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

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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 weddelli*) 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

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**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).