

Everything you wanted to know about Northern Elephant Seals reproduction but refused to ask.

Heat or Estrus Period

It is not clear how males detect estrus in females. It doesn't appear that scent is involved. For research purposes, and since there are no visible signs, scientists define estrus as the time between the first and last mating of the season. Depending on the female this is usually the last week of nursing^{1,2,3}, and more than one male may be involved⁴. Note that mating means actual copulation, not attempted matings that may occur at any time the female is on the beach².

Breeding

Typically females are sexually mature at 2 years of age; the most common age for a first birth is four.⁵

Males do not court or investigate the perineal area of the female prior to mounting; they seem to be testing the receptivity of the female. They mount from one side without any preliminaries and seemingly attempt to overpower the female. Males use the great bulk and weight of their forequarters, a fore-flipper clasp, and a neck bite to restrain the animal. They mount pregnant females, those giving birth, females soon after birth, and females in estrus. Only the frequency not the form of these mating attempts varies with estrus. A mount may end in copulation; by the mounter being repulsed by an alpha; or simply because the male ceases the attempt.⁴

Females respond to male mounts by active protest or passive acceptance. A female protests by issuing a virtually continuous train of vocal threats and by whipping her hindquarters vigorously from side to side. Because of their relative positions her rear flippers often strike near the males penile opening. She may also flip sand directly at the males head and face, nip his neck, or struggle to get away. Alternatively the female may remain passive throughout the mount or may facilitate by spreading her hind flippers. Females were not observed to court or solicit copulation.⁴

Estrus as well as non-estrus females protest the majority of mounts attempted by males. In one study of almost 1500 mounts: 79% were protested for the entire duration of the episode, 14% were partially protested and 7% were not protested. All mounts directed to marked non-estrus females were totally protested. Of the mounts to marked females known to be in estrus 63% totally protested, 24% partially protested and 13% did not protest. Thus protesting throughout the duration of a mount is not necessarily a sign of non-estrus while no protest or partial protest is a reliable indication of estrus⁴

Early estrus females protest all mounts. As estrus proceeds protesting is reduced. No-protest is the most common response on the last day of estrus. Females tend to stop protesting toward the end of a mount of long duration. Males mounting estrus females are more likely to be driven off by nearby males when the female protests. Young, small, and low ranking males are interrupted most frequently and most quickly. Duration of mounts protested by females is also a function of a male's age and social rank. Young low ranking males were interrupted more quickly and even when they were not moved by a dominant male they did not persist as long in their copulatory attempts as higher-ranking males—this because they were nervous about being attacked⁴

Even when mounts are not interrupted by dominant males, estrus females are more apt to protest totally if the encounter is with an immature male. Also, young males were least likely to encounter estrus females that did not protest. One explanation is that young males were unable to obtain access to non-protesting females, usually females in the process of departing from the rookery. These females attracted a great deal of attention, and the most mature, high-ranking males on the periphery of the harem kept all of the younger subordinate males away from them.⁴

Young males were prevented from entering the harem, chased out of the harem, or were interfered with in their attempts to mate. Even if they eluded the males, the females made it difficult for them to copulate.⁴

It is possible that a female distinguished a high-ranking male from others by the duration and vigor of the mounts and simply stopped protesting when mounted by the former. Females that protest mounts at the beginning of estrus increase the probability that their first copulation will be with the highest ranking male because it alerts nearby males who threaten the subordinate mounter and prevent copulation (female incitation of male competition).⁴

The probability of a female mating with a high-ranking male depends in part on the number of females in the harem. As the number of females in the harem increased, more males copulated, including young, low ranking, and previously non-breeding males. The latter were more successful when males dominant to them were fighting, mating, or sleeping. From the female point of view, an increasing harem size means that the odds of mating with a mature, high-ranking male decrease⁴

Because there is a limit to how many females an alpha male can inseminate (overwork) it would be advantageous for a female to mate early. Thus we might expect females to compete among themselves to arrive early in the breeding season to secure a position near the alpha male and of course to protest all mounts vigorously up to the point of copulation. We know females that arrive early form the center of the harem and are more likely to copulate with the alpha than females on the periphery. Centrally located females are aggressive to females on the edge and keep them from entering the harem.⁴

Polygyny in this species is extreme; studies done during the 1968 through 1973 breeding seasons indicated the 5 most active males were responsible for about half and in some case up to 90% of the copulations observed with up to 470 females.^{3,6}

Data collected over 20 years and 19,000 births shows the odds are about 1 in a thousand of a female dying as a result of mating with a male.⁹

Pregnancy and Reproduction

The sex ratio of pups at birth is 50% male, 50% female²

Typically about 95% of the adult females will give birth each year⁷, with mid-age animals being the most productive.⁵ This number is reduced during years of high environmental stress (El Niño), when it may be more difficult to find food, and thus more difficult to bring a fetus to term.^{5,8} Females that successfully wean a pup tend to return to the same place to give birth. Those that are unsuccessful more readily move to a new site.⁷

Non-pregnant females

The familiar series of events: pregnant female arrives, gives birth, nurses, and mates for next year has one problem. How does a female become pregnant the first time? How does an adult female who aborted a fetus become pregnant again?

Virgin females are sometimes seen on the beach after the males begin to arrive in late November. In addition, these females are seen on the beach in winter for a few days, and have been seen to mate with subordinate males. Furthermore, sub-adult males are on the beach during the breeding season and much of the juvenile molt, and have the potential to mate with juvenile females. However, according to observations made by Burney Le Boeuf and others, the number of matings seen is not large enough to account for all the juvenile females that become pregnant in any given year. He theorizes that most females mate for the first time at sea.^{10, 11, 12}

Mature Females

Mature, non-pregnant females that hauled out during the breeding season usually were on land for 1 or 2 days, some as little as a few hours. Most of them mated with subordinate males, sometimes in the water. A few mature, non-pregnant females remained on land 10-12 days during the breeding season and gave birth the following breeding season.⁵

Typical birth

Each year, births occur over a 6-8 week period extending from late Dec to about the 10th of February. The female gives birth on average 6 or 7 days after arrival on the rookery. The peak period for births was the last 2 weeks of January during which approximately 50% of the pups were born.

A four-year study at Ano Nuevo of over 1000 births found that only 8% occurred during the day. Of the day births, 9:00 to 10:00 a.m. and 4:00 to 5:00 p.m. were the peak times.

The pregnant female becomes somewhat restive during early stages of labor shifting her weight from her belly to one side or the other. In the final phase the female lays on her belly and elevates her perineum 1-2 ft above the ground and swings it slowly from side to side. At the same time her fore flippers may be extended and her head and neck raised; her posture giving a u shaped appearance. This posture is usually assumed during contractions from the time the fetus is visible to the moment of expulsion and is a reliable signal that parturition is imminent. Females move very little during this period, although a few will circle as the fetus is being expelled. The laboring female may look straight ahead and may close her eyes from time to time. The female may emit a low vocalization similar to low intensity encounters with other females. The amount of blubber makes it difficult to monitor contractions. Defecation may occur just prior to the appearance of the fetus, which is first surrounded by amniotic membranes. These usually rupture by the time the head or rear flippers are visible. The female usually turns immediately to face her pup, which breaks the umbilical cord. As she turns she usually begins emitting a warbling sound in the pup's direction and touches its body with her nose. She does not lick or clean the newborn. The newborn usually responds to the mother's warble with a vocalization of its own. All pups make this sound within an hour

after birth and some vocalize almost immediately. The placenta is delivered with the pup or within an hour after birth.

The arrival of the newborn increases female aggression in the vicinity. Nearby females may approach the pup, sniff it, bite it, threaten, or in a few cases move the mother away and take the pup as their own.

About 60% of births were head first and 40% rear flipper first. The time for delivery for head or rear flipper presentation ranged from 1 to 30 minutes with an average of about 7 minutes. The percentage of rear end first presentations is a lot higher than land mammals but doesn't cause any problems because of the lack of pelvic bones in the birth canal, which in breech presentations cause major problems in land mammals. The weight of the placenta (about 10 lbs.) is consistent with other mammals of the same size. Complications with the delivery of the placenta are rare.

In the 4 years studied, only 4 stillbirths were observed. Premature pups of this species have never been observed at Ano Nuevo.²

Nursing Period

Weaning success is positively correlated with increasing age and size of mothers. About three-fourths of females (6yrs or older) nurse their own pups exclusively until weaning^{2,17}, however some females lose their pups and adopt orphan pups and raise them as their own. In the crowded main breeding harem at Ano Nuevo a quarter to more than half of the pups – depending on the year - were separated from their mothers over the 1977-1980 period. In a follow-up study of separated pups at Ano Nuevo: 5% reunited with their mother, 27% were adopted by foster mothers and 68% remained orphaned and died. Factors causing mother/pup separations and mortality were: female density, males moving through the harem, wandering pups, female aggression and inclement weather. Most reunions were effected by the mother¹³ If they don't reunite, starvation is the most likely outcome.¹⁶ Nearly all pup deaths occur within 2 weeks after birth.¹⁵ Pup necropsy results often show internal injuries caused by male trampling, and skull fractures that may be caused by female bites.²

Young females (3-5 years of age) have lower weaning success because: 1. They lack mothering experience and make mistakes such as confusing the newborn with a neighbor's pup, 2. Older, larger females may cause them to be separated from their pup and make re-unification difficult, 3. They are shunted to the periphery of harems where they are exposed to aggressive male attempts to mate while nursing, as well as high surf conditions and high tides, 4. They produce less milk energy and their pups weigh less at birth and at weaning.⁷ Following the loss of a pup these females usually attempt to foster an orphan the same age as the pup that was lost. Adoption of a single pup was most common but pupless females would attempt to steal suckling pups, adopt a weaned pup, adopt multiple pups or indiscriminately nurse any pup that approached. Superweaners are suckled by 2 mothers or are adopted by a pupless female after being weaned by their mother.¹²

Pups and nursing

Males weigh more than females both at birth and weaning. Males are nursed an average of a day longer. Males are more persistent and more successful at stealing milk than females. Permanent canine teeth erupt before weaning in females and 4 weeks after

weaning in males.¹⁴ This may facilitate milk stealing in males, and account in part for the slightly longer nursing period.

Pups do not suckle continuously during a suckling bout. The daily pattern is quite variable in the same individual and across individuals. For example, some pups suckled several times in one day and others did not suckle at all. 60% of the marked pups suckled their mother until they were weaned but only 22% exclusively. 80% of the pups suckled an alien female occasionally. Separated pups were more apt to survive if fostered exclusively by one alien female.²

The female allows the pup to sleep next to her and she responds to its suckling attempts by assuming the nursing position unless she is already in it. She never solicits suckling directly. Mother and pup do not move much around the harem. Close association begins at birth between mother and pup and is well formed by the end of the pup's first week. However, if the mother is separated from her offspring for several days during this period she may reject attempts to suckle when the pair are reunited. Except for cases like the above, no marked mother was ever seen biting or behaving aggressively toward her pup.²

A subtle cue that weaning is imminent is that pups may attempt to nurse more frequently because mom is drying up. Securing additional milk after weaning gives an individual an advantage because it prolongs the growth period while others are fasting and losing weight daily. Pups may lose 25% of their body weight between weaning and their departure from the rookery.¹⁴

Vocalizations

Pups have one type of vocalization, which is a shrill, cry repeated several times at intervals of 1 sec. Females have 2 distinct vocalizations. One is an attraction call to the pup, a high pitched warbling sound when the newborn cries. Sometimes she moves toward the pup while warbling, although she usually waits for the pup to come to her. The second is used when the pup is threatened. This sound is a loud prolonged low frequency, rasping noise with the mouth held wide open. The open mouth threat usually precedes a bite.²

Weaner mortality

Sources of injury leading to weaner mortality were observed at Ano Nuevo rookery. These included: 1. Head wounds when being sexually accosted by subadult and adult males; 2. Bites on head inflicted by adult females; 3. Falling down cliffs or getting stuck between holes in rocks; 4. Storms with attendant high surf caused injuries and deaths by drowning or by dashing weaners on the rocks; 5. Predators, such as great whites sharks and killer whales, killed some weaned pups before they departed the Ano Nuevo rookery.¹⁴

Up to 50% of the weaned elephant seal pups in the rookery at Ano Nuevo at the end of the breeding season showed evidence of being mounted by males. Most male inflicted injuries on weanlings were superficial. Although deep gashes and punctures that bled and exposed blubber were seen.¹⁵

Female departure

Females near the end of estrus rarely protest mounts and readily accept copulation with peripheral males. During the last hour on land females were extremely receptive to all males.

Seventeen of 20 females copulated on the waters edge as they were leaving the rookery. Most females copulated with the highest-ranking adult male present among the 10-12 males on the periphery of the harem. This change in behavior we interpret as a female's means of insuring fertilization. Another interpretation is that receptive females receive fewer blows capable of inflicting injury than non-receptive females. This may then be a behavior in the context of gaining safe passage.⁹

On the day of weaning the female moves toward the periphery of harem; this may take several hours if she is moving past females dominant to her and if she is near the center of the harem. Her pup may or may not follow her. She may start her move while the pup is sleeping and she doesn't seem to mind if the pup follows or not. This is the end of the filial relationship. While it may happen that a female returns to molt before her pup has left the rookery, mothers and weaners do not seem to reunite.¹⁴

Typically, the time from birth to departure is 28 days, +/- 4 days.

Delayed Implantation

Many pinnipeds have delayed implantation, which assures a yearly reproductive routine no matter what the gestation period is. What this means for NES is that no matter when the females mate (early or late in the season) the fertilized egg (embryo) does not implant and begin growth until about 7 ½ months before a January delivery. The embryo is maintained in a state of dormancy while unattached to the uterine wall. While much of the molecular regulation involved in activating dormant embryos is known, the mechanism that keeps the embryo in suspension is not clear, though it might be mediated through the hormones estrogen and progesterone. The NES exhibits seasonal implantation (as opposed to implantation associated with lactation), which is a mechanism that allows pinnipeds to time the birth of their offspring to favorable environmental conditions.

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