada), the Smithsonian Institution and the Friends of the National Zoo.

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