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## Northern Elephant Seal

*Mirounga angustirostris* Gill, 1866

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### *Genus and Species*

The Northern elephant seal, *Mirounga angustirostris*, is one continuous species throughout its range with no subspecies or races currently recognized. Bonnell and Selander (1974) surveyed five breeding colonies electrophoretically and found no polymorphisms among 21 proteins encoded by 24 loci. It was originally described by Gill (1866). A more recent discussion of the taxonomy is found in Scheffer (1958). The northern elephant seal is the largest pinniped in the northern hemisphere and second only in size to the southern elephant seal, *Mirounga leonina*. There are the only two species in the genus *Mirounga*.

### *External Characteristics and Morphology*

At birth northern elephant seal pups weigh from 30-34 kg and have a mean nose-to-tail length of 127 cm. The pup's weight increases to a

mean of 158 kg at weaning (LeBoeuf *et al.*, 1972). They are born with a moderately thick, black pelage and essentially no subcutaneous fat (Fig. 1). After the one-month nursing period they undergo a moult in which the black fur is replaced with a silvery hair coat (Fig. 2). By this time they have also acquired a thick subcutaneous fat layer which functions as body insulation throughout life.

Adult cows (Fig. 4) rarely exceed 900 kg and are about 3 m in length. They exhibit the standard phocid body form with only a slight elongation in the nasal region. Adult bulls reach a maximum size of about 2700 kg and 6 m total length (Scheffer, 1958). In addition to its massive size, the male northern elephant seal develops a greatly enlarged and elongated nasal chamber which, as the species name suggests, is elephantine (Fig. 3). They also develop at maturity, a pink and grey mottled cornified skin layer on the ventral neck and chest regions. Both sexes have a light brown hair coat with little shading. Both the hair and the surface epidermal layer is replaced in an annual moult. Even though the hair coat has essentially no insulative value compared to the thick subcutaneous fat layer (McGinnis, 1973),



FIG. 1 Nursing black furred pup, approximately three to four weeks old. Note the contrast of pelt colour and texture between the pup and the buff-coloured hair coat of the adult.



FIG. 2 Weaned pups in various stages of moulting. The lighter animal on the right has completed the process and now possesses a silvery hair coat.

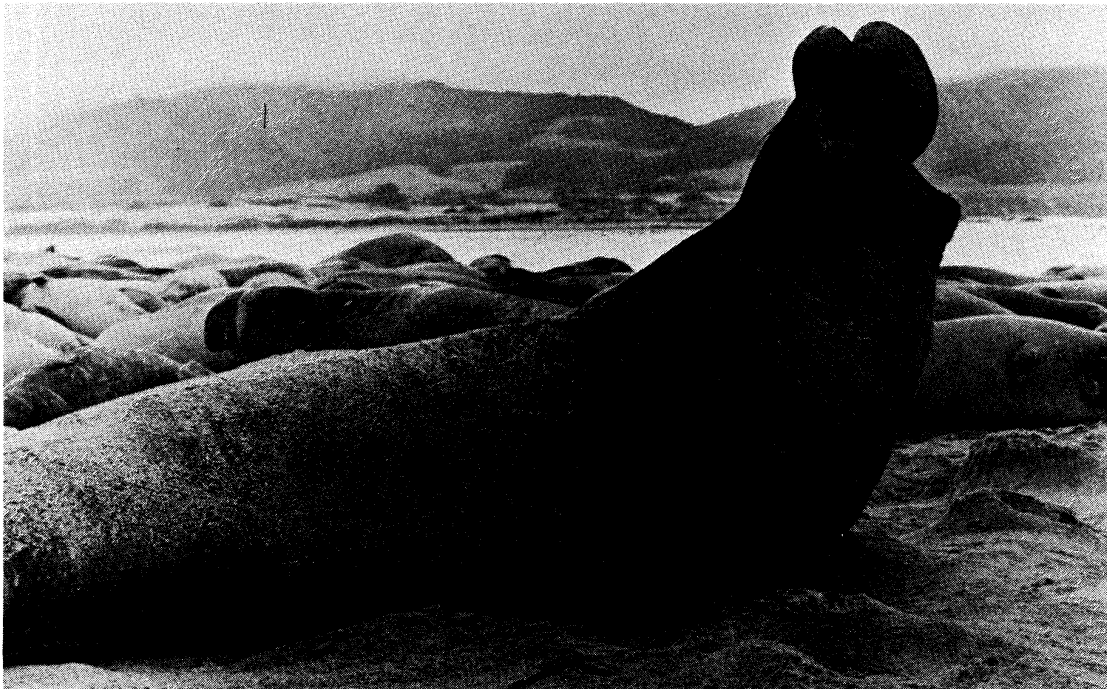


FIG. 3 Typical breeding bull posture while emitting the “clap-threat” vocalization. Note the elevated posture and sand layer deposited on back by backward scooping motion of fore flipper.

moulting apparently must take place on land. Also, it appears that moulting and reproductive activity are not compatible since only weaned pups moult on the breeding rookery. All others return at various times according to their age and sex group throughout the remainder of the year to moult at the rookery site (Orr and Poulter, 1965).

The hind limbs on the northern elephant seal are similar in form and function to those of other phocids. However, the forelimbs differ with respect to their extreme digital dexterity (Fig. 4). This ability permits precise scratching of most portions of the body including the back and dorsal neck and head regions. It also makes possible the scooping action by which the thermoregulatory and displacement behaviour of sand flipping are accomplished.

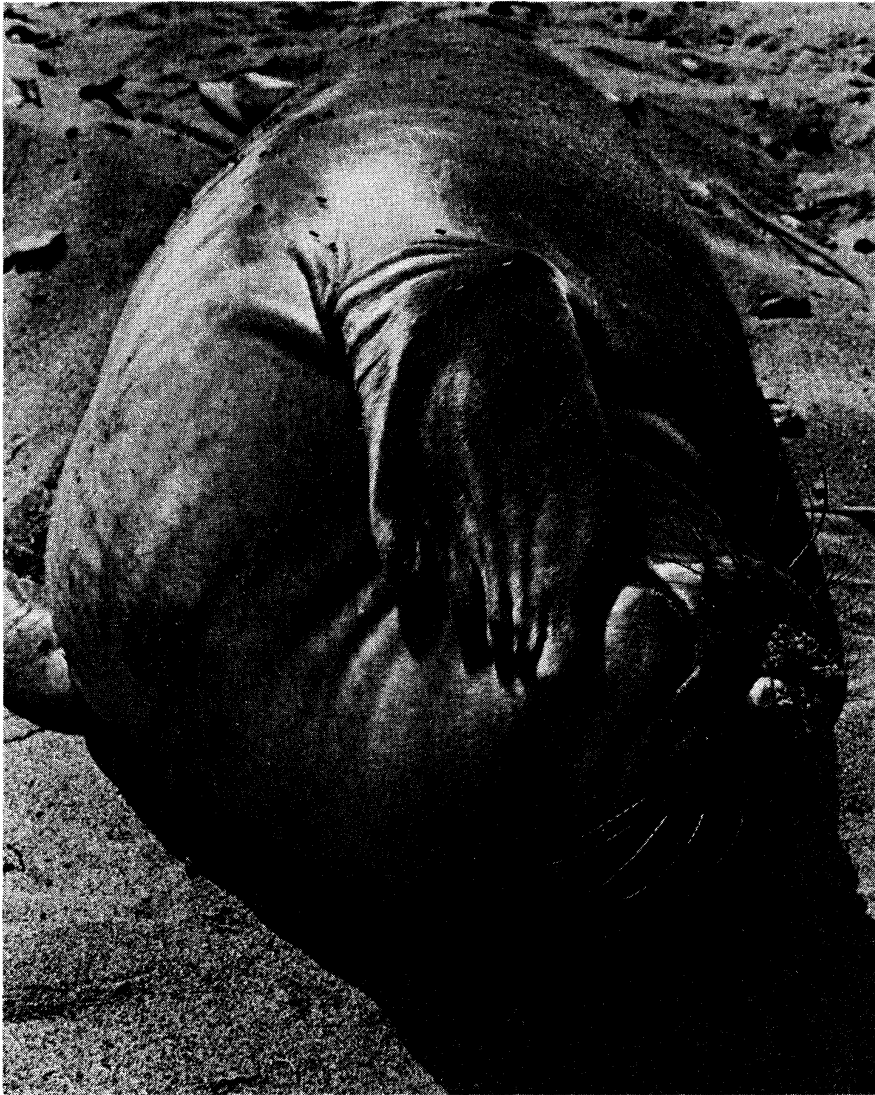


FIG. 4 Female northern elephant seal exhibiting the high degree of manipulation of the fore limb.

### *Distribution and Migration*

The present range of the northern elephant seal is from Cedros Island off the Pacific coast of central Baja California, Mexico, north to the -Farallon Islands, due west of San Francisco, California, USA. Non-breeding individuals are often seen offshore along the west coast of North America up to Vancouver Island, Canada (Scheffer, 1958). The most northerly sighting was by Willett, 1943, who recovered a fresh carcass of a subadult male on Prince of Wales Island, Alaska, nearly 3000 km from the most northerly breeding sight. Except for such occasional marine sightings and carcass recoveries, we have no knowledge of this species' activities and movements once it leaves the breeding or moulting grounds. Tagging operations conducted by LeBoeuf and his associates at the University of California, Santa Cruz, clearly show an annual homing to the birth sight each year for breeding and/or moulting. In one sense, then, the northern elephant seal may be considered a migratory species in that there are yearly movements from unknown feeding grounds to specific rookery sights.

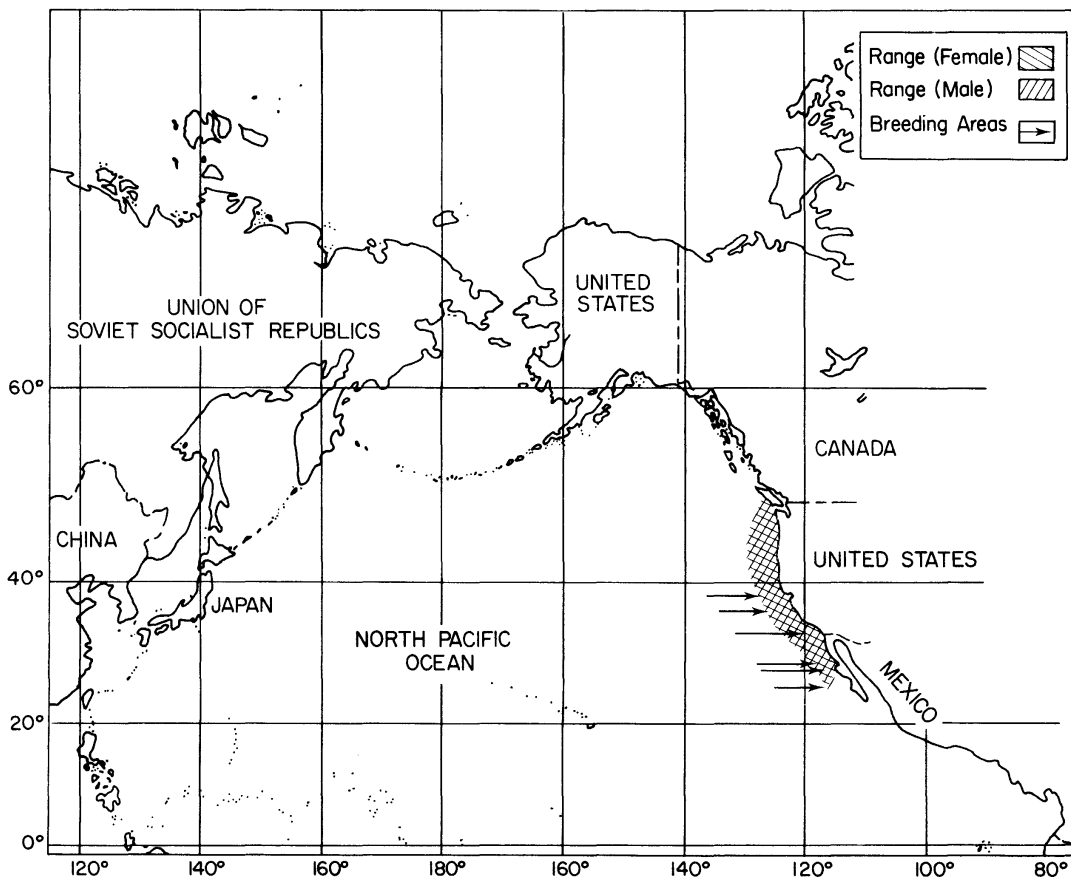


FIG. 5 Distribution of Northern elephant seal.

### *Abundance and Life History*

As a brief sketch of the life history of the northern elephant seal we present the annual cycle as observed on Año Nuevo Island off the coast of Central California as viewed by these authors over the past decade. Adult bulls haul out on the island to begin the breeding season in late November and remain until March. Although some bulls enter the water during this time, it is doubtful that they feed. In mid-December adult females arrive, give birth, nurse their pups for about one month, come into oestrus, copulate, and depart. They rarely enter the water during this period and, like the bulls, apparently metabolize subcutaneous fat stores. Both cows and bulls appear considerably thinner at the time of departure.

After weaning, the pups, now referred to as "weaners", gather in pods on the beach where they remain for about one month. During this time they do not feed but instead also metabolize fat reserves laid in during the nursing period. Weaners make short excursions into tide pools around the breeding beach during this time and appear to be learning to swim and dive. They leave the rookery in small groups unaccompanied by any adults. Apart from reproduction, the only other apparent reason for returning to the land is to moult.

The recent population dynamics of the northern elephant seal have indeed been just that, dynamic! It was the prime target for commercial sealing because of its extensive subcutaneous fat layer which from a bull four m long yielded about 325 l of oil (Scammon, 1874). Exploitation of this species began about 1818 and continued until 1869 when the species was considered commercially extinct. By 1890 only one herd of about 100 northern elephant seals on Guadaloupe Island was reported (Bartholomew and Hubbs, 1960). This was perhaps a count of a breeding colony and did not take into account juveniles which were out at sea. Yet the fact remains that the species was at a dangerously low level. From this nucleus population on Guadaloupe Island, Mexico (29 °N), the species rapidly increased and recolonized its former breeding islands and beaches. In 1918 the San Benito Islands (lat. 28.5 °N), closest to Guadaloupe, were recolonized (Rice *et al.*, 1965). This first step in recovery was aided by a law affording the northern elephant seal complete protection passed by the Mexican Government in 1922.

The United States soon followed suit. The re-occurrence of the species on other islands followed in this order: San Miguel Island (34 °N) 1925; The Coronado Islands (32.5 °N) 1948; Santa Barbara

Island (33.5 °N) 1948; San Nicolas Island (33.3 °N) 1949; Año Nuevo Island (37 °N) 1955; Anacapa Island (28.5 °N) 1958; the Farallon Islands (37.6 °N) 1959; Cedros Island (28.5 °N) 1965; and Santa Rosa Island (34 °N) 1965.

In their publication, Bartholomew and Hubbs (1960) estimated a total population size of 13 000 animals in 1957. LeBoeuf (in press) estimated that in 1976 there were 47 684 northern elephant seals in existence. Thus within 20 years the population has more than tripled. LeBoeuf has summarized the initially observed locations, the initiation of breeding, Colony size, number of breeding females, and total colony numbers (Table 1).

TABLE 1 Northern elephant seal breeding colonies, the time of colonization, and estimates of colony sizes.<sup>a</sup>

Colony	Seals initially observed	Breeding began	Colony size	
			Number of breeding females at peak season	Estimated total animals
Isle of Guadaloupe	—	—	4 652	18 596
Islas San Benito	1918	1930s	2 382	9 238
San Miguel Island	1925	1930s	3 842	13 980
Los Coronados	1948	1950s or later	44	152
Santa Barbara Island	1948	late 1950s	68	252
San Nicolas Island	1949	late 1940s	616	2 214
Año Nuevo Island	1955	1961	687	2 718
South-east Farallon Island	1959	1972	60	260
Isla Cedros	1965	1960s(?)	63	274
Population totals			12 414	47 684

<sup>a</sup>The last are based on censuses taken in late January during the 1976 breeding season on all rookeries except the Isle of Guadaloupe (1975), Islas San Benito (1970), and Isla Cedros (1970). The number of breeding females was obtained from peak censuses taken in late January. Approximately 10-15% of the breeding females in each colony are still at sea at this time. Estimate of total animals in each colony was calculated by simply doubling the censuses in late January (LeBoeuf, 1977).

As may be seen from the latitude sequence of island re-occupancy, colonization of the former range has not been a direct progression northward. Instead it appears that perhaps the most suitable breeding sights, i.e. those with good sand or gravel beaches remote from human activity, were occupied first, and the less suitable rookery sights were occupied sometime thereafter. The pattern of colonization which these

authors witness over the past decade on Año Nuevo Island and which has been reported by LeBoeuf *et al.* (1974) for the Farallon Islands had allowed the following synthesis of the process:

1. The closest colonized breeding islands supply the initial stock to a new sight. In the case of the Farallon Islands there were Año Nuevo, San Miguel and San Nicolas Islands (LeBoeuf *et al.*, 1974).

2. The colonizers are young of the year which use the new sight as a hauling out place for the summer or fall moult.

3. The first breeding at the new site involves subadult males (six to seven years) and adult females. Subadult females do not usually participate in the early stage of colonization. One may view these first breeders as wanderers from an established colony with a large established population. The first incidence of breeding on the Farallons in 1972 was characterized by the arrival first of several cows followed by the subadult bulls (LeBoeuf *et al.*, 1974). This is the reverse of the sequence in an established colony.

4. Once established the new colony grows rapidly and the harem-type breeding structure gradually changes. In the early 1960s the harems on Año Nuevo Island were for the most part successfully defended by an alpha bull, and most of the breeding was accomplished by relatively few bulls (LeBoeuf and Peterson, 1969). By the late 1960s, however, the breeding beaches were literally covered with adult bulls and females with no possibility of a discrete, well-defended harem existing. The result was breeding by a greater number of bulls and increased pup mortality. The latter was studied on Año Nuevo Island by LeBoeuf and Briss (in press) between 1968 and 1976. They found that throughout this period pup mortality ranged from 13% to 26% with the two main sources of pup death being aggression of females towards foreign pups and trampling by bulls. These are the same sort of conditions which exist apparently on a permanent basis on Guadaloupe Island. It is perhaps this "full house" condition which stimulates the roving of breeding animals to a new rookery site. This idea is supported by the fact that breeding occurred for a decade on Año Nuevo Island before adult females ventured less than 200 km north to the Farallons. The increase in pup mortality in the rookery with the increase in size of the breeding population is also an excellent example of intra-population regulation of animal numbers, since the factors causing increased pup mortality in the full beach condition are all density dependent.

Population kinetics as studied on Año Nuevo and south-east Farallon Islands by LeBoeuf *et al.* (1974) and on San Nicolas Island by Odell (1974) show a similar pattern in all three even though the



Farallons have only recently been colonized. The breeding populations all peak in February, juvenile peaks occur in April-May and again in November. The beach populations reach their lowest points in August.

Perhaps the most significant colonization event to date took place on Año Nuevo Point Beach, the mainland shore opposite the island, in 1975. For more than a decade, adult and subadult bulls from the island have been swimming to the mainland and spending days and weeks on the beach and in the surrounding sand dunes. In early January, 1975, a pregnant female hauled out on the beach and gave birth to a pup. She was chaperoned from the start by the dominant beach bull with which she later bred. The following season a total of seven cows with pups were ashore at this locality. Mainland colonization at Año Nuevo Point Beach has continued to grow rapidly during the past three years, and in 1979 there were approximately 90 females, 80 pups and 260 bulls. This is the first known instance of a mainland breeding colony since the species' recovery from near extinction. It now appears that a full recolonization of the original range via the establishment of a breeding colony at the Point Reyes National Seashore (38 °N) is most probable.

### *Internal Characteristics and Morphology*

Adult bull skulls at the museum of Vertebrate Zoology, University of California, Berkeley, average 50 cm in total length and 27 cm in width at the zygomatic arch. In contrast, the average nursing pup skull in this collection is 20 cm long and 13 cm wide (Fig. 6). The adult dental formula is

$$I \frac{2}{2} C \frac{2}{2} PC \frac{5}{5}$$

and the deciduous formula is (Harrison, 1974)

$$I \frac{2}{2} C \frac{1}{1} PC \frac{3}{3}$$

Total upper canine length of an adult bull when removed from the skull ranges from 5-6 cm. However, only a little more than half this length protrudes beyond the gum. These are the teeth which inflict most of the wounds during bull combat, but their functional length is less than half the skin-fat layer on most parts of the body. The implication that

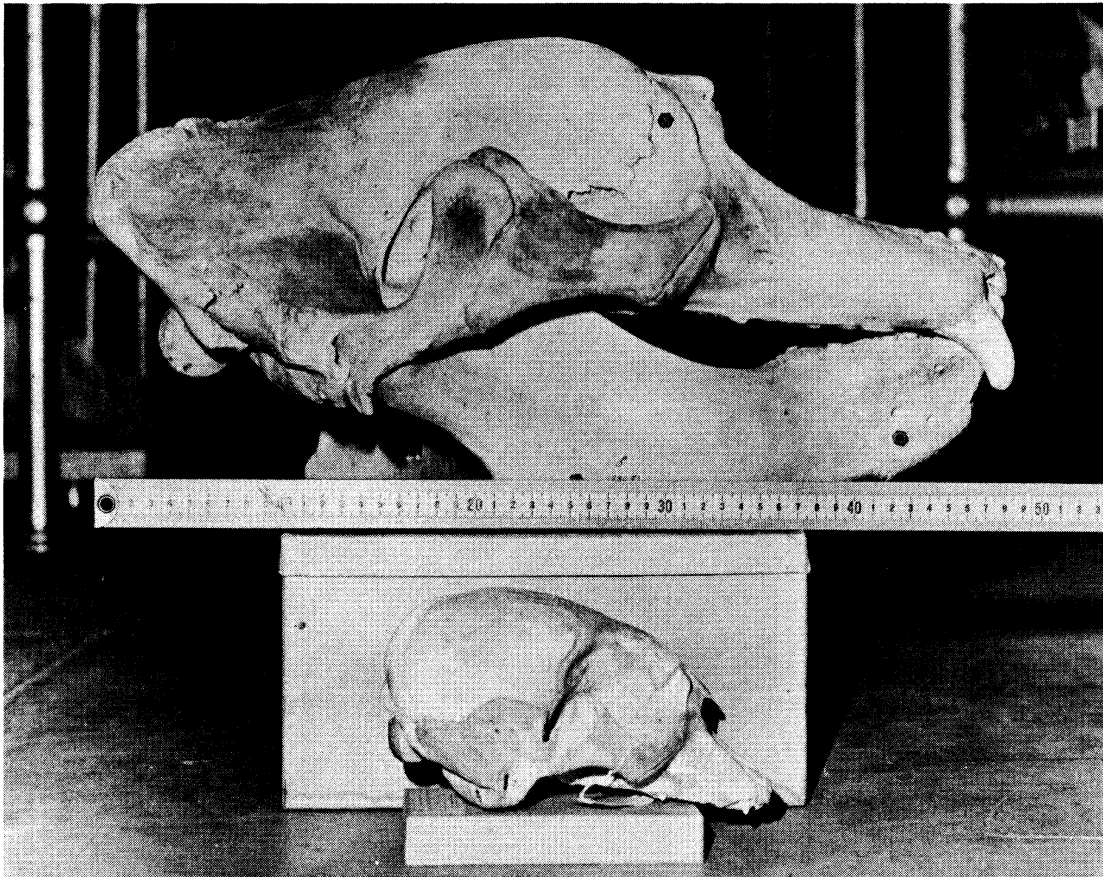


FIG. 6 Skull of an adult bull and nursing pup northern elephant seal, photographed at the Museum of Vertebrate Zoology, University of California, Berkeley.

relatively short canine length is a selective feature which prevents high bull mortality is born out by the results of an autopsy of an adult bull by Robert Jones, Museum of Vertebrate Zoology, Berkeley. This animal died as the result of an eight-hour running fight with another bull on Año Nuevo Point, California. Although there were numerous cuts in the neck shield area, no deep artery or vein was severed. Instead death was due to a shattered scapula which punctured the thoracic cavity.

Subcutaneous fat forms a major part of the mass of the northern elephant seal. In a recent dissection of a two-year-old female we found that the skin and fat layer weighed slightly more than the remainder of the body. Fat-layer thickness in this animal ranged from 87 mm in the dorsal thoracic region to only a few millimetres near the nose and naked portions of the hind flippers.

As for other aspects of internal anatomy, the literature is almost completely lacking with respect to the northern elephant seal, except for a few minor observations (Ridgway, 1972). This is in sharp contrast

to the southern elephant seal, *Mirounga leonina*, for which much information can be found. This is no doubt due to the unavailability of fresh wild specimens of the northern elephant seal for anatomical study due to its complete protection by the United States and Mexico. Many of the findings for the southern elephant seal probably apply to the northern species as well, although this must still remain speculative.

## *Behaviour*

### *Thermoregulation*

Initial interest in the body temperature of the northern elephant seal was stimulated by Bartholomew (1954) when he obtained rectal temperatures of sleeping animals in a rookery and found a surprisingly wide range of body temperatures. McGinnis and Southworth (1967) obtained similar results from a captive juvenile which led to a more detailed telemetry study of both wild and captive animals of various age groups (McGinnis and Southworth, 1971). In this work they found that most wild northern elephant seals were very stenothermic with the exception of undernourished pups and bulls at the end of the breeding season. However, numerous long-term captive animals all exhibited marked eurythermy as previously discussed.

Insulation in the adult and weaned young is entirely by subcutaneous fat deposits. New-born pups, however, possess no subcutaneous fat. Instead they rely to a great extent on an abnormally high metabolic rate to offset excessive body heat loss until the fat insulation can be acquired (Heath *et al.*, 1977). The black pelage of nursing pups, though a better insulator than the adult hair coat, (McGinnis, 1973) does not make up for the lack of subcutaneous fat. Body heat dissipation is primarily by vasodilation of blood vessels in the hind flippers (McGinnis *et al.*, 1970). Sand flipping also provides an avenue for body heat dissipation, especially if the sand is moist when flipped on the back. Excessive activity on land, especially on warm days, results in elevated body temperature (McGinnis and Southworth, 1971) and apparently cannot be tolerated for very long.

### *Diving*

Both direct and indirect evidence presented here under feeding behaviour indicate that the northern elephant seal is capable of long, deep dives. Various physiological blood properties associated with

diving presented by Lenfant (1969) and Simpson *et al.* (1970) suggest that this species is far more similar in diving ability to other deep diving species of pinnipeds and cetaceans than to the surface-feeding, shallow-diving forms. Elsner *et al.* (1964) demonstrated that the inferior vena cava of *M. angustirostris* may expand to such an extent during a dive as to contain one-fifth of the total blood volume. In this manner it acts as a storage compartment for de-oxygenated blood during a dive. Marked bradycardia during simulated diving has been reported both for adults (Van Citters *et al.*, 1965) and nursing pups (Hammond *et al.*, 1969).

Because of the large size of adults in this species many direct tests in laboratory chambers, now so prevalent for smaller species, are lacking here. However, there appears to be ample indirect evidence that long-term, deep diving is a major feature of the physiological niche of the northern elephant seal.

### *Feeding behaviour*

In a stomach content analysis of a 2.5 ton male, Huey (1929) found rat fishes, dogfish, shark, puffer, shark-skates and squid. All of these prey are deep water inhabitants. They are found at depths of approximately 22 m. Scheffer (1964), reported that northern elephant seals were hooked on fishing lines at depths of 183 m. Although sea lions can dive to 250 m (Ridgway, 1972), elephant seals probably dive much deeper permitting this species to exploit a food niche which is not available to other pinnipeds on the west coast of North America.

Census data on Año Nuevo Island and Southeast Farallon Island correlates with fluctuations in salinity, water temperature, coastal upwellings and possible elephant seal food (LeBoeuf *et al.*, 1974). This suggests that abundant food prey is most likely to be available from May to September.

### *Sensory perception*

Virtually nothing is known about the sensory systems of elephant seals. It is likely that acoustic, visual, olfactory and tactile cues account for various aspects of social orientation, feeding orientation and migrating behaviour.

Comparative histology of retinas from four pinniped species revealed that the northern elephant seal had the highest ratio of receptor to ganglion cells (Landau and Dawson, 1970). This suggests that although *Mirounga* may have relatively poor visual acuity, its sensitivity to light may be greater than other pinniped species.

### *Vocalizations*

The most detailed structural and functional analysis of northern elephant seal vocalizations was originally given for the breeding population on San Nicolas Island, California, by Bartholomew and Collias (1962). These investigators presented excellent spectrographs of the major types of phonations emitted by males and females at different ages. Later work, primarily of a comparative nature was done at Año Nuevo Island, California (LeBoeuf and Peterson, 1969b; LeBoeuf and Petrinovich, 1974a; LeBoeuf and Petrinovich, 1974b; Petrinovich, 1974; Sandegren, 1976).

Although Sandegren (1976) distinguishes between four different adult male vocalizations, the two most commonly heard during the breeding season are the "snort" and the "clap-threat". Both are threat vocalizations with the former often given from a prone position or in water. The clap-threat is always associated with other elements of threat behaviour and is clearly related to aggression and dominance. The clap-threat consists of a series of pulses which are guttural and low-pitched with most of the energy concentrated below 2500 Hz. Sandegren (1976) found that the spectral characteristics of these pulses are different for individuals and could be used for individual recognition. LeBoeuf and Peterson (1969b) and LeBoeuf and Petrinovich (1974a) found that the pulse repetition rate of the clap-threat varied significantly from one colony to another, indicating the presence of a dialect. Finally, LeBoeuf and Petrinovich, 1974b, found species differences in both temporal and pitch parameters of the clap-threat emitted by *M. angustirostris* and *M. leonina*.

When a pup is ready to suckle or has been separated from its mother, or has in some manner been stressed by another adult, it emits a shrill distress cry of 0.3 s duration, repeated several times at intervals of about one second. The fundamental frequency is about 1000-1500 Hz with harmonics above 5000 Hz. Adult females frequently respond to their own pup's distress calls with a pup-attraction call having a fundamental frequency between 600 and 1000 Hz with rises and falls in pitch five to six times per second. Petrinovich (1974) has experimentally demonstrated individual recognition of pup distress calls by their mothers. Females also have a threat vocalization which is loud and prolonged, having most of its sound spectral energy below 700 Hz.

### *Male dominance hierarchies*

Studies of social behaviour in the northern elephant seal began in

earnest with the work of George Bartholomew (1952). Brief and relatively inaccurate statements regarding their reproductive behaviour were first made by Scammon (1874) and later by Townsend (1912). Since 1968 LeBoeuf and his associates at the University of California, Santa Cruz (LeBoeuf, 1974; LeBoeuf and Briggs, 1977), have studied reproductive behaviour of elephant seals on Año Nuevo Island, California in relation to demographics in remarkable detail.

Soon after adult males (eight years old) arrive on the breeding grounds they begin to fight for dominance status within a social hierarchy, and with repeated encounters among several males the emerging alpha male acquires greater access to females than lower-ranking males (Bartholomew, 1952; LeBoeuf and Peterson, 1969a; LeBoeuf, 1974). High-ranking males are involved in more aggressive interactions than lower-ranking males, but overt fighting is usually infrequent (6% or less) relative to the total number of aggressive encounters (LeBoeuf and Peterson, 1969a; Sandegren, 1976). Threat exchanges among participants include such motor elements as an elevated posture of the neck and/or body to about a 90-degree angle with the substrate, an inflated proboscis, a head toss, a slamming of the body to the ground (Fig. 3), a "snort" vocalization and a series of low-pitched guttural pulses (Sandegren, 1976). Defeated males retreat backwards while facing their foe, taking a low body posture. The most frequent behaviour of submissive males when threatened at some distance by a dominant male is to turn and move away. Submission by a beta individual when alpha is within striking distance includes one or more of the following: lateral swimming motions with the hind-quarters, wide-eyed scared expression, proboscis retraction, relaxed open mouth, nip-biting (Sandegren, 1976). When a bull is in a fight-or-flight conflict he uses his fore flippers to flip sand on the back (Heath and Schusterman, 1975).

### *Reproduction*

As already mentioned, the complete protection afforded this species during most of its population recovery has precluded in-depth investigation of all aspects of internal anatomy, particularly those pertaining to reproductive biology. Therefore, such suspected phenomenon as delayed implantation has yet to be documented for this species. Harrison (1969) presents numerous data on the reproductive physiology of the southern elephant seal, *M. lionina*, much of which

probably applies to the northern elephant seal as well, but with no direct field data this can only be speculative.

We do know, however, that the females come into oestrus just at or about the weaning period which is quite different from western otariids. The bulls, like all phocids, have internal testis, which poses the question of sperm viability and body temperature. Bryden (1967) found that the testicular temperature of two immobilized southern elephant seal bulls was about 60 °C below deep body temperature but does not postulate a mechanism to account for this. The shunting of cool venous blood from the hind flippers to a plexus surrounding the testis could account for such a thermal differential.

### *Perinatal, maternal and pup behaviour*

Perinatal behaviour of *M. angustirostris* females and their young has been studied during four breeding seasons by LeBoeuf *et al.* (1972) at Año Nuevo Island, California. Although females can give birth during their third year, the majority start giving birth during their fourth or fifth year of life. Arrival time of females to time of parturition is six to seven days, with a nursing period of about 28 days. An oestrus of three to five days occurs during the final days of nursing and females wean their young and depart approximately 34 days after arriving. An oestrus female mates promiscuously. After departing the breeding grounds females feed at sea for a few weeks, return to the rookery to moult and rest for nearly a month, and return to sea for the next eight to nine months before the next reproductive season.

The peak period for births throughout the northern elephant seal's range is 20 January to 1 February. Generally, most births occur at night or during the coolest hours of the day while the female is in a "harem" or clumped together with other females. Individual distance among females varies from light contact to one or two m (LeBoeuf and Briggs, 1977). A detailed description of a birth is given by LeBoeuf *et al.* (1972). In the final phase of parturition, the female assumes a "U"-shaped posture. Immediately after birth, the mother turns, faces the newborn (thereby breaking the umbilical cord), vocalizes towards the pup and appears to smell the pup. The precocial pup vocalizes in return and this behavioural sequence in which mother and pup learn to recognize one another continues for about an hour. Females become considerably more aggressive after giving birth and attempt to keep nearby females, who are frequently attracted to new-borns, away by vocal and postural threats. Small and less aggressive mothers (probably primiparous) often have their pups bitten by larger and more

aggressive nearby females almost as soon as the pup is expelled. Pups of subordinate females were much more likely to be bitten and eventually become orphaned than pups of dominant, aggressive and probably older cows (Christenson, 1974).

Duration of parturition from the time the foetus is barely visible ranges from approximately 1 to 30 min with a mean of about 7.3 min. LeBoeuf, *et al.* (1972) observed 29 presentations of which 62% were cephalic and 38% were caudal. In the majority of births, delivery of the placenta, which weighs about (10 lb) 4.5 kg occurred within two min of birth. Usually gulls consume the entire afterbirth within 24 h.

A new-born pup's eyes are open, it can scratch, flip sand on its back and move forward as well as vocalize and hold its head somewhat erect. Suckling, which occurs within 15 min to one h after birth, takes place two to four times per day and increases in frequency and duration with age (Fig. 1). The close filial relationship during the nursing period of four weeks not only ensure nurturance of the pup, but also its protection by its mother from injury by other females. This close association between mother and pup ends abruptly when the female leaves the harem and returns to sea, leaving the pup on the rookery and no longer interacting with it on land. The weaned pups or "weaners" as they are called, leave the female harem and form weaner pods or aggregates. Recent observations suggest that some weaners, mainly males, re-enter the harem and try to obtain additional nourishment by suckling nursing females (Reiter, 1975).

Generally, females nurse their own pups (36 of 50 marked pairs) and reject suckling attempts of alien pups. In many of those cases where a female suckled an alien pup or weaner, the female was asleep and did not discriminate between her offspring and the alien, or the female had lost her own pup and was probably physiologically primed to respond maternally (LeBoeuf *et al.*, 1972). These findings contradict those of Klopfer and Gilbert (1967).

Swimming and diving skills of weaners improve gradually as they spend increasing amounts of time in the water (Reiter, 1975). "Mock fighting" by weaners resembles adult agonistic interactions and is sexually dimorphic, both quantitatively as well as qualitatively. Male mock-fight more frequently and for longer periods of time than do females. Male weaners had long bouts of mock-fighting interactions including throat-pressing, neck-biting, rear and slam, etc., while female weaners briefly faced each other with open mouths emitting loud vocalizations. Detailed descriptions of the motor patterns involved in self- and object-manipulation by weaners is given by Rasa (1971) who also discusses the adaptive significance of these early behaviour



patterns. Weaners departing from the rookery in mid-April and early May, a period of coastal upwellings and phytoplankton blooms, are about 14 weeks old (Reiter, 1975).

### *Copulatory behaviour*

As indicated earlier, status within the male social hierarchy determines access to the female harem or aggregate, and since high-status males prevent subordinates from approaching, mounting or copulating with females, there is a high positive correlation between social status and the estimated number of females inseminated (LeBoeuf, 1974). The high positive correlation between status and reproductive success among males depends to some extent on the number of oestrus females, the number of competing males and the location of the female harem. The more difficult it is to defend a harem, either because of its size or location, the more likely younger males will begin copulating (LeBoeuf, 1972; LeBoeuf, 1974). Generally, males begin copulating at eight or nine years of age and highly successful males may breed for three or four successive years with as many as approximately 250 females. However, the reproductive success of most males is zero or low because many succumb before attaining reproductive status, and those that do are prevented from mating by high-status males. According to LeBoeuf (1974) the mortality of males may be as high as 97% prior to reaching age eight and as high as 86-93% before reaching six or seven years of age.

Copulating activity is highest during the third week in February. Copulation is initiated by the male without any preliminary courtship (LeBoeuf, 1972). Mounting is from the side with the male using the great weight of his head and neck, and fore flipper clasp or a neck-bite to restrain the female. All females are mounted, those which are pregnant as well as those in oestrus, although the latter are mounted more frequently. A cooperative female is passive and may facilitate intromission by assuming the lordotic posture and spreading her hind flippers. Intromission last about five min on land and about six min in water. Males usually terminate intromission.

When a male attempts to mount an unreceptive female, she continually emits vocal threats, swings her hindquarters from side to side, vigorously flips sand (Heath and Schusterman, 1975) with her fore flippers back into the male's face, and struggles to get away. Many of these protested mounts occur during early oestrus and result in either the male stopping his attempted copulation and the female moving away, or the mounter being interrupted by the threatening actions of a

more dominant male or a completed copulation. Cox and LeBoeuf (1976) found that the loud protests of mounted females are likely to result in the interruption of mounts by low-ranking males and not high-ranking males. Thus, females during early oestrus incite male competition with the result that they mate primarily with high-status males, thus increasing their own inclusive fitness.

### *Captivity*

Northern elephant seals have been kept successfully in several zoos in the United States including St Louis, San Diego, Chicago, Washington D.C. and the New York Aquarium. As is true with other pinniped species, they are difficult to breed in captivity and there have been no known successful breeding programmes. The activity patterns or time budgets of two yearlings were quantified by Schusterman (1968) who gives the percentage time that each animal spent in mock-fighting, grooming, environmental manipulations, etc. McGinnis and Southworth (1971) found that long-term captive northern elephant seals were strikingly eurythermal compared to stenothermic wild specimens. They suggest that the captive diet of frozen herring does not permit a constant resting metabolism. Lenfant (1969) reports a decrease in blood haemoglobin content in captivity which also suggests dietary deficiencies.

In recent years at least two oceanaria, Sea World in San Diego and Marineland near Los Angeles, have made considerable progress in rehabilitating sick pups that come to mainland beaches. Both organizations currently maintain captive colonies of elephant seals.

### *Diseases*

Lists and discussions of major pinniped diseases, some of which may be found in the northern elephant seal, are presented by Ridgway (1972) and Hubbard (1968). The most complete case history of a disease in this species is that of an incidence of obstructive emphysema by Saunders and Hubbard (1966). Given that the literature on disease in *M. angustirostris* is very sparse, three separate reports on emphysema as a direct cause of death make this malady the most prevalent to date.

## *Acknowledgement*

In the preparation of this manuscript R. J. Schusterman was supported by Contract N00014-72-C-0186 from the Office of Naval Research.

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