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Lactation and mother–pup behaviour in the Mediterranean monk seal *Monachus monachus*: an unusual pattern for a phocid

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This paper presents baseline information on maternal behaviour and lactation in the Mediterranean monk seal, with particular focus on the age at which pups are weaned. The study was conducted in the western Saharan population, the only surviving colony of the species. The first moult finished at a mean pup age of 72.3±17 d (N=17) and, in contrast to other taxonomically-related phocids, this process was not associated with weaning. Lactation lasted a mean of 119.4 d (N=9; range: 103–149 d) in the pups that could be monitored until full weaning had taken place. This period almost doubles the maximum lactation length reported in other phocid species. During the first week after birth the mother–pup bond was well developed and mothers always remained with their pups. The time invested in nursing (17%, SD: ±36) and in mother-pup interactions (14%, SD: ±32) was higher during this period than afterwards (8%, SD: ±23 and 4%, SD: ±19, respectively). After the first week, nursing continued but mothers started to leave their pups in order to feed at sea. Weaning occurred gradually. Already since birth, pups were active and mobile, and swam frequently before moulting or weaning occurred. Fostering and milk stealing were common patterns of behaviour for both lactating females and pups. In 26.6% of the suckling episodes observed in mother–pup pairs of known identity, pups suckled from females other than their mothers. Some females nursed more than one pup, at least occasionally, and in some cases a pup was fostered long-term by an alien female. The Mediterranean monk seal exhibits maternal-care characteristics that are more like otarids than phocids. This observation contradicts previous proposals that a short lactation period is a phylogenetic characteristic of phocids. Several of the unusual maternal traits observed may be favoured by year-round access to abundant food supply, availability of breeding sites, and mild climatic conditions. This information should be taken into account when designing conservation strategies for the species and, very particularly, in the implementation of pup rehabilitation programmes.

INTRODUCTION

The Mediterranean monk seal is one of the most scarce mammal species worldwide. Its original distribution range originally extended throughout the Black Sea, the Mediterranean Sea and the temperate waters of the eastern North Atlantic. However, its numbers were severely depleted by sealing and other adverse interactions with humans, mainly with fishermen, well before the end of the last century; consequently, it has vanished in many of the areas that were originally inhabited. In recent decades, the overall trajectory of the various populations shows a continuous decline in all regions. Thus, many localities where monk seals were present in the 1960s (Winjgaarden, 1962) are no longer occupied (Aguilar, 1999), and the remnant populations are heavily fragmented. This isolation of subunits further hinders the recovery of the species. There are no reliable figures available on the total number of animals surviving. The population was thought to number approximately 500 in recent years (Reijnders et al., 1993). However, in spring 1997 a large-scale mortality struck the large western Saharan population and reduced estimated worldwide numbers to only about 250–300 (Aguilar, 1999).

The rarity of the species during this century, and the fact that all surviving populations are cave dwellers, has hampered the ability to study the biology of the species. This is particularly true for the reproductive aspects, which are critical for designing conservation strategy and action. The limited information available indicates that gross reproductive rates are remarkably low as compared to other phocids (Gazo et al., 1999; Gucu et al., 2004), and that this low rate may be an effect of the extremely low genetic variability of the species and potentially associated inbreeding depression (Pastor et al., 2004). However, little is known of the fate of newborns apart from the fact that their mortality may in some periods be extremely high as a consequence of storms (Gazo et al., 2000). The only large colony of Mediterranean monk seals that survives today and, therefore, the only aggregation that still displays the social structure and biological cycle typical of the species, is located on the western Saharan coast (Aguilar, 1999). Before suffering a mortality event in 1997, the population numbered about 317 individuals but this was reduced to an estimated 109 individuals (Forcada et al., 1999).

Information on maternal care and lactation is of relevance to understand the role of phylogeny versus the environment

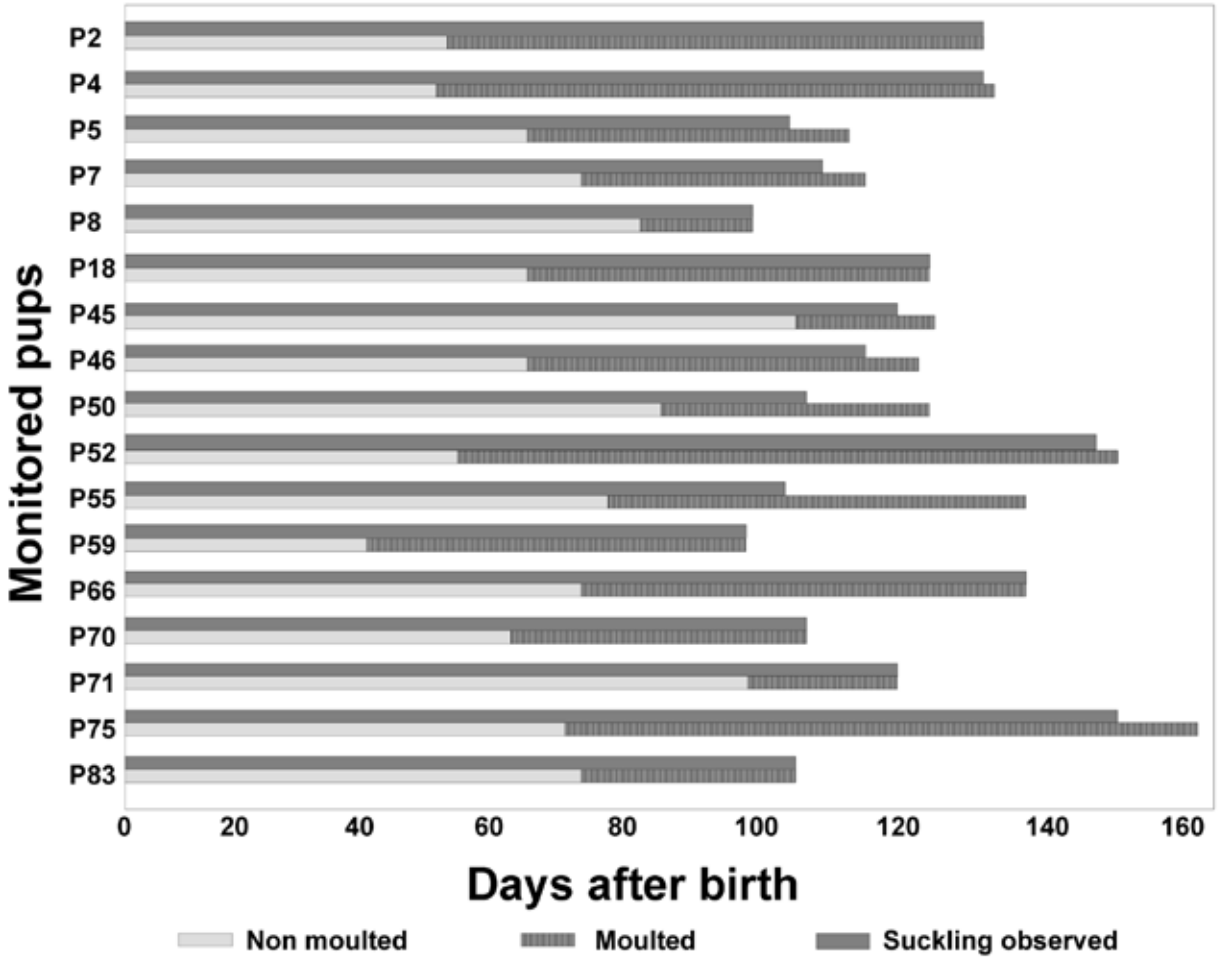

Figure 1. Diagram showing the chronology of moulting and weaning in 17 identified Mediterranean monk seal pups. The limit of the lower bar indicates the duration of the monitoring period for each pup.

in shaping the maternal strategy of pinnipeds. It is also critical for the conservation of the species, in particular for monitoring maternal reproductive effort and success, identification and rehabilitation of pups in distress, and potential captive breeding programmes. The objective of the present study, carried out in the Mediterranean monk seal colony of Cap Blanc, in the western Sahara, is to produce baseline information for the species on maternal behaviour and lactation, with particular focus on the age at which pups are weaned.

MATERIALS AND METHODS

The study was carried out on the Mediterranean monk seal population inhabiting the 'Seals Coast', a segment of coastline located on the western side of the Cap Blanc peninsula in the western Sahara. Data were collected from January 1995 to November 1999 but excluding the period when the population suffered a large-scale mortality (May–September 1997) because the seals' behaviour was then much altered. Monitoring effort focused on Caves 1 and 3, the two main caves occupied by the reproductively active fraction of the population and where over 80% of births occur (González et al., 1997; Gazo et al., 1999).

We monitored activity patterns and behavioural interaction between lactating females and pups either by direct observation from standpoints located at the entrance of the caves or by remote control video cameras installed on the roof of the entrance, as described by Gazo et al. (1999). We identified individual pups by their unique ventral coloration patterns (Badosa et al., 1998) and through marking (Gazo et al. 1999). Adults were identified by their natural markings (Forcada & Aguilar, 2000). We observed the behaviour of 55 pups, but monitoring from birth to weaning was only possible for 17.

Maternal care

We defined maternal care as any interaction between the mother and the pup that implied direct contact, protection, or care of the pup. As in other phocids, it involved vocalizations, approach by the mother, close olfactory inspection, and physical contact. It also included postures of the mother to protect the pup from the waves or other seals. We defined an encounter as the approach and subsequent contact between a female and a pup after a period of separation of at least 10 min. A mother–pup encounter rate was calculated as: encounters h^{-1} $month^{-1}$.

Table 1. *Proportion of time (as percentage of total ±SD) spent by pups of various developmental stages in distinct behaviours.*

	Pup stage			
	WP	NMP	MP	PMP
	Mean±SD	Mean±SD	Mean±SD	Mean±SD
Idle	58±45	76±36	70.7±44	73.4±41
In locomotion	11±30	11±26	10±28	14.2±30
Interacting with other pups	0	0.9±9	1.1±10	0.7±7
Interacting with mother	14±32	4±19	6.4±25	4.2±7
Interacting with adult male	0	0.3±2.5	1.3±10	0.2±2.6
Suckling	17±36	8±23	10.5±28	7.3±23
N	71	257	126	456

WP, wrinkled pups; NMP, non-wrinkled non-moulted pups; MP, moulting pups; PMP, post-moulted pups; N, number; SD, standard deviation.

Nursing

Scan sampling was recorded in blocks of 10–15 min on all animals on the beach inside the cave, at 30–60 min intervals and *ad libitum* sampling between scanning sessions (Altmann, 1974). We estimated time budgets for the behaviour of the distinct pup stages from 910 observations. Pups were classified into two categories: non-moulted and moulted pups or youngsters. For certain behavioural traits, three developmental stages within non-moulted pups were distinguished: wrinkled pups (WP), which were newborns or very recently born, non-wrinkled non-moulted pups (NMP) and moulting pups (MP) (Gazo et al., 1999).

We defined nursing as any event in which the pup established oral contact with the teats. Following Oftedal et al. (1987), we defined a suckling session as the total period during which a pup was continuously on-teat or during which the off-teat breaks were shorter than 10 min. We considered that a long break (>10 min) or transition to another activity terminated a session. Weaning of a given pup was estimated to have occurred when no more observations of suckling were made. A seal was considered a pup during the period from birth to weaning. We defined fostering as any event in which females allowed a non-filial pup to suckle. Milk stealing was defined as any suckling event in which a pup suckled from a female, other than its mother, and that female was sleeping or was unaware of the presence of the pup.

RESULTS

We followed 17 pups from birth until they completed moulting. In these individuals, the age at the onset of moulting averaged 48.5 d (SD: ±12 d; range: 21–59 d). Moulting lasted an average of 23.7 d (SD: ±8.9 d; range: 9–43) and the pups were completely moulted at an average age of 72.3 d (SD: ±17 d; range: 40–101 d). In eight cases (pups P2, P8, P18, P59, P66, P70, P71, P83) the pup disappeared or monitoring was interrupted before weaning occurred (Figure 1). These pups were therefore useful to assess a minimum period of lactation but not its actual duration. The mean calculated for this group was 112 d (range: 97–131 d). Monitoring of the other nine pups (P4, P5, P7, P45, P46, P50, P52, P55, P75) continued after they had reached weaning and their mean time at weaning was calculated to be 119.4 d (range: 103–149 d).

Mothers spent the first week after birth on land lying close to their newborn even during high tides, and were aggressive towards other seals that approached the pup. During this stage, mother–pup bonding was well developed and recognition was established by frequent nuzzling and vocalizations. Table 1 details the time budget of pups in the various pup growth stages. We observed no trend in time spent idle, in locomotion or in interacting with individuals other than the mother. The time invested in nursing and interacting with the mother was highest while the pup was wrinkled but decreased afterwards, although differences between periods were not significant, possibly because of the high variability observed and limited sample size. The mother–pup encounter rates were significantly higher (Mann–Whitney *U*-test, U=3, $P<0.05$) for non-moulted pups (0.168±0.06 for non-moulted pups vs 0.068±0.02 for post-moult pups). An encounter was followed by a suckling session for 63.3% of non-moulted pups, and 85.7% for post-moult ones (Table 2); differences were non-significant ($t = -1.68$, df=10, $P=0.123$).

We observed 70 suckling sessions, during which 218 on-teat events were recorded. In 34 of these sessions we monitored the mother–pup pair from beginning to end in order to determine their duration (Table 2). When comparing non-moulted vs post-moult pups, neither the mean duration of

Table 2. *Behavioural characteristics of suckling sessions.*

	Pup stage			
	Non-moulted pups		Moulted pups	
	N	%	N	%
% of encounters followed by suckling session	36	63.3	14	85.7
	N	Mean±SD	N	Mean±SD
Duration of suckling session (min)	25	13.5±7.05	9	17.8±7.75
% of time on-teat during suckling session	25	69.6±14.00	9	72.6±17.8
Duration of on-teat events (sec)	144	14.6±5.60	74	11.6±2.01

N, number; SD, standard deviation.

the suckling sessions (t =−1.54, df=32, P>0.05), the mean time on-teat (t =−1.76, df=32, P>0.05), nor the duration of individual on-teat events (t=1.64, df=32, P>0.05) showed significant differences.

We identified the mothers of 34 pups. A total of 220 suckling events were recorded for these 34 mother–pup pairs, although not all from beginning to end. In 48% (N=105) of these events we identified the mother; in 73.3% of cases the attending female was the mother, while in 26.6% the nursing individual was an alien female. We observed an adult female suckling four different pups successively and, on three occasions, we recorded a female simultaneously nursing three pups, of which two were non-filial. In eight cases we observed females disputing a pup, particularly when one had lost her pup. In two such cases, the conflict ended with the fostering of the pup by the alien female. Such plasticity in maternal interactions was common. For example, in 13 suckling sessions by pup P18, five took place with the putative mother and eight with an alien female that eventually became the foster mother.

DISCUSSION

The Mediterranean monk seal has an extremely protracted whelping season. In the Mediterranean, its season extends from about June to December (Gucu et al., 2004). In Cabo Blanco, probably because seasonal climatic variation is less marked, it reproduces throughout the year although there is a small peak of births in October (Gazo et al., 1999; Pastor & Aguilar, 2003). This lack of a definite peak in the yearly distribution of births precluded the determination of the duration of lactation using the overall activity patterns of the population. Therefore, in our study this variable was calculated by continuous long-term monitoring of identified individuals.

Previously, three captive pups from Greece were observed to moult at 82, 85 and 102 days old (Hart & Vedder, 1990; SRRC, 1991). These values are relatively high compared to those observed in Cabo Blanco (mean: 72.3; SD: ±17 d; Figure 1), although they fall within the ranges (40–108 d). However, the age of the Greek pups was unknown when the animals were collected, therefore the determination of their age at moulting may be incorrect. Also, moulting is likely to be altered in individuals that have been subject to deficient feeding or stress. In the elephant seal (*Mirounga* spp.) and the Hawaiian monk seal, both close relatives of Mediterranean monk seals, weaning is associated with the first moult (Riedman, 1990). However, our results indicate (Figure 1) that in Mediterranean monk seals these events are not related and that there is a considerable delay in weaning once moulting has occurred.

During the first week after birth, the bond between mother–pup pairs was well developed and mothers always remained with the pups in the caves. The time invested in nursing and in mother–pup interactions was higher during this period than afterwards. Once this period was finished, both direct observation and the monitoring of a lactating female with a time–depth recorder (Gazo & Aguilar, 2005) showed that mothers started their trips to sea for feeding. Upon their return, the mother actively looked for the pup and, when this happened, a suckling session commonly followed; because the feeding trips appeared to be more frequent towards the end of the lactation, mother–pup encounters and suckling sessions subsequent to the mother's absence were also more frequent when the pup had moulted. However, the time budget of the suckling periods is similar in moulted and non-moulted pups (Table 2). Mothers used nuzzling and vocalization to recognize their pups. Contrarily, female Hawaiian monk seals cannot recognize their pups by voice (Job et al., 1995). In other phocids, such as the harp seal (*Phoca groenlandica*), besides spatial, visual and auditory signals, olfactory cues also provide the definitive means of identification between mother-pup pairs when mothers return from the water (Kovacs, 1995). In our study, we never observed adult males to display any caring behaviour towards pups or participate in their rearing.

Pups were active and mobile soon after birth (Table 1), a fact that was both confirmed by direct observation and monitoring with time–depth recorders (Gazo et al., 2006). Pups started to swim in the first weeks of life, and movements between caves, which are 1.1 km apart, were not rare; these trips were occasionally undertaken independently of the mother. Nursing pups of phocid seals which do not moult *in utero* rarely venture into open waters (Bowen, 1991). Exceptions to this general pattern appear to be the pups of grey seals (*Halichoerus grypus*), harp seals, Weddell seals (*Leptonychotes weddellii*), and Hawaiian monk seals, which have occasionally been observed to swim during the nursing period (Lydersen & Hammill, 1993).

The most striking aspect of lactation in Mediterranean monk seals is its duration. Pups suckled in all cases for at least over 98 d and some for up to 148 d, the best estimate being 119 d. These periods may even underestimate the true lactation period because in the last stage suckling events are sparse and may therefore go unnoticed by observers. Also, in several cases monitoring was discontinued before the pup was weaned; therefore lactation in these pups was likely to be more protracted than that recorded. Such a long nursing period is exceptional. It almost doubles the maximum lactation lengths observed in other phocid species (for reviews, see Oftedal et al., 1987; Hammill et al., 1991; Schulz & Bowen, 2004). Previous estimates of the suckling period in the Mediterranean monk seal had always been based on fragmentary and indirect observations which did not exceed 50 d (Sergeant et al., 1978; Boulva, 1979; Kenyon, 1981). The only exception was that by Mursaloglu (1984) who, after monitoring a pup in a cave in Turkey for several months, reported that it had been suckling for over 4 months, but this finding was generally disregarded or considered an exceptional case (Marchessaux, 1989). Our results indicate that this protracted nursing period is a common feature of the species rather than an exception.

The information available on the identity of the lactating females in this study was in some cases fragmentary. Thus, we cannot rule out that pups may attain these long lactation periods because they suckle females other than their mother after being weaned. However, in at least some cases, such as the pup described by Mursaloglu (1984) and pup P75 (Figure 1), suckling was limited to a single female during 150 d.

A 98–119 d nursing period would be impossible to sustain under continuous fasting by mothers. Although no

quantitative observations were made, we did not observe lactating females in the impoverished condition that typical phocids exhibit toward the end of the nursing period (e.g. Hammill et al., 1991; Arnbom et al., 1997). Thus, we assume that ingestion of food during lactation is substantial. This again differs from most other phocids, including the congeneric Hawaiian monk seal, which typically fasts or feeds little during lactation (Kenyon, 1981; Bonner, 1984). However, it is unclear how frequently or efficiently the Mediterranean monk seal mothers feed. Feeding trips in otariids usually last several days (Gentry & Kooyman, 1986), while those of other phocids that combine feeding with nursing span some hours or, at the most, a day (Lydersen & Kovacs, 1993; Lydersen et al., 1994). We lack reliable information on this aspect of the Mediterranean monk seal because the identification of adult females was difficult. However, the presence of pups in the caves with no accompanying adults was frequently observed, although the duration of the periods was not established.

Weaning in Mediterranean monk seals occurs gradually, again contradicting the typical phocid pattern, characterized by an abrupt termination of suckling (Trillmich, 1996). Application of time–depth recorders to moulted pups from Cabo Blanco that were still sporadically involving in suckling showed that they undertook bouts of diving associated with foraging (Gazo et al., 2006). Furthermore, we observed pups playing with prey in their mouths; in some cases at least, this appeared to be ingested. The observation of a gradual transition from suckling to ingestion of solid food is further supported by the fact that the time devoted to maternal care and nursing was longer in non-moulted pups than in moulted ones.

Fostering and milk stealing was common. In 26.6% of the suckling episodes observed in mother–pup pairs of known identity, pups suckled from females other than their mothers. Suckling from an alien mother was in some cases more frequent than from the putative one, and in some cases it eventually led to the fostering of the pup by an alien female. These events did not necessarily occur after a mother had lost her pup, as they do in other phocids like the harbour seal (Boness et al., 1992). Some females nursed alien pups during the period in which they nursed their own offspring. This behaviour has also been observed, although rarely, in other phocids (Fogden, 1971; Riedman & Le Boeuf, 1982; Boness, 1990; Arnbom et al., 1997). Some females were seen nursing more than one pup simultaneously. Both fostering and milk stealing are widespread among phocids (Bowen, 1991) including the congeneric Hawaiian monk seal, in which this behaviour is particularly well developed (Boness, 1990). Allomaternal care and adoption are more frequent in species that nurse their young in cohesive aggregations (Lunn, 1992; Boness et al., 1992). Because Mediterranean monk seals, at least on the western Saharan coast, breed in caves where space is limited and the density of individuals, often closely related, is high (Gazo et al., 1999), the incidence of fostering or maternal care for alien pups is likely to be enhanced.

Although the relative importance of phylogeny in determining the lactation strategy exhibited by a species is debatable (Schulz & Bowen, 2004), maternal strategies in pinnipeds are classified into three categories, which are traditionally associated with each pinniped family. Odobenid females take their pups with them to open waters and nursing takes place both at sea and on land; lactation lasts for two or three years, milk is low in fat, and weaning is gradual. Otariid females alternate feeding trips at sea with the nursing of pups on land, and therefore they make limited use of their blubber fat reserves during lactation; concomitant with this, the nursing period is protracted (4–24 months), weaning is gradual, lipid content of milk is low, and pup growth rates are slow. Phocid females usually fast and do not engage in foraging trips during lactation; lactation is short (4–60 d), weaning occurs abruptly, milk has a high lipid content, and growth rates of pups are rapid (Oftedal et al., 1987; Boyd, 1991; Trillmich, 1996). However, these strategies are not necessarily family-specific and the harbour seal, which is a phocid, engages in foraging during the final stages of lactation (Boness & Bowen, 1996).

The Mediterranean monk seal exhibits a maternal-care system that lies between the phocid and the otariid pattern, perhaps being closer to the latter. Lactation length is much longer than usual among phocids, including the harbour seal, and indeed lies at the lower end of the duration range for otariid nursing (Boyd, 1991). Moreover, lactating female Mediterranean monk seals alternate foraging trips with nursing and do not undergo substantial changes in body condition during lactation, as is the case for most other phocid females. Weaning is gradual and, when the pup reaches this stage, it has probably developed the foraging skills necessary to acquire the nutrients, a trait that is common in otariids but rare in phocids (Trillmich, 1996; Burns et al., 2004). All these observations contradict the conclusion of Boness & Bowen (1996) that a short lactation period is a phylogenetic characteristic of phocids and supports the proposal by Trillmich (1996) that differences in maternal strategies should be interpreted as adaptations to environmental conditions rather than attributed to phylogenetic inertia.

Mediterranean monk seals that inhabit the western Saharan coast live in a productive and stable environment where food supply, access to breeding sites, and climatic conditions are optimum for raising pups throughout the whole year (Gazo et al., 1999; Pastor & Aguilar; 2003). Such a stable ecosystem does not impose the limitations that force phocids inhabiting higher latitudes to adjust biological cycles to strict time budgets. The Hawaiian monk seal, the other remnant phocid species that inhabits tropical waters, also has a low degree of pupping seasonality and protracted lactation (5–6 weeks) as compared to most other phocids (Kenyon, 1981; Johanos et al., 1994), although it is not as long as in Mediterranean monk seals. In otariids, pup dependency periods increase with decreasing latitude. In phocids, this pattern is complicated by distinct maternal strategies associated with breeding substrates (i.e. pack ice, fast ice, or land), but it is likely that such a relationship remains valid (Oftedal et al., 1987). The western Saharan population is the most southern (21°N) of all Mediterranean monk seal populations and, together with the conspecific Hawaiian monk seal (15–20°N), it occupies the lowest latitudes of all phocids.

Phocids appear to have originated in warmer latitudes than those that they currently occupy and their original lactation patterns may have been devoid of the marked seasonality

that commonly governs the biological cycles of the extant species today (Perry et al., 1995). Most phocids later evolved while moving to higher latitudes. In these regions seasonal changes in environmental conditions are more marked, and this encouraged the acquisition or reinforcement of seasonality in reproductive cycles (Perry et al., 1995). The Mediterranean monk seal and the congeneric Hawaiian monk seal are the most primitive members of the Phocidae family (Repenning & Ray, 1977), and probably still present the ancestral mothering system and lactation pattern from which the other phocids evolved.

Our results show that the lactation and maternal behaviour of the Mediterranean monk seal markedly differ from what has been commonly accepted. This species has a unique reproductive biology among phocids, and this should be taken into account when designing management and conservation strategies for the surviving populations. In particular, the results show that the occurrence of a lone pup on a beach or inside a cave should not be taken as evidence of abandonment by the mother, as has been commonly assumed by pup rehabilitation programmes. Also, the fluid mothering behaviour suggests that, in the case of the mother's death or disappearance, if another lactating female is available in the area fostering may be a more effective and natural alternative than rehabilitation.

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