# Marine Mammal Science

# The mating system of the Mediterranean monk seal in the Western Sahara

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## ABSTRACT

The mating system of the Mediterranean monk seal was studied combining the use of diverse technologies. Sexual dimorphism in size was limited. Sexual activity was only observed to occur in the water. The different segments of the population segregated spatially: females, pups, and juveniles aggregated inside two main caves, whose entrances were controlled by a small number (2–3) of territorial males that defended aquatic territories situated at the very mouth of the caves. Other territorial males defended aquatic territories located further away (5–30 km). The tenure of aquatic territories was nonseasonal and spanned several

years. Relatedness among pups belonging to the same cohort was low or null, indicating a low level of polygyny, which is not surprising for an aquatically mating phocid with a protracted reproductive season. However, in addition, genetic relatedness showed a remarkable temporal periodicity. These results in combination point to the existence of a complex social structure in this species.

Based on behavioral observations, most pinnipeds were initially thought to have breeding systems based on strong polygyny, mating on land, showing marked sexual dimorphism, and having a short mating season with males competing for access to large aggregations of females (Bartholomew 1970). However, recent molecular studies have often revealed the presence of alternative mating strategies. Thus, while otariids and the northern and southern elephant seals (*Mirounga angustirostris* and *M. leonina*) all appear to be strongly polygynous, evidence of female choice has been found in the Antarctic fur seal, *Arctocephalus gazella* (Hoffman *et al.* 2007). Similarly, in the gray seal, behaviorally dominant males are not as successful as their behavior would suggest and females may show some level of mate fidelity (Amos *et al.* 1995). Elsewhere, many phocid seals breed on ice or have an aquatic mating system and exhibit reduced sexual dimorphism, suggesting much lower male reproductive skew (Boness *et al.* 2002, Ralls and Mesnick 2002). The reproductive system of the Mediterranean monk seal, *Monachus monachus*, is poorly characterized, although the information available suggests that at least some aspects of its reproduction may not fit the typical phocid pattern. This species has an unusually long lactation period (Aguilar *et al.* 2007), and as a consequence females perform regular foraging dives (Gazo and Aguilar 2005), weaning occurs gradually (Aguilar *et al.* 2007), and in the only extant colony surviving from the species and located at the Peninsula of Cap Blanc (Western Sahara), breeding females aggregate, forming large defensible groups (González *et al.* 1997). However, other traits match the typical phocid pattern; for example, mating has occurred underwater on the few occasions in which it has been witnessed (Sergeant *et al.* 1978, Marchessaux and Pergent-Martini 1991, Pastor and Aguilar 2003).

While the congeneric Hawaiian monk seal, *M. schauinslandi*, is not sexually dimorphic and seems to be a promiscuous species (Stirling 1983), coloration in the Mediterranean monk seal appears to be sexually dimorphic (Samaranch and González 2000) and reports of the mating strategy are contradictory. Some studies have suggested that the species is monogamous (Marchessaux 1989), while others have indicated that it is promiscuous (Riedman 1990), polygynous (Sergeant *et al.* 1978, Riedman 1990), or undetermined (Godwin 1990, Boness *et al.* 1993). This scarcity of information is due to the elusive and cave-dwelling habits of the species, and also to the existence, as mentioned above, of only one extant socially structured colony where mating strategies can be studied. Indeed, the Mediterranean monk seal is one of the most highly endangered species in the world, and no more than 400 individuals exist worldwide (Aguilar 1999, IUCN 2008). Most of the current population is fragmented into groups that are dispersed all over its geographical range, and with the exception of that at Cap Blanc, the sizes of these groups are so small that the colonial structure has been lost.

The present study was conducted at the Cap Blanc colony, which is composed of a few hundred seals that haul out inside large caves with open-air entrances, providing excellent opportunities for the observation and identification of individuals. In this paper we present information on the mating system of the Mediterranean monk seal in the Western Sahara for the first time. This information was obtained through the combined use of a number of different methodologies: photo-identification, length measurements, visual observation of behavior, video-camera recordings, monitoring of movements of individuals through theodolite and GPS recordings, and molecular analysis.

## METHODS

### Study Area

This study was conducted on the Mediterranean monk seal population that inhabits the Cap Blanc peninsula in the Western Sahara (21°02′N, 17°03′W; Fig. 1). The coastline stretching from Cap Barbas, in the north, to the Tip of Cap Blanc, in the south, consists of a succession of high cliffs interspersed with sandy beaches. The cliffs are constantly beaten by the swell and form deep caves that collapse periodically, thus producing frequent changes in the shape of the coast. González *et al.* (1997) provided a detailed description of the distribution of the seals along the peninsula and the pattern of occupation of caves. Seals occupied three different, distinct locations (see Fig. 1):

### Las Cuevecillas

This is a 3.2 km long area where seals of both sexes and all ages hauled out inside two breeding caves, numbered according to Marchessaux and Muller (1987): Cave 1 (21°02′72″N, 17°03′82″W) and Cave 3 (21°03′32″N, 17°03′82″W), located 1.1 km apart. Both caves contain beaches and are large enough to shelter several dozen individuals. In between there are two caves that are occupied sporadically by a small number of seals: Cave 2 (21°03′02″N, 17°03′88″W), a small cave that does not contain a beach and Cave 5 (21°02′83″N, 17°03′82″W), which contains a small beach. Thirty meters north of Cave 3 is Cave 7, which is also occupied occasionally by some seals.

### Zone 4-Tarf el Guerguerat

This is a 7.6 km long area beginning approximately 5 km to the north of the breeding caves and stretching from 21°05′78″N, 17°07′54″W to Tarf el Guerguerat (21°10′52″N, 17°03′04″W). This area consists of a series of high cliffs with a sandy beach of about 1 km (the Duna Blanca) and is occupied exclusively by territorial males. Some segments of this area, particularly Tarf el Guerguerat, do not contain caves. In contrast, in the area known as "Los Arcos," there are two spectacular natural archways and many large and deep caves. Access to Zone 4-Tarf el Guerguerat is limited due to the presence of land mines and by military restrictions applied to both land and sea.
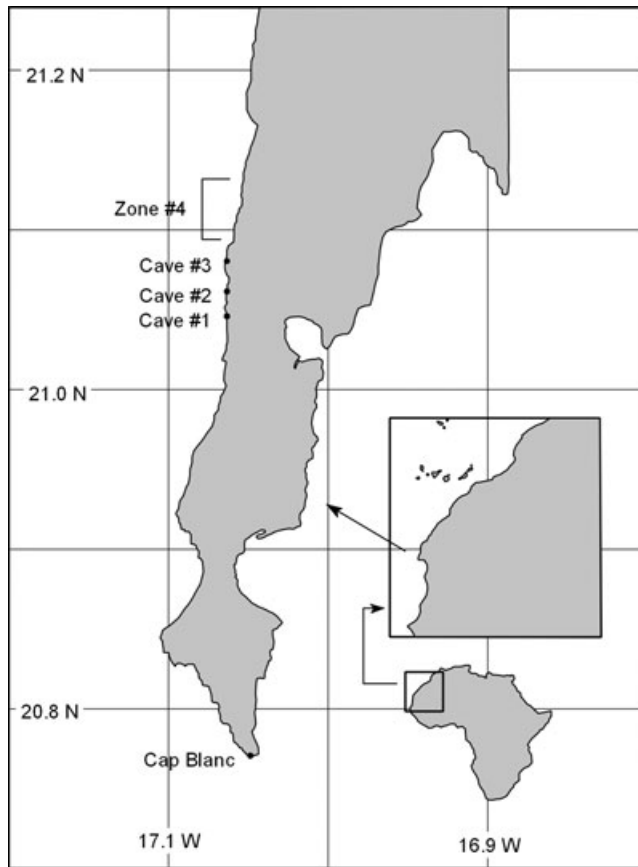
*Figure 1.* Distribution of seals and location of aquatic territories at the Peninsula of Cap Blanc. The bulk of the colony—females, pups, and males—aggregate inside two breeding caves (Caves 1 and 3), whose entrances are controlled by two (occasionally three) territorial males. The rest of territorial males defend aquatic territories at Zone 4-Tarf el Guerguerat (5 km north of the breeding caves) and at the Tip of Cap Blanc (30 km south).

*Tip of Cap Blanc*

This segment of the coastline is located 30 km south of the Las Cuevecillas area and is composed of a series of cliffs that conform to the southern end of the Cap Blanc peninsula. As in Zone 4-Tarf el Guerguerat, it is occupied only by territorial males. This area has been protected and belongs to the Réserve Satellite du Parc National du Banc d'Arguin, which also includes a fringe of 400 m of sea water around the cape.

*Surveys*

From May 1993 to December 1999, we conducted an annual series of surveys that included monitoring and periodic counts of individuals through photo-identification

and tagging. The observation effort and the timing and duration of these surveys varied between areas and years (see Pastor and Aguilar 2003 for further details).

During 1993 most of the effort was dedicated to establishing field facilities in the Las Cuevecillas area (where the breeding caves are located), developing field methods, and building a photo-identification catalog, while later work focused on the monitoring of individuals. We monitored seals swimming outside Caves 1 and 3 almost daily with the help of binoculars, and monitored those inside the caves using either a hanging platform lowered into the cave entrance or, after August 1995, by means of two remote-controlled cameras installed on the roofs of the caves (see Pastor and Aguilar 2003 for further details). We performed periodic counts of the number of seals inside and outside the breeding caves and classified individuals according to the morphological categories established by Samaranch and González (2000). We also carried out counts every 6 mo at the Tip of Cap Blanc to improve estimation of the total number of adult males. As access to Zone 4-Tarf el Guerguerat is limited by military restrictions both by land and by sea, we were only able to carry out eight expeditions in Zone 4-Tarf el Guerguerat during the whole study period, most of which lasted two consecutive days (Table 1). These surveys included observation with binoculars and photo-identification sessions.

*Individual Identification and Size Dimorphism*

We distinguished adult males by their size and morphology (black pelage, white ventral region, and a well-developed throat), and we identified individuals using markings and scars on their heads and backs (Forcada and Aguilar 2000) and by the unique shapes and spotting patterns of individuals in the ventral region (Samaranch and González 2000). Conversely, distinction of females and subadults was more difficult because these animals presented a gray pelage with no distinctive ventral pattern (Samaranch and González 2000); these individuals were identified using natural marking that were only apparent in adult seals, and using tagging studies.

We measured standard body length (Scheffer 1967) of 95 adults (39 males and 56 females) found dead ashore, mostly during an epizootic die-off in May–June 1997 (Hernández *et al.* 1998). The poor state of the carcasses precluded the identification of most corpses and the extraction of good quality DNA.

*Behavioral Analysis*

During 1994 and 1995, we observed seals inside the caves from the hanging platform lowered into the entrance of the two breeding caves. From August 1995 to 1999, this procedure was substituted with remotely controlled TV cameras installed on the roof of the caves. These allowed behavioral activities to be recorded using instantaneous scan sampling, focal animal sampling, and *ad libitum* observations (Altmann 1974). Instantaneous scan samplings of groups of seals at 60 min intervals were also recorded on VHS video tapes in periods of approximately 10 min over 15 d sparsely distributed from July to October 1995 (the total duration of recordings was 9 h). No observations could be carried out after dusk. We classified seals according to their morphology and recorded their behavior as being: (1) inactive (resting), (2) active (changing topographical location on the beach), (3) aggressive interaction, and (4) sexual interaction. Simultaneously, we carried out focal animal sampling of adult males for individual identification.

*Table 1.* Annual presence of identified males in aquatic territories. In the breeding caves and Tip of Cap Blanc areas, monitoring was regular, while in Zone 4 monitoring was reduced to sporadic expeditions. Territorial males that were detected sometimes resting inside the breeding caves are highlighted in bold. In June 1997 there was a die-off that eliminated a large number of males.

| Territorial males in the breeding caves | | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | Territorial males in the Zone 4 | 1994 | 1995 | 1996 | 1997 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cave 1 | 14 | | | | | | | 52 | | | | |
| | 53 | | | | | | | 202 | | | | |
| | 4 | | | | | | | 203 | | | | |
| | 214[a] | | | | | | | 207 | | | | |
| | | | | | | | | 213 | | | | |
| Cave 2 | 210 | | | | | | | 214[a] | | | | |
| | | | | | | | | 215 | | | | |
| | 36 | | | | | | | 217 | | | | |
| Cave 3 | 66[b] | | | | | | | 218 | | | | |
| | 261 | | | | | | | 220 | | | | |
| | 412 | | | | | | | 221 | | | | |
| | | | | | | | | 222 | | | | |
| | | | | | | | | 223 | | | | |

Territorial males at the Tip of Cap Blanc (30 km south of breeding caves)

| | | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **204** | | | | | | | | | 226 | |
| 205 | | | | | | | | | 228 | |
| **208** | | | | | | | | | 230 | |
| 209 | | | | | | | | | 233 | |
| 211[c] | | | | | | | | | 234 | |
| 212 | | | | | | | | | **235** | |
| 225 | | | | | | | | | 236 | |
| 246 | | | | | | | | | 237 | |
| 248 | | | | | | | | | **238** | |
| 252[d] | | | | | | | | | 239 | |
| | | | | | | | | | 247 | |
| | | | | | | | | | 253 | |
| | | | | | | | | | 254 | |
| | | | | | | | | | **255** | |
| | | | | | | | | | 257 | |
| | | | | | | | | | 258 | |

[a]Had a territory in Z4 in 1995 and a territory in Cave 1 in 1997.
[b]Established a territory from Cave 3 to Cave 7.
[c]First described in 1984 by Marchessaux 1989.
[d]Swam in a large territory.

The behavior of adult males in the water was observed *ad libitum* from the top of the cliffs and with binoculars. Activities were classified as: (1) resting (idle movement on the water), (2) patrolling (repetitive short dives within well-delimited borders), (3) aggressive interactions (puffs, dives persecuting an intruder, subaquatic fights), (4) foraging, and (5) sexual interactions (sexual harassment, mounting attempts,

sexual play). We defined sexual play when two seals were rolling nonaggressively over themselves and the male had an erect penis. The other seal could be either a female or another male (young or subadult).

### Aquatic Territories

We classified an adult male as "territorial" if it was observed to display territorial behavioral traits in the water, such as patrolling a delimited area or performing aggressive interactions with another seal in what would be its aquatic territory. We evaluated the fidelity of territorial males to their aquatic territories by comparing their geographical positions in different seasons across years. These were estimated from the top of the cliff located perpendicular to the aquatic territory using a GPS (Magellan GPS 300, San Dimas, CA). When possible, we characterized aquatic territories by recording exact positions of territorial males using theodolite tracking, a method that has been widely used to track the movements of vessels or cetaceans spotted from cliffs (Würsig et al. 1991, Bedjer and Dawson 2001). A theodolite provides both the vertical ($\alpha$) and horizontal ($\delta$) angles to a target, which, together with the altitude of the theodolite and the position of an horizontal reference point, permit the position of the target in coordinates to be determined accurately. We took measurements from two sites. In Cave 1, we set the theodolite on the top of the cliff overlooking one of the two cave entrances and determined the position of one territorial male; in the Cap Blanc area, we set the theodolite in a central location relative to the territories and determined the positions of three territorial males. Taking into account the height of the cliff (13.74 m in Cave 1 and 22.51 m in Cap Blanc) and that of the theodolite (1.46 m in Cave 1 and 1.51 m in Cap Blanc), we converted theodolite readings into UTM coordinates using Vincenty's (1975) formula and loaded these coordinates into Quantum GIS software to determine the surface area of the territory using minimum convex polygon analysis.

### Molecular Analysis

Preliminary behavioral observations suggested that the Mediterranean monk seal adopts a polygynous system in Cap Blanc, with a small number (2–3) of territorial males controlling the entrances of the two breeding caves. We estimated the level of polygyny through the proportion of half-siblings. Because pinniped females are limited to one pup per year, a high number of half-siblings would indicate that there are few males siring pups, and hence that polygyny effectively predominates. Alternatively, a low number of half-siblings would mean that the contribution to reproduction of a large number of males is high, and therefore that polygyny is relaxed or nonexistent. Paternity analyses were excluded for several reasons: active sampling of adults in the caves was completely discarded to avoid disturbances in such an endangered species, the samples obtained from carcasses during the die-off were in poor condition, and in most cases they corresponded to unidentified individuals.

For half-sibling analysis, we collected skin samples from 71 pups (50 from the rear flippers during tagging and 21 from carcasses found washed ashore during 1994–1999). This set of samples included at least two known female-pup pairs: females #403 and #408, born and sampled as pups in 1994, and their respective pups, #5138 and #5137, born and sampled in 1998. We initially preserved samples in 20% DMSO saturated with salt but once in the lab, the skin pieces were frozen

until analysis. When the exact age of the pup was unknown, we estimated its date of birth according to its morphology when sampled following Gazo *et al.* (1999) and Pastor and Aguilar (2003).

We genotyped pups for 13 single-locus microsatellite loci used in a previous study (Pastor *et al.* 2004) and known to be polymorphic and not X chromosome-linked. The presence of null alleles was tested both by the analysis of the two known mother–offspring pairs (#403-#5138 and #408-#5137) and by analysis of homozygote excess. In a previous study, neither differences in allele frequencies nor in genotypes were detected between pups born or found resting in the two caves (Pastor *et al.* 2004), so all samples were pooled together for the half-sibling analysis. Probabilities of identity (siblings and nonsiblings) were calculated using the software Cervus 3.0 (Marshall *et al.* 1998).

We calculated relatedness coefficients ($r$) among pups pairs using the Queller and Goodnight (1989) statistic ($r_{xy}$), which is an unbiased estimate of the true relatedness between individuals $x$ and $y$. The long-standing presence of territorial males in the breeding caves suggests that strong polygyny spanning several years may be present (Table 1). In order to test whether this is the case, we estimated the overall genetic relatedness between all pairs of pups from the whole sampling period and compared the obtained distribution with that expected if the pups were related as full-siblings ($r = 0.5$) or half-siblings ($r = 0.25$), or if pups were not related ($r = 0$). These distributions were generated by simulating the pups' allele frequency dataset using the relatedness calculation option and the simulation routine implemented in the Kinship v.1.2 software (Goodnight 1998).

Although males may appear to be territorial over several years, we also tested the possibility that individual males had most of their success during a year or less. For this, we calculated pairwise $r$-values among classes of pups established by years and months of birth using the Relatedness v. 5 software (Goodnight and Queller 1998). All pups had the same weight and errors were estimated by jack-knifing over all 13 unlinked loci. In addition, we analyzed temporal distribution of relatedness by examining potential associations between relatedness values and dates of birth. Finally, we implemented a simulation-based approach using the program GroupRelate (Valsecchi *et al.* 2002). Here, the average pairwise relatedness among pups within a year was compared with an equivalent value generated by replacing all genotypes with randomly selected alleles, preserving the same structure of the original dataset in terms of missing data.

<center>RESULTS</center>

*Individual Identification and Size Dimorphism*

We identified 51 adult males during the study period. Unfortunately, the 1997 die-off drastically reduced the number of seals in this portion of the population (Forcada *et al.* 1999). Standard length measurements showed that Mediterranean monk seal males ($n = 39$) are significantly ($t = 4.61$, df $= 93$, $P < 0.01$) longer (5%; $251 \pm 14$ cm *vs.* $238 \pm 13$ cm) than females ($n = 56$).

*Behavior*

Territorial males patrolled the boundaries of their territory by performing repetitive short dives over well-established borders. They were often seen foraging in their

territories. In general, they did not tolerate the presence of other adult males in their aquatic territory and showed aggressive behavior (puffs, dives seeking intruders, or subaquatic fights). Territorial males with territories away from the breeding caves were occasionally seen resting inside the breeding caves. To enter the caves, males crossed the aquatic territory of the male at the territory near the entrance to the cave by performing long dives directly into the cave, avoiding swimming at the surface. Inside the caves, all males were inactive 95% of the time, resting alone or in a group. No sexual activity was detected. When observed, although infrequent aggressive behavior was used to dispute a place to rest on the beach. Territorial males posted in the area near breeding caves regularly displayed sexual behavior (sexual play, mating attempts) in their aquatic territories. Conversely, we failed to observe sexual behavior in the territories away from the area near breeding caves. The only cases when we observed males with territories away from the breeding areas attempting sexual activity was when they were in the area near breeding caves area and the breeding cave territorial male was absent.

*Aquatic Territories*

The aquatic territories were unevenly distributed along the coast (Fig. 1); most territories were located at Zone 4-Tarf el Guerguerat and at the Tip of Cap Blanc, while the number of aquatic territories was limited near the breeding caves. One territory (occasionally two) was located at the entrance of Cave 1, another was located at the entrance of Cave 3, and for a short period another was located at the entrance of Cave 2, a cave that was only sporadically occupied by females (Table 1).

At the Tip of Cap Blanc, the total surface area of the territories of the three males (#204, #212, and #246) measured 1,123 m$^2$, 3,868 m$^2$, and 640 m$^2$, respectively (Fig. 2). Near Cave 1, the total surface area of territorial male #4's aquatic territory, which was located at the southern entrance of Cave 1, was 17,500 m$^2$, but this male remained within a subarea of 4,741 m$^2$ most of the time. Another territorial male (#53), whose aquatic territory could not be estimated, controlled the main access to the cave.

In general, site fidelity of a given male to a given aquatic territory was not affected by season and was long-lasting (Table 1). The average tenure was 1.5 yr (range 0–3.5 yr) in the area near breeding caves and 2.2 yr (range 0–13) at the Tip of Cap Blanc. In this latter location, we were able to recognize one individual (#211) that was first identified in 1984 from identification sketches (Marchessaux 1989), and that was still defending an aquatic territory from 1992 to 1997, that was in roughly the same location as its territory in 1984. This male was seen to haul out occasionally in an open sandy beach located at the coastal margin of his aquatic territory. In Zone 4-Tarf el Guerguerat, where observations were made infrequently due to the presence of land mines, males were located approximately in the same positions during the different surveys.

Despite the observed stability in the location of the territories, the presence of males in specific territories was not permanent. Thus, we detected territory-holding males from the Tip of Cap Blanc or from Zone 4-Tarf el Guerguerat that were occasionally resting inside the breeding caves. Indeed, the average daily number of resting males inside the caves was 5 ± 5.7 (range: 0–24), or 16% of the total number of seals. However, absences from territories were sporadic and males were generally
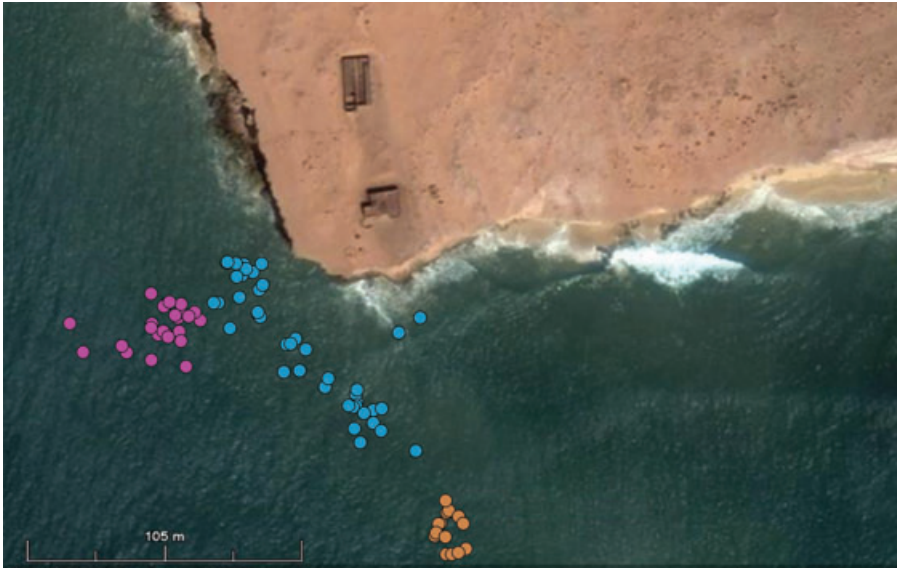
*Figure 2.* Theodolite positions of territorial males at the Tip of Cap Blanc. The total surface area of the territories of the three males (#204, #212, and #246) measured 1,123 m$^2$, 3,868 m$^2$, and 640 m$^2$, respectively.

present in their territories throughout the year with no apparent temporal variation in their numbers.

On two occasions, both of which occurred in Cave 1, we witnessed a territorial male being replaced by a new territorial male. In the first case, the replacement of the former territorial male (#14) was gradual. A month before the territorial male definitively disappeared, and while he was temporarily absent from the territory, a younger male (#52) occupied the territory displaying the usual behavioral traits of a territorial male: it examined the rocks surroundings the entrance of the cave, undertook mating attempts, and threatened seals that passed nearby by performing aggressive open-mouth displays. However, this newcomer did not succeed in keeping control of the territory and eventually moved to Zone 4-Tarf el Guerguerat, where it did establish an aquatic territory. Sometime after #14 disappeared, five other young males (#4, #53, #58, #66, #76), which had recently molted to the black adult pelage, appeared in the area. All of these males were observed attempting to mate in the territory. Finally, two of them (#4 and #53) managed to establish themselves as territorial and split the previous aquatic territory into two. Each male was positioned in front of one of the two available access points of the cave: male #53 controlled the main entrance and extended its territory to the north, while #4 controlled a lateral entrance and extended its territory to the south. At least two fights of 3–4 h duration were recorded between these two males. A year later, another of the unsuccessful males (#66), succeeded in establishing a territory, located further north, which extended from Cave 3 to Cave 7.

The second observed replacement took place after the 1997 die-off. Male #214, which formerly possessed a territory in Zone 4-Tarf el Guerguerat, moved to Cave 1 and became the territorial male there. However, in this case, instead of patrolling
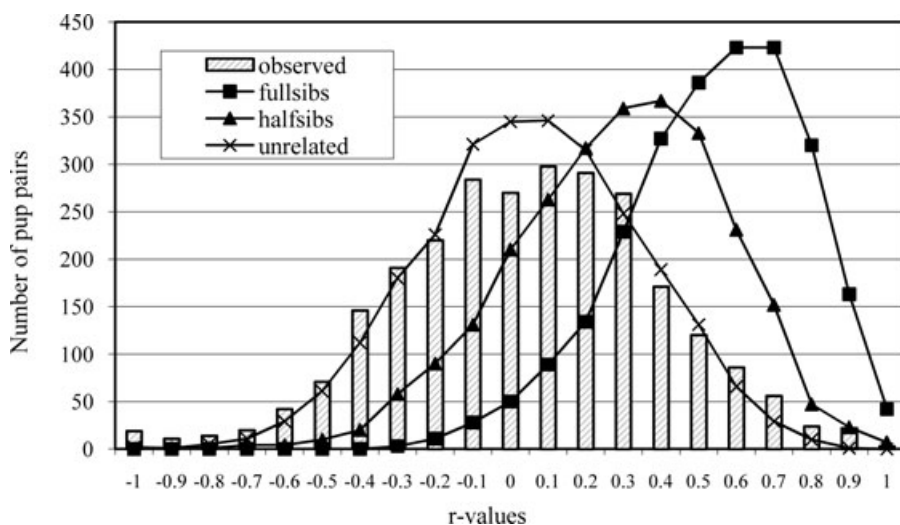
*Figure 3.* Distribution of relatedness values for all pairs of sampled pups born between 1994 and 1999. Simulated distributions for unrelated, half-sibling, and full-sibling relationships expected from the allelic frequencies.

a large aquatic territory, it only controlled the aquatic zone at the main entrance of the cave, as if the territory had been exceptionally reduced to only the cave hall. In this scenario, we observed several males entering the cave exclusively through the lateral southern entrance and not the main entrance controlled by this new territorial male.

*Molecular Analysis*

All pups could be distinguished from each other. The combined nonexclusion probability of identity was $2.83 \times 10^{-5}$ and the combined non-exclusion probability of sibling identity was $6.01 \times 10^{-3}$. As expected, the two female-offspring pairs produced *r*-values of 0.54 and 0.65, respectively, values that do not differ from the expected value of 0.5, indicating that they reflect the true relationship between pairs of individuals reasonably well. The proportion of sampled pups relative to born pups was 63%, indicating that a sample bias might exist. However, for a consecutive 3 mo period (June–August 1995), we were able to sample all pups born and the *r*-value average was still zero (Table 2).

The overall genetic relatedness for the 2,485 pairwise combinations of pups was 0.0615 (SD = 0.0183), and values matched a distribution consistent with unre-latedness (Fig. 3). *R*-values were zero for pups born during 1994 ($r = -0.0004$, $n = 9$), 1995 ($r = 0.0033$, $n = 22$), 1996 ($r = -0.0498$, $n = 11$) and 1999 ($r = -0.0709$, $n = 7$), indicating unrelatedness, and was positive for those born during 1997 ($r = 0.3765$, $n = 8$), 1998 ($r = 0.1237$, $n = 11$). When analyzed using the program GroupRelate, a similar pattern was found, with the year 1997 show-ing significantly higher mean relatedness than expected if all pups were unrelated ($P = 0.007$, significance obtained from 10,000 randomizations). Because the num-ber of pairwise comparisons rises with the square of the number of pups, the higher

*Table 2.* Relatedness (*r*) values for pairs of pups by year- and month-classes *n* is the number of pups. *r* values among the 5 most related pups are also indicated

| Year | Group | Pups % analyzed/born | *r* | *n* (*n* >2) | Std. Error: |
|------|-------|----------------------|-----|--------------|-------------|
| 1994 | May | - | 0.0304 | 4 | 0.1182 |
|      | June | - | −0.1948 | 2 | 0.3318 |
|      | Whole year | | *−0.0004* | *9* | *0.1034* |
|      | 5 most related | | 0.6034; 0.5510; 0.4998; 0.4666; 0.4350 | | |
| 1995 | April | 100 | 0.2298 | 3 | 0.1836 |
|      | June | 100 | −0.0204 | 4 | 0.1354 |
|      | July | 100 | 0.0909 | 5 | 0.1167 |
|      | August | 100 | −0.2672 | 4 | 0.0793 |
|      | September | 40 | 0.1782 | 2 | 0.3565 |
|      | October | 17 | 0.0415 | 2 | 0.2567 |
|      | Whole year | | *0.0033* | *22* | *0.0474* |
|      | 5 most related | | 0.9280; 0.8628; 0.8248; 0.7663; 0.6922 | | |
| 1996 | April | 33 | −0.4052 | *2* | 0.3481 |
|      | June | 33 | −0.2387 | *2* | 0.3285 |
|      | September | 40 | −0.535 | *2* | 0.3671 |
|      | November | 29 | 0.0665 | *2* | 0.4409 |
|      | Whole year | | *−0.0498* | *11* | *0.1004* |
|      | 5 most related | | 0.5812; 0.5375; 0.4955; 0.4526; 0.3684 | | |
| 1997 | April | - | 0.0372 | 3 | 0.2321 |
|      | Whole year | | *0.3765* | *8* | *0.1231* |
|      | 5 most related | | 0.8942; 0.8642; 0.8465; 0.7062; 0.7034 | | |
| 1998 | September | 75 | 0.1877 | 3 | 0.1854 |
|      | October | 57 | 0.1961 | 5 | 0.106 |
|      | Whole year | | *0.1237* | *11* | *0.1202* |
|      | 5 most related | | 0.8119; 0.7642; 0.6439; 0.6377; 0.6170 | | |
| 1999 | July | 100 | 0.5735 | *2* | 0.2261 |
|      | September | 100 | −0.3213 | *2* | 0.4786 |
|      | October | 18 | −0.2439 | *2* | 0.2275 |
|      | Whole year | | *0.0709* | *7* | *0.1161* |
|      | 5 most related | | 0.5466; 0.5449; 0.4280; 0.3762; 0.2713 | | |
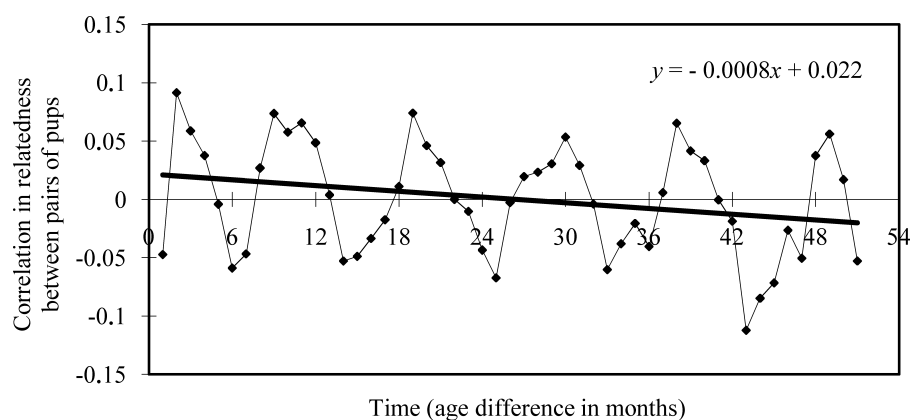
*Figure 4.* Correlation between *r*-values between pairs of pups and age difference (in months).

*r*-values generated by any given proportion of half-siblings will be increasingly di-luted as sample size increases. For example, if a sample is made up entirely of pairs of otherwise unrelated siblings, five pairs will contribute five high *r*-values among 45 comparisons (11%) while 50 pairs will contribute 50 high values among 4,950 comparisons (1%). Mean *r* should therefore be more effective at detecting shared paternity in smaller samples. In an attempt to circumvent this bias, we modified the GroupRelate program to focus only on the top five relatedness values found, asking whether the average of the five highest values in the actual dataset was significantly higher than in an equivalent data set comprising randomized, unrelated genotypes. Our results were essentially the same as we obtained using the other approaches, again revealing significance in 1997, but not in other years (data not shown).

To explore possible temporal patterns of relatedness we plotted average pairwise relatedness against the temporal difference in birth dates (Fig. 4). We found a rather striking periodicity, with "peaks" and "valleys" of relatedness. The immediate expectation would be that the cycle should be annual, driven by the same females breeding at similar times of year. However, the total profile covers just over 4 yr, while there are almost six complete cycles.

<div align="center">

DISCUSSION

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Our findings modify, complete, or challenge currently accepted knowledge of the mating strategy of the Mediterranean monk seal. On average, adult males of Mediterranean monk seals were found to be only 5% longer than females as opposed to other phocid species, like the northern and southern elephant seals, in which males can be 3–10 times larger than females (Haley *et al.* 1994). This can be explained by the fact that the Mediterranean monk seal appears to mate exclusively inside the water unlike these species, which mate on land. Continuous monitoring showed that no sexual activity occurred inside the caves. Instead, we recorded frequent sexually related behavior in the aquatic territories located at the entrances of their caves. Dimorphism in aquatically mating seals is usually small, and may even be reversed, because a smaller size favors agility in water (Riedman 1990) or because males have

the opportunity to forage during the mating season and therefore do not need to accumulate large fat reserves as terrestrial breeders do (Harcourt *et al.* 2007*a*).

The aquatic territories were not continuous along the coastline. A small number of males (two, occasionally three) defended aquatic territories surrounding the entrance to the breeding caves while a larger number of males defended aquatic territories located along cliffs situated approximately 5 km north (Zone 4-Tarf el Guerguerat) or approximately 30 km south of these caves (Cap Blanc), which were therefore situated far away from the caves used by females. Interestingly, Cebrian (1998) also described the presence of males defending aquatic territories in areas not suitable for pupping (*i.e.*, islets without caves or small islands with no suitable caves for reproduction) in the eastern Mediterranean population (Zakintos and the Cyclades areas). Similarly, male harbor seals in Scotland also appear to defend aquatic territories at three different places: in the water around haul-out sites, on foraging grounds up to 50 km from pupping sites, and on transit routes between these two areas (Van Parijs *et al.* 1997).

Territories were often adjacent to one another and their boundaries seemed to be marked by external topographic elements such as rocks or coastal prominences, or by underwater cues. The latter was apparently confirmed by the fact that males periodically performed repetitive short dives along the boundaries. The size of the four estimated aquatic territories was heterogeneous and ranged from 640 to 17,500 m$^2$, with the territory located in front of the breeding cave area being over four times larger than the largest territory at Cap Blanc. Moreover, territories changed in size when the proprietor changed: the territory at the breeding Cave 1 was reduced to approximately half its size when ownership shifted from male #14 to male #4. All of these territory sizes are of the same order of magnitude as those described by Hayes *et al.* (2004) for Pacific harbor seals.

The tenure of the aquatic territories was nonseasonal, which is consistent with the fact that pupping (and hence mating) occurs throughout the whole year (Pastor and Aguilar 2003). In the breeding caves, the average tenure was 1.5 yr (range 0–3.5 yr) and at the Tip of Cap Blanc 2.2 yr (range 0–13 yr). Indeed, in at least one case, tenure lasted for 13 yr, the longest tenure described for an aquatic-mating male. Such a long tenure is possible for several reasons: occupancy of the territory by males is not a full-time endeavor, and males neither fast nor need to undertake distant migrations to feed because the colony is located in one of the world's most productive areas, with a semipermanent upwelling that ensures high productivity all year round (Ansa-Emmim 1982). Thus, behavioral observations and a time-depth recorder (TDR) deployed on an adult male for 51 d (from 18 June to 7 August 1996), showed that, indeed, Mediterranean monk seal males not only forage while they defend their coastal aquatic territories, but they also forage during daily trips that they undertake offshore (Gazo 1997).

The limited size of the territories and the fact that foraging also occurs offshore seem to indicate that the function of the territories is mostly reproductive, as appears to be the case in other aquatic-mating phocids (Coltman *et al.* 1997, Hayes *et al.* 2004, Harcourt *et al.* 2007*a*). Females have to pass through the territories located at the entrances to the breeding caves when they enter the cave for breeding, nursing pups, or resting, and the territorial male of this area can thus intercept and mate with females in this location. Apparently confirming this, all the cases of sexual harassment that we recorded took place in this area. However, we observed very few copulations, suggesting that mating either predominantly occurs at night or that mating also takes place elsewhere and is therefore likely to involve territorial males away from the breeding area as well. The latter option is supported by the

genetic relatedness analysis, which shows that although some few pups may be paternally related, most of them born within a season are not. Indeed, the overall genetic relatedness for all pairwise combinations of pups born during the period 1994–1999 was zero, though this is likely due to the way in which, in large data sets, modest numbers of true related pairs contribute a tiny minority of all possible pairwise relatedness values. As a consequence, a strong polygyny spanning several years is not likely, even if a territorial male may hold a territory in the breeding cave area for up to 3.5 yr. Nonetheless, evidence of shared paternity was obtained for 1997 and, to a lesser extent, in 1998. However, these may be viewed as unusual. In 1997 only a few pups could be sampled due to a die-off that killed two-thirds of the population just before the pupping peak (Forcada *et al.* 1999), while those born in 1998 were conceived in 1997, when there were fewer males left to mate. Thus, while our analysis appears to rule out strong polygyny, it seems that some skew in male success is possible, though whether this is the norm and mean relatedness lacks the power to detect it in most years, or is due mainly to exceptional circumstances remains to be determined. Likewise, the relatedness analysis cannot discern whether the shared paternities corresponded to the territorial males in the area near breeding caves or to any other territorial male.

Thus, the role played by the distantly located aquatic territories defended by the other territorial males is unclear. One possibility is that these territories are located along the route to areas used by females to forage, and thus might be convenient places to intercept females, as it has shown to occur in harbor seals (Van Parijs *et al.* 1997). In combination with or independent of this hypothesis, these distant territories may also serve as *leks*, a mating arena in which males would perform their displays to attract females visiting the area. Indeed, a lek-type mating behavior has been suggested to occur in the two subspecies of harbor seals (Hayes *et al.* 2004, Boness *et al.* 2006) and in the Pacific walrus *(O. rosmarus divergens)* that breeds in the pack ice (Riedman 1990). Our results are not decisive in this respect: the genetic data would not contradict a lek-type mating strategy, but our field observations, although limited in these segments of the coastline and restricted to day-light hours, never indicated that females were visiting the distant territories. However, visits may indeed occur at night; a TDR deployed on a lactating female showed that by the end of lactation, night time dives increased in frequency (Gazo and Aguilar 2005).

An alternative explanation for the function of these distant territories is that they serve as a spot where territorial males measure their ability to establish the hierarchical ranks that would create a male-dominated system. Such a system, in which males fight for status, has been described in the closely related northern and southern elephant seals (Hoelzel *et al.* 1999) and in gray seals (Anderson and Fedak 1985). In our study, during an episode of replacement of the territorial male in the breeding cave area involving several candidates, we observed that, after the new male was established, one of the losers established an aquatic territory in the distant Zone 4-Tarf el Guerguerat area. We also observed the opposite process; a male initially occupying a territory in the distant Zone 4-Tarf el Guerguerat area eventually became territorial at Cave 1 after the die-off eliminated the male originally holding that post. Some degree of fluidity and a connection between territories situated in different locations is therefore apparent.

There is, however, a third potential explanation that cannot be discarded: the current population of Mediterranean monk seals at Cap Blanc is known to be only a fraction of the population that occupied the area in the past, and thus the distribution of the territories observed today may simply be reminiscent of an original breeding

structure established when the number of seals was larger. In this sense, the mating behavior observed in the species today may change as the population increases. In a hypothetical scenario, the whole coastline along the Cap Blanc peninsula in the past would have held a continuum of breeding areas, including open beaches, and associated aquatic territories, of which only the aquatic territories in cliff areas remain today. The aquatic territories that now are far from the breeding area would formerly have been adjacent to it. In this context, it is worth noting that there is some indication that today some small breeding caves may be located to the north of Zone 4-Tarf el Guerguerat (González *et al.* 1997). This appears to be supported by questionnaires circulated among local fishermen and Moroccan military personnel, which confirmed seal sightings along this segment of coastline. However, even if this was true, the number of seals concerned would be very low because a recent at-sea survey failed to observe any seals in the area (Fernández de Larrinoa *et al.* 2007). According to this hypothesis, the original mating system at Cap Blanc would resemble that described for the current population in the Cilician Basin, in the eastern Mediterranean, where the social structure shows habitat partitioning in subregions and further subgrouping among the monk seals of a subregion; there appear to be one or more reproductive females selectively using the same caves within the range of control of a single adult male (Guçu *et al.* 2003).

Whatever the case, the low levels of relatedness among cohort pups found in this study indicate that the level of polygyny currently operating in the colony of Cap Blanc is low. Even if Mediterranean monk seal females in the Cap Blanc colony cluster spatially in two single breeding caves forming defensible groups, mating is exclusively aquatic and the mating season is extremely protracted (Pastor and Aguilar 2003). These are severe handicaps for controlling females. Furthermore, 10 d after parturition, females start performing daily feeding trips offshore (Aguilar *et al.* 2007) so they may disperse when coming into estrus (Pastor and Aguilar 2003). Hence, the low level of polygyny observed at Cap Blanc is not surprising and is comparable to that obtained for the other aquatically mating species studied: the two harbor seals subspecies (Coltman *et al.* 1998, Hayes *et al.* 2006) and the Weddell seal (Harcourt *et al.* 2007*b*).

Finally, relatedness between pups exhibits a remarkable periodicity, oscillating from 9 to 12 mo. Such a pattern seems most likely to be driven by shared maternity rather than shared paternity. Several phenomena could explain this stratification of relatedness. Firstly, females that lactate their pups for approximately 2 mo tend to give birth around the same period across years (Pastor and Aguilar 2003). Thus, we might expect pups born around 12 mo, and multiples of 12 apart, to have a much increased chance of shared maternity and hence higher mean relatedness compared with pups born with other temporal separations that are unlikely to share either parent. Secondly, reproductive cycles are not strictly annual, *i.e.*, they do not last invariably 365 d. Their duration depends on the duration of the lactation (Pastor and Aguilar 2003). Each time a female loses her newborn pup, she reduces her annual cycle up to 15 d; therefore a female that loses her pup three consecutive years will present subannual cycles. Mortality of newborns is very high in the area, in the order of 60%, depending on the season (Gazo *et al.* 2000). Consequently, females that tend to birth earlier each year appear to be common in this colony. A further phenomenon that would also contribute to this stratification of relatedness is that there seems to be a 6 mo shift between the observed month of birth of a female and the month when it would subsequently deliver its offsprings (Badosa *et al.* 2006).

In conclusion, at present the colony would organize according to a relatively relaxed polygynic structure, with some internal stratification in relatedness.

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