Chapter 3
Maternal Behavior in Otariids and the Walrus

Maritza Sepúlveda and Robert G. Harcourt

Abstract The most energetically costly phases of female reproduction in placental mammals are gestation and lactation. For the young, the success of this relationship is based on obtaining as much maternal care as they can take in, even if this may result in a cost to future reproductive success of the mother. On the other hand, the mother should retain sufficient resources to be able to invest in future offspring, thus ensuring her own future reproductive success. These competing demands lead to a conflict between mothers and their young that eventually results in the weaning of the young, often initiated by the mother. In this review, we describe the main strategies of lactation and maternal care in fur seals, sea lions and walrus. The maternal care strategy in income-breeding pinnipeds with prolonged lactation periods, such as otariids and walrus, is influenced by group-living, and these two factors have been subject to strong selection. Maternal care in pinnipeds is influenced by both social and environmental constraints. This information plays a major role in our understanding of the social and exploratory behavior of the young, as well as into the interaction between maternal care and the development of offspring.

Keywords Maternal care · Income breeding · Lactation · Mother-offspring conflict · Otariid · Fur seal · Sea lion · Walrus

M. Sepúlveda (✉)
Centro de Investigación y Gestión de Recursos Naturales (CIGREN), Facultad de Ciencias, Universidad de Valparaíso, Valparaíso, Chile
e-mail: maritza.sepulveda@uv.cl

R. G. Harcourt
Marine Predator Research Group, School of Biological Sciences, Macquarie University, Sydney, NSW, Australia
e-mail: robert.harcourt@mq.edu.au

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3.1 Introduction

In placental mammals, gestation and lactation, periods during which young are energetically dependent on their mothers, represent the two most energetically costly phases of female reproduction. For most mammals, caring for the young is principally carried out by the mother, not only through the provision of milk, but also by other behaviors associated with care such as social interactions, recognition and nurturing, protection aggressive conspecifics, vigilance, anti-predator defense, and in some, teaching of tools required for their survival once independent. For the young, the success of this relationship is based on obtaining as much maternal care as they can take in, increasing its chance of survival at a time when mortality is typically high (Caughley 1966), even if this may result in a cost to the future reproductive success of the mother. On the other hand, the mother is selected to retain sufficient resources to be able to invest in future offspring, thus ensuring her own future reproductive success. These competing demands lead to a conflict between mothers and their young that eventually results in the weaning of the young, often initiated by the mother.

In this chapter, we describe the main strategies of lactation and maternal care in income breeding pinnipeds, the fur seals, sea lions and the walrus (*Odobenus rosmarus*). Much of our knowledge on this topic comes from their habit of giving birth and nursing on land or ice, as this has allowed researchers to examine strategies used by mothers to ensure survival and welfare of their young.

3.2 Gestation Length and Maternal Attendance Patterns

A limited amount of data currently exists regarding physiological changes that occur during gestation of marine mammals, particularly those in their natural habitat. Due to the high-energy cost of maintaining a developing fetus while engaging in thermoregulation and foraging activities, most pinniped females carry a single fetus. Few exceptions have been reported, but occasionally twin pups do survive to weaning and this has been reported in subantarctic (*Arctocephalus tropicalis*, Bester and Kerley 1983; de Bruyn et al. 2010), Antarctic (*A. gazella,* Doidge 1987; Bonin et al. 2012) and New Zealand fur seals (*A. forsteri*, Dowell et al. 2008) and Steller sea lions (*Eumetopias jubatus*, Maniscalco and Parker 2009). Bonin et al. (2012) demonstrated genetically that not all putative twins were in fact siblings; rather, there was a mix of full siblings, half siblings and adoptions. Although rare, reports of twin fetuses typically result in spontaneous abortions by the female at some point during gestation (Spotte 1982).

Development rates *in utero* seem relatively fixed, and to coordinate timing of breeding, otariids and walrus are not able to simply adjust developmental rates. In fur seals and sea lions, gestation lasts 8–10.6 months, with a delayed implantation / embryonic diapause of 1.4–4 months post conception, and this allows them to

Table 3.1 Lactation in fur seals, sea lions and walrus

Species	Lactation duration
Otariids	
Guadalupe fur seal	8–11 months
Juan Fernandez fur seal	7–10 months
Galapagos fur seal	18–36 months
South American fur seal	8–12 months. . .12–24 months
New Zealand fur seal	10–12 months
Antarctic fur seal	3.5–4 months
Subantarctic fur seal	9–11 months
South African fur seal	9–11 months
Australian fur seal	11–12 months
Northern fur seal	4 months
New Zealand Sea lion	6–12 months
Australian sea lion	17 months
South American sea lion	6–24 months
California Sea lion	6–12 months
Galapagos Sea lion	10–12 months
Steller Sea lion	12–36 months
Odobenids	
Atlantic walrus	24 months
Pacific walrus	24 months

Adapted from Riedman (1990) and Berta et al. (2006)

complete their cycle annually, or in the case of the Australian sea lion (*Neophoca cinerea*) 17-18 months and walrus 2.5 years (Boyd 1992; Boness et al. 2002; McIntosh and Pitcher, Chap. 26). Walrus have a 15–16 month gestation including a 3–4 month delayed implantation, resulting in a 2 year breeding cycle, the longest of all the pinnipeds (Boness et al. 2002; Miller and Kochnev, Chap. 22).

Like gestation length, maternal care pattern and lactation duration vary greatly among fur seals, sea lions and walrus (Table 3.1) (Trillmich 1990; Boness et al. 2002). Lactation strategies comprise either mothers leaving their offspring periodically and regularly, alternating foraging cycles of female foraging at sea with fasting nursing periods ashore (Costa and Valenzuela, Chap. 2), or females and their offspring staying together on land and at sea, with their offspring nursing in the water and staying with the mother while she forages.

Otariids exhibit an alternating foraging/fasting cycle, but the duration of lactation is highly variable. At its one extreme, the near-polar living Antarctic fur seal (Doidge et al. 1984) and northern fur seal (*Callorhinus ursinus,* Loughlin et al. 1987), both of which migrate away from the breeding area during the harsh polar winters, have relatively short lactation periods of 4 months. By contrast, Galapagos fur seals, *A. galapagoensis* (Trillmich 1986) and Steller sea lions (Gentry 1970) regularly suckle their pups for up to 3 years. Many of the temperate fur seals display a lactation that lasts 300–360 days (Table 3.1), but Australian sea lions suckle their pup until the birth of their subsequent offspring approximately 18 months later (Higgins and Gass

1993; see McIntosh and Pitcher, Chap. 26, for explanatory hypotheses). Otariid females give birth 1–2 days after arrival in the colony. They remain with their newborn pup for a period of 7–14 days before departing for their first foraging trip (Bonner 1984). Over the course of the entire duration of the maternal attendance period, females alternate suckling while ashore with these foraging trips to sea. Milk ingestion by the pup is intermittent, with intensive suckling periods interspersed with fasting periods while the mother is away foraging (Gentry and Kooyman 1986).

The duration of foraging trips, and thus the duration of the pup's fasting, varies within and across species, and is influenced by intrinsic factors such as age of the pup (Oftedal et al. 1987), and external factors such as productivity of the area (Bailleul et al. 2005), which may vary seasonally (Harcourt et al. 2002) or with unpredictable environmental oscillations such as El Niño (Soto et al. 2006). For instance, the duration of foraging trips in subantarctic fur seal females increases during the lactation period, starting from 15 days on average during the summer to 30 days on average during the winter (Beauplet et al. 2004). These seasonal differences are likely explained by a seasonal variability in food availability, combined with the growing pup's enhanced ability to fast.

Walrus alone exhibit the strategy of aquatic nursing, characterized by a long lactation phase during which the females feed. Both North Atlantic and Pacific walrus subspecies exhibit this strategy. Mothers nurse their calf for 1–2 years but this can be extended to a third year or even longer if another pregnancy does not occur (Fay 1982). Females are diestrous, with a behavioral estrus in late summer and a second heat through February.

Calves are relatively precocious, able to swim competently within a few hours of birth, and stay in permanent contact with their mothers (Stewart and Fay 2001). While moving to foraging grounds or to find floating ice, females often carry their young calf on their back.

3.3 Parental Care

In pinnipeds, care of the young (i.e. protection and nurturance) is provided only by the mother, as males are not involved in the pup's life. For terrestrially breeding colonial species, mothers must protect their pups from three main threats, neighboring females, bulls, and in some colonies, predators (Fig. 3.1). Aggressive females may bite neighboring pups, sometimes severely, especially in high density colonies (Marlow 1972; Harcourt 1992a, b; Cassini 2001). Danger to the pup is compounded by movements of males through the colony, whether to secure a breeding position or for thermoregulation (Marlow 1972; Carey 1992; Harcourt 1992a; Hofmeyr et al. 2007). Male-male competition often leads to pups being trampled and suffering crush injuries as the bull pursues a rival (Marlow 1975). Mothers attempt to protect their pups from invading predators; for example, South American sea lion (*Otaria byronia*) males raid South American fur seal (*A. australis*) colonies in Peru and Uruguay to steal pups, and mothers either flee (Peru) or defend (Uruguay) their

Fig. 3.1 Subadult male of the South American sea lion (*Otaria byronia*) kidnapping and biting a newborn pup. Photo by Guido Pavez

offspring (Harcourt 1992a; Cassini 2001). For young pups, these raids may result in mother-pup separation and this can be fatal if the mother-pup bond has not yet formed. All together, aggressive/defensive behaviors from adult females and disruptive male behavior contribute to a high proportion of pup mortality. For these reasons, mothers spend much of their time protecting an area around their pup, especially during the perinatal period (Harcourt 1992a, b; Phillips 2003). Such maternal protection seems to be correlated with colony density (Le Boeuf and Briggs 1977; Doidge et al. 1984; Harcourt 1992b; Cassini 2001; Hofmeyr et al. 2007), and also with the quality of the substrate, including proximity to water, tide pools, presence of shade, or a flat area (Doidge et al. 1984; Fernández-Juricic and Cassini 2007).

In walrus, mothers are strongly bonded with their calves and are highly protective against any predator, including humans (Fay 1982; Nowak 2003). If females perceive danger, they push their calf into the water and join it. Interestingly, other conspecifics also become actively protective of the calves. It is common to see both female and male walruses forming tight formations i.e. *herding* when a calf produces distress calls (Fay 1982; Nowak 2003).

Fostering, allosuckling or allonursing are the different terms used in the literature for nursing of a non-filial pup by a female, once or for a more prolonged time of several days. In some species of pinnipeds, allosuckling behavior has been described. But, overall, allomaternal care in otariids is extremely rare, except for New Zealand sea lions (*Phocarctos hookeri*) (Fig. 3.2) (6%: Childerhouse and Gales 2001) and Antarctic fur seals (7%–11%: Lunn 1992; Gemmell 2003).

In otariids, most species have developed a highly reliable mother-pup recognition system (higher vocal stereotypy and occurrence of mutual recognition—see

Fig. 3.2 Allomaternal carers: Australian sea lion (*Neophoca cinerea*) female simultaneously nursing two young pups. No aggressive behavior was observed for any of the pups (from Pitcher et al. 2011). Photo by Clarence Kennedy

Charrier, Chap. 14) and so non-specificity of recognition of young by mothers is unlikely to explain the higher rates observed in New Zealand sea lions or Antarctic fur seals. Instead, age of the female may be an important contributing factor in the frequency of allonursing. Young and/or primiparous females reportedly accept non-filial pups more easily than older and/or multiparous females (Georges et al. 1999), with multiparous females highly aggressive towards non-filial pups (Trillmich 1981). Fostering unrelated pups may provide young females opportunities to gain maternal experience, especially those having lost their pup (Riedman 1982).

However much more commonly, pups may attempt to steal milk (sneak-suckling) from non-mother females (e.g. Roux 1986; Lunn 1992; Porter and Trites 2004; Pitcher et al. 2011). This behavior is likely intentional and pups do not suckle the wrong female by mistake. In most reports, the thieving pup quietly approaches a female that is asleep, suckling until the female becomes aware that the suckling pup is not her pup and rejects it (Porter and Trites 2004). Sometimes the female's own pup alerts the mother that an unrelated pup is present (Sepúlveda, pers. obs.). This behavior is frequently observed in pups that are nutritionally stressed when they are separated from their mother for a long period of time, a common phenomenon given the alternating feeding cycle in otariids. Such attempts can be quite risky since females are highly aggressive towards non-filial pups (Harcourt 1992a), suggesting that the benefit of gaining even a small supply of milk may outweigh the risk of immediate injury from bites, since starvation is the likely alternative (Roux 1986). Early research considered milk stealing by pups to be uncommon. However a growing number of observations suggest that this behavior is widespread (de Bruyn et al. 2010), and requires detailed further investigation.

3.4 Mother-Offspring Conflicts and Weaning

That conflicts are likely to occur between mother and her offspring is a tenet of evolutionary theory. Trivers (1974) proposed a conflict for the amount of energy transfer between mother and her offspring will occur intensively at the end of lactation, i.e. near weaning. Thus, weaning bestows an advantage for mother but not for the suckling offspring. For offspring, acquiring energetic resources for a longer period may enhance their chance of survival and thus increase their own reproductive success. From the mother's perspective, providing nutrition for a longer period of time will further decrease her own body resources and so may impact survival of her next offspring and therefore her own future reproductive success (Desprez et al. 2014). Such theory predicts an increase in mother's aggressive behavior towards offspring near weaning and a decrease in successful suckling bouts.

In many otariids, parent-offspring conflict occurs when mothers nurse their young for an extended period, and older pups are still present in the colony when mothers have their next offspring (Fig. 3.3). This parent-offspring conflict can be exacerbated when food resources are highly seasonal and unpredictable. There are frequent observations of mothers having to defend themselves against their offsprings' aggressive begging; for example, in older pups of Galapagos fur seals and sea

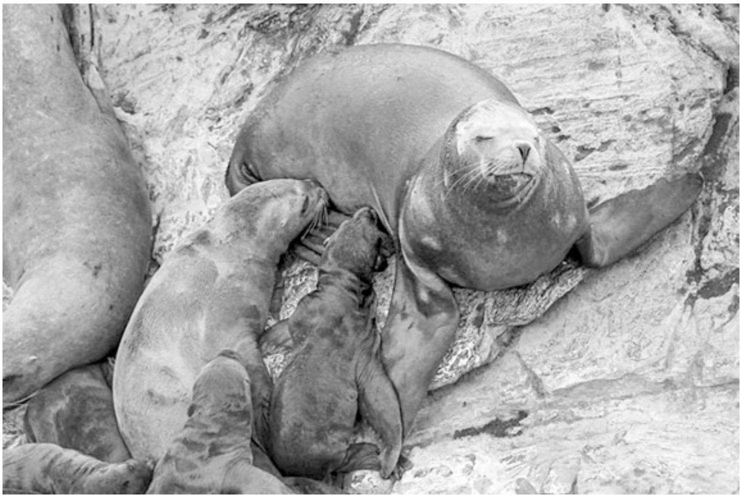

Fig. 3.3 South American sea lion (*Otaria byronia*) female simultaneously nursing a juvenile born in the previous year and a newborn pup. Photo by Guido Pavez

lions (*Zalophus wollebaeki*, Trillmich and Wolf 2007), South American fur seals (Majluf 1987), Australian sea lions (Marlow 1975) and South American sea lions (Sepúlveda, pers.obs). Moreover, sibling conflict occurs in some otariids when females with yearlings give birth to lighter newborns that are at greater risk of mortality due to the presence of older siblings (Trillmich and Wolf 2007). In contrast to these tropical otariids, the Galapagos fur seals and sea lions, no evidence for aggressive behavior or decrease in suckling has been observed in other species showing prolonged lactation, including New Zealand fur seals (Hasse 2004) and Steller sea lions (Marcotte 2006), with young weaning themselves. Self-weaning has been also observed in northern fur seals (Macy 1982) and Antarctic fur seals (Doidge et al. 1984), two species with a short lactation period, where when ready, pups leave the colony to forage before their mothers return from a trip. In most otariids, the absence of parent-offspring conflict may be explained by the fact that young complement their milk diet with solid food obtained during short foraging trips, and thus learn the location of foraging grounds and prey capture techniques. While it has been suggested that pups might learn from their mothers, recent findings on Australian sea lions have shown that pups do not have similar foraging patterns to their mothers. Given that in all otariids, pups complement their milk diet with solid food obtained in short feeding trips, this may presumably be where they first learn to forage - whether independently or by observation of unrelated conspecifics (Lowther et al. 2012).

3.5 Conclusions

Habitat, establishment of social units, and mating system have clear impacts on pinniped maternal care and the relationship between mothers and their young. Lactation strategy and duration are a good illustration of the complexity of maternal care patterns which consider effects of social and environmental constraints, as well as the development of a reliable mother-young recognition system. In otariids, lactation is prolonged, forcing mothers to undertake feeding trips, which along with the usual high density of animals on land leads to the development of a complex and precise recognition system. Maternal care strategies appear complex in group-living species. In pinnipeds, it is unknown whether contact between the mother and her offspring continues after weaning. Long-term recognition is present in some otariid species which, combined with natal site fidelity (i.e. philopatry), provides a mechanism for the development of some degree of association with relatives. However, in other species, kin associations are only weak compared to philopatric drivers of social associations. Further information on post-weaning interactions between mother and offspring will play a major role in our understanding of the social and exploratory behavior of the young, as well as into the interaction between maternal care and the development of offspring.

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