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Steller Sea Lion

Eumetopias jubatus (Schreber, 1776)

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Introduction

The Steller sea lion (*Eumetopias jubatus*), (Family Otariidae, genus *Eumetopias* Gill, 1866 known also as the northern sea lion or Steller's sea lion is the largest of all the eared seals or otariid pinnipeds. Despite the fact that the California sea lion (*Zalophus californianus*), is more tropical in its distribution than the Steller sea lion, the two sea lions show considerable overlap in their distributions along the coasts of Oregon and northern California and are occasionally mistaken for one another. The misidentification usually occurs between juvenile or subadult male *Zalophus* and yearling or subadult female *Eumetopias*. However, fully grown male *Eumetopias* are indeed massive, weighing three times the amount of their *Zalophus* counterparts and fully grown female *Eumetopias* are at least four times the size of fully grown female *Zalophus*. Moreover, *Eumetopias* is a light tan or yellowish brown—considerably lighter in colour than *Zalophus*. Unlike *Zalophus*, which is found in nearly all oceanariums, zoos and circuses, *Eumetopias* (because

of its massive size and relatively higher aggressivity) has not been popularized in captivity, is rarely seen in oceanariums, zoos and circuses, and is seldom trained to perform tricks.

Eumetopias is named after George Wilhelm Steller, the German naturalist, who was a member of the discovery expedition to Alaska in 1741 (Steller, 1751). Among the earliest accounts of this sea lion's morphological characteristics (including size, weight, pelage, skull, teeth, skeleton, etc.) and behavioural characteristics (vocalizations, breeding, locomotion, capture, migration, etc.) are those given by Allen (1880) and Scammon (1874). The latter was probably the first observer to suggest migratory movements of *Eumetopias*. Because of the species' relatively low commercial value, little was known about the biology of *Eumetopias* until the 1960s. Recent census information, originally spurred by the possible predation of *Eumetopias* on commercially valuable fishes, was obtained in Alaska by Kenyon and Rice (1961) and Mathisen and Lopp (1963). Smaller populations have been censused in southern California (Bartholomew, 1967; Bartholomew and Boolootian, 1960) and in northern California (Orr and Poulter, 1965). Seasonal fluctuations in Oregon from 1968 through 1970 have been quantified by Mate (1973). Feeding studies and surveys have been conducted by Mathisen *et al.* (1962), and Fiscus and Baines (1966). Several investigations are available on the growth of *Eumetopias* (Fiscus, 1961; Mathisen *et al.*, 1962; Orr and Poulter, 1967) but data on population dynamics are still relatively sparse. Until 1970, life history and reproductive behaviour had been briefly surveyed in Alaska (Mathisen *et al.*, 1962; Thorsteinsen and Lensink, 1962) and in California (Bonnot, 1928; Bonnot, 1951; Evermann, 1921; Evermann and Hanna, 1925; Starks, 1918; Orr and Poulter, 1965; Orr and Poulter, 1967). From 1967 through 1969, Gentry (1970) conducted the first extensive and quantitative field investigation dealing with the social behaviour of a northern California population of Steller's and at the same time Sandegren (1970) did a detailed study of the breeding and maternal behaviour in an Alaskan population. In the present chapter most of the material dealing with reproductive behaviour will summarize the data presented in these two excellent monographs. The most extensive laboratory studies on the sensory perception and social behaviour of *Eumetopias* have been done by Schusterman and his collaborators (e.g. Schusterman, 1968) and by Poulter (e.g. Poulter and DelCarlo, 1973). Volumes edited by Harrison *et al.* (1968), Andersen (1969), Ridgway (1972) and Kinne (1975) review some of the most recent laboratory studies on the behaviour and physiology of Steller sea lions.

Genus and Species

Details regarding taxonomy of the North and South American genera from the subfamily Otariinae (i.e. *Eumetopias*, *Zalophus* and *Otaria*) are given by Allen (1880, pp. 231-233 and pp. 291-296). A more recent discussion of the name *Eumetopias jubata* may be found in Scheffer (1958, pp. 56-59). The present author prefers the common name of Steller sea lion which is currently used most frequently. However, “northern sea lion” and “Steller’s sea lion” are still found in contemporary references to *Eumetopias*. The common name “Steller’s sea lion” may be confused with the common name “Steller’s Sea-cow” (*Hydrodamalis stelleri*) and the common name “northern sea lion” may sometimes be confused with the common name for *Callorhinus ursinus*—the “northern fur seal”.

External Characteristics and Morphology

As in all otariid forms *Eumetopias* shows a decided sexual dimorphism (Figs 1 and 2). Mathisen *et al.* (1962) presented data on the length of bulls, cows, yearlings and pups. The mean length of 46 bulls ranging in



FIG. 1 Copulation in Steller sea lions. Note female lies passive with saliva running from her mouth while male lies with head and neck outstretched. An adult female vocalizes behind the mating pair.



FIG. 2 Territorial display involving three males in the oblique stare posture. The displays occurred at the mutual boundary of all three territorial males. Note the forward position of the whiskers.

age from five to 19 years old was 286.8 ± 34.7 cm and the mean length of 49 cows ranging in age from nine to 22 years old was 240.3 ± 13.6 cm. Seventeen yearlings averaged 177.8 ± 16.8 cm in length and 22 pups had a mean length of 100.6 ± 7.3 cm. Thorsteinsen and Lensink (1962) presented data on the mean length of males ranging in age from nine to 17 years old. The corresponding mean lengths were 287.0 cm and 299.7 cm. They found no change in the mean length of males after the age of 13 years. Fiscus (1961) presented sex and age changes in body length. One male yearling was 178 cm while three male 10-year-olds had a length of 301 cm and two male 16-year-olds had a body length of 325 cm. A two-year-old female's body length was 180 cm and the lengths of three 12-year-old females were 243 cm. The kind of detailed information readily available on the body length of *Eumetopias* is not, to my knowledge, available on their weight. Generally speaking, fully grown males weigh about 1000 kg and fully grown females weigh about 273 kg. Scheffer (1945) found that the mean weight of three newborn males was 17 kg and that both male and female pups of 6-10 weeks old weighed approximately 40 kg.

On the basis of the body length data summarized from Fiscus (1961) and Scheffer (1945), Bryden (1972) has developed postnatal growth curves for male and female *Eumetopias* which show that like the northern fur seal, early growth in the Steller sea lion is rapid for both

sexes and that sexual and physical maturity are attained following a relatively long developmental period. Growth continues for considerably longer in *Eumetopias* males than females.

The coloration of adults of both sexes is light to reddish brown and there is little or no pigment in the epidermis (Sokolov, 1959, 1960, as cited in Ling, 1974) but abundant pigment in the hair follicles (Scheffer, 1962). Ling (1974) has recently reviewed the integument of marine mammals and includes much data on *Eumetopias*. Pups are dark brown to blackish. Wet adult animals appear darker than dry ones. Scheffer (1962) has described in detail the arrangement, abundance, and size of hairs on the mid-back region of male and female *Eumetopias*. Comparison of the development of skin and hair of *Eumetopias* with that of *Callorhinus* has been described by Belkin (1963, 1964) as cited in Ling (1974). Adult males develop a secondary sexual characteristic in the form of a massive muscular neck with a thick pelage of long coarse hair (see Figs 1 and 2). Although not as prominent as *Zalophus*, *Eumetopias* males also develop a sagittal crest on the skull.

Distribution, Abundance and Migration

Eumetopias breed on the Pribilof Islands, Aleutian Islands and on the Alaskan-Canadian coastline down to San Miguel Island off southern California (Fig. 3). In Asian waters, there are breeding populations on the Kurile Islands, Kamchatka and on islands in the Okhotsk Sea. There is an estimated world population of 250 000 Steller sea lions (Kenyon and Rice, 1961).

The most intensely studied *Eumetopias* population over the longest period of time is the one located on Año Nuevo Island, California, where a breeding population of nearly 2000 Steller sea lions has remained relatively constant for 50 years (Evermann, 1921; Rowley, 1929; Ripley *et al.*, 1962; Orr and Poulter, 1965; Gentry, 1970). The southern California population peaked at 2000 in 1938, then declined precipitously to approximately 100 individuals in 1964 (Bartholomew and Boolootian, 1960; Bartholomew, 1967). It is believed that the southern extent of the *Eumetopias* breeding range has been most affected by increasing water temperatures in the area (Bartholomew, 1967).

Sex ratios during the breeding season at Año Nuevo Island, California, from 1967-69 were: female to male pups 1.08:1.00; females to males of reproductive size 10.7:1.0; females to pups 2.85:1.00 (Gentry, 1970). Similar data collected by Mate (1973) on two breeding

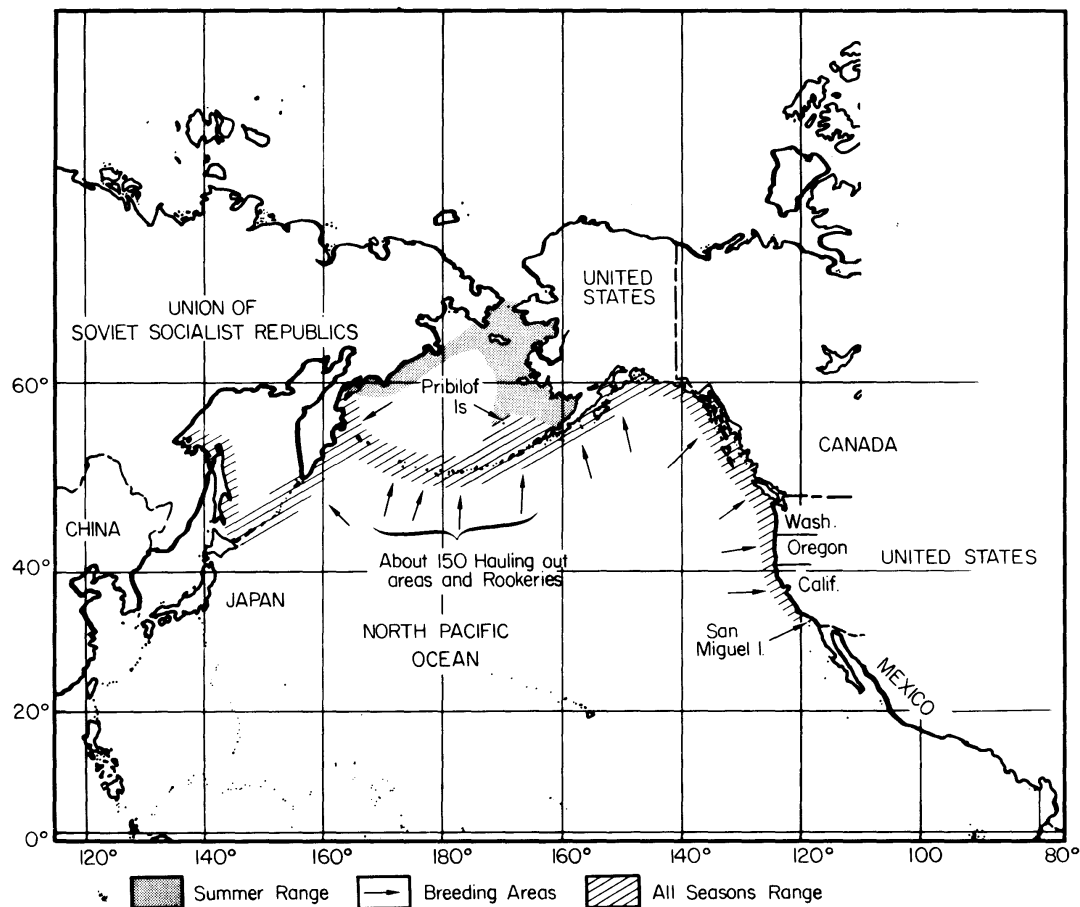


FIG. 3 Distribution of *Eumetopias*.

colonies in Oregon show sex ratios at the smaller colony at Simpson Reef, Oregon, from 1969-71 were: breeding adult females to territorial bulls 13.4:1.00; breeding adult females to pups 1.53:1.00. During the same period, the ratios at the larger rookery at Orford Reef, Oregon, were: breeding adult females to territorial bulls 6.8:1.0; breeding adult females to pups 1.81:1.00.

Eumetopias pup mortality in British Columbia, Canada, has been described as "low" (Pike and Maxwell, 1958), while at Año Nuevo Island it has been called "high" (Orr and Poulter, 1967). Gentry's (1970) figure for pup mortality in this area was less than 10%. On Lewis Island, Alaska, pup mortality was given at 12.5-14% for two-week-old pups (Sandegren, 1970). Probably the most accurate figures on *Eumetopias* pup mortality over a three-year period are those given by Mate (1973) for his two study sites in Oregon. Pup mortality ranged from 22% to 83% and was correlated with weather conditions. No figures have been given regarding the factors responsible for pup mortality. However, these include: (a) drowning (possibly the most

important single factor); (b) stampede; (c) rejection of the neonate by the mother in favour of her unweaned yearling or subadult (usually at the insistence of the latter—see Sandegren, 1970); (d) bitten by cows other than its mother.

Termination of breeding occurs in August in all known *Eumetopias* populations. Adult males are the first to leave, followed by the bulk of the females in September and October. In California, there is a northward migration, while in Alaska there is a southward migration. Little about the details of these migrations are actually known other than that they occur.

Internal Characteristics and Morphology

In presenting new data thoroughly covering both the gross and microscopic functional anatomy of the digestive system of the Weddell seal (*Leptonychotes weddelli*), Eastman and Coalson (1974) have reviewed the literature regarding the digestive system of other pinnipeds including *Eumetopias*. Most of the work on the gross anatomy of the digestive system of *Eumetopias* was done in the nineteenth century by Murie (1874) and later by Fahrenholz (1937) as cited by Eastman and Coalson (1974). The work by Murie and then by Fahrenholz consists of descriptions of the tongue, salivary glands, pharynx, and the alimentary canal (including the liver and biliary system and the pancreas).

Even the limited work on the gross and microanatomy of the central nervous system, endocrine system, cardiovascular system and lymphoid system of *Zalophus* (see Odell, this volume), has not been repeated in *Eumetopias*. Simpson and Gardner (1972) have studied the microanatomy of the lung and found one striking difference from *Zalophus*. "The California sea lion has only a single capillary within each alveolar septum. We have been confounded by the apparent presence of a double alveolar capillary supply (as in Cetacea) in the Steller's sea lion." The skeletal and muscular systems have been described by Murie (1872).

The skull and teeth were first described in some detail by Allen (1880). Fiscus (1961) gave skull measurements broken down into age and sex and on the basis of such measurements concluded that growth rate tends to reach an asymptotic level at about eight years in females and ten years in males. Fiscus found that the basioccipital-basisphenoid suture closes at about four years of age in both sexes and



FIG. 4 Skull of fully grown adult male (courtesy of Dr Charles Reppenning).

that a sagittal crest is strongly developed in males by seven years of age (see Figs 4 and 5). Sexual dimorphism is apparent in most skull characteristics. Most recently, Orr and Poulter (1967) have described several characteristics of the teeth of *Eumetopias* including: (a) the distinct generic trait of a marked space between the last two upper postcanines; (b) a decided sexual dimorphism in the permanent teeth; and (c) the distinctions between deciduous and permanent dentition (see also Spalding, 1966).



FIG. 5 Skull of five-month-old male (courtesy of Dr Charles Reppenning).

Testis and baculum weights are given for different aged *Eumetopias* bulls ranging in age from approximately six years to 17 years (Thorsteinsen and Lensink, 1962). The weights of the testis differed little between these ages and the mean weight of the testis of 49 ten-year-old bulls was 89.2 ± 2.3 g. The mean baculum weight of 38 ten-year-old bulls was 36.9 g. To my knowledge there are no other published data on organ weights.

Blood characteristics

Hubbard (1968) gives the following data (the present author calculated the mean values) on the blood of 11 newly arrived pups (1-4 weeks of age) at the laboratory: RBC count, $4.99 \times 10^6 \text{ mm}^{-3}$; haemoglobin (g per 100 ml), 16.2; PCV, 48.6%. Hubbard (1968) also gave the WBC count, the differential leucocyte counts and serum chemistry values. Unpublished data by Hubbard are given by Lenfant (1969) in order to describe the O_2 -Hb dissociation curve. Florkin and Redfield (1931) have constructed the O_2 and CO_2 dissociation curves for *Eumetopias*. Oxygen capacity of the blood is given as 20.10 ml O_2 per 100 ml blood, and oxygen combining capacity is 1.30 ml O_2 per g Hb. Also included are values for CO_2 transport (Lenfant, 1969). Serum lipoprotein analyses were done on a 14-month-old Steller sea lion by Puppione and Coggiola (1966). They presented the concentrations and percentage composition of each lipoprotein.

Milk composition

Poulter *et al.* (1965) give the following information on *Eumetopias* milk based on analyses done by Frank A. Silver in 1945 and Michael Pilson in 1964: water, 61.8%; solids, 33%; fat, 20-21%; protein, 11%; ash, 1%; lactose, 0.

Behaviour

Diving and swimming capabilities

Most of the prey species found in the stomachs of *Eumetopias* suggests that this sea lion dives to depths of approximately 180 m (Fiscus and Baines, 1966). On the basis of what he considered to be accurate, albeit anecdotal information, Kenyon (1952) reported that Steller sea lions were hooked on fishing lines at depths of as much as 183 m. Thus, the

only available data at the present time indicate that free-swimming *Eumetopias* dives to depths of at least 180 m.

The cardiovascular and respiratory systems of *Eumetopias* have not been studied during diving. Recent general discussions of diving physiology in pinnipeds may be found in Harrison and Kooyman (1968), Kooyman and Andersen (1969) and Elsner (1969).

It has been suggested that the cavernous tissue in the mucous membrane of the middle ear of the Steller sea lion fills with blood during a dive, filling and reducing the air space within the middle ear (Odend'hal and Poulter, 1966). Thus, the cavernous tissue inside the bulla probably serves a pressure-equalization function during relatively deep dives.

Sandegren (1970) studied the swimming development of *Eumetopias* pups in great detail in the field and divided their approach to aquatic life into three phases: the terrestrial, the littoral, and the pelagic. The pups stayed on land for a mean number of 14 days (range 12-20 days) following parturition. During this period, water activity was restricted to awkward swimming with head held high out of water and signs of fear when they were washed into the sea. The terrestrial phase was characterized, according to Sandegren, by frequent front "flipper exercise" which consumed a good deal of the pups' time between 5 and 12 days *post partum* and disappeared when the pups initiated water activity. The principal component of this exercise is the forward stretching of the flipper along with dorsal bending of the distal phalanges. During the littoral phase the mother and pup stayed in the intertidal zone and the mother comforted the pup when it showed fear of the water and frequently stimulated the pup to join her at sea by calling. At the end of the littoral phase, pups have coordinated flipper movements and breathing and are relatively skilful in moving about in water 2 m deep. During the pelagic phase, the mother repeatedly calls the pup (a mean age of 28 days) to accompany her on swimming tours which gradually become longer until the pup overcomes its fear of leaving the rookery and entering deep water. At the termination of this phase (36-41 days of age) the pups have developed the swimming and coordinated breathing rhythm of adults in pelagic swim.

Thermoregulation

In amphibious mammals like pinnipeds a heat transport system must limit the rate at which heat is conducted away from the submerged

body in the hydrosphere while stopping the retention of excessive heat in the atmosphere. Research leading to the notion that pinnipeds deal with thermoregulatory problems by modifications of the integument, blood circulation, metabolism, respiration and body surface area have been reviewed most recently by Irving (1969, 1970).

In the laboratory, McGinnis (1968) has shown that deep-body temperatures recorded by biotelemetry in *Eumetopias* pups over a 48-hour period ranged from 37.7° to 38.1°C. Hubbard (1968) gives the mean rectal temperatures for eight Steller pups as 37.8°C.

Thermoregulation in *Eumetopias* has been studied in the field most comprehensively and quantitatively by Gentry (1970, 1973), who found that the resting postures of the animals were highly correlated with solar radiation and that social consequences of thermoregulatory behaviour were very important since males who were most likely to copulate had territories where females remained under various thermal conditions. At low substrate temperatures (10-15°C) *Eumetopias*, like other otariids, concealed their flippers and exposed a minimum of body surface area to the air. Like all other sea lions, and unlike most fur seals, Steller females huddled against one another at low temperatures, suggesting that, like fur, huddling attenuates the outward flow of heat (Gentry, 1973). As temperatures increased to 15-20°C Steller sea lions were more likely to expose their flippers to air and then become wet. At 30°C and above, most females became wet, indicating that heat loss at high temperatures occurs as a result of evaporative and conductive cooling. Territorial males drink salt water which may be exaggerated by thermal stress and simultaneous fasting (Gentry, 1981).

Food and feeding

Fiscus and Baines (1966) suggest that *Eumetopias* feed near land or in relatively shallow water (180 m). Hobson (1966) commented on the significance of vision in the feeding behaviour of sea lions. As is true of many species of pinnipeds, Steller sea lions are opportunistic predators but their food preferences and their feeding behaviour have not yet been studied in any great detail. Stomach content analysis is reviewed by Keyes (1968) in which he cites the findings of Fiscus and Baines (1966), Mathisen *et al.* (1962), Pike (1958) and others. Stomachs of Steller sea lions, taken off California and Oregon, have contained flatfishes and rockfishes and those taken in Alaskan waters contained capelin, sand lance rockfishes, sculpins and flatfishes, and one animal's stomach contained salmon. Other fish food (see Keyes' review) included flounder, halibut, cod, pollock, smelt and greenling. In examining 114

stomachs, Mathisen *et al.* (1962) found that of the total volume of food, 27% was fish, 35% squid and octopus, 20% common bivalves, and 8% shrimp and crabs. One two-year-old Steller sea lion consumed 9.4% of its body weight. Nesterov (1964), as cited in Keyes (1968), states that cephalopods played a prominent role in the nutrition of Steller sea lions of the Commander Islands, USSR.

Gentry (1970), in California waters, and Sandegren (1970), in Alaskan waters, observed females usually leaving the rookery in the early evening (1600 hours) and returning the next morning (0600 hours). This was a relatively consistent pattern in California and it was assumed by both investigators that nocturnal feeding took place during these absences. Gentry (1970) reports that although females went to feed singly during the early and middle part (May and June) of the breeding season in California, towards the later part of the season (July) females departed in large groups. Contrary to Gentry's and Sandegren's observations, Fiscus and Baines (1966) reported on feeding behaviour by Steller sea lions in Alaskan waters and noted that they left their hauling grounds in early morning in compact groups of from several hundred up to several thousand sea lions, dispersing into smaller groups of less than 50 animals five to fifteen miles from land, re-forming into large groups again late in the afternoon and returning to the hauling grounds. Fiscus and Baines (1966) report that large massing of sea lions occurs when they are feeding on schooling fishes or squid and that in the absence of schools of prey they feed singly or in small groups (two to five animals). Thus *Eumetopias*, although primarily feeding at night, also hunts large schools of prey during the day. Group feeding apparently aids in controlling the movement of schooling fishes and squid facilitating the exploitation of large schools of prey. Robert Gisiner (personal communication) has seen female Steller sea lions gather together and engage in a great deal of locomotion as well as vocal and tactile behaviour patterns just prior to their departure to the sea suggesting that such behaviours serve to synchronize group feeding.

Territorial behaviour

Gentry (1970) provides detailed descriptions of the establishment and maintenance of territories by *Eumetopias* bulls during the breeding season. Repeated ritualized threat displays (in which the bulls may first roar, then face each other in a prone position with mouths open and vibrissae forward, followed by an oblique stare—see Fig. 2) delineate each bull's boundaries at several points. Most boundaries follow

natural topographical features such as cracks, faults, or ridges in the rock. All territories at Gentry's study site (Año Nuevo Island, California) were located on shale sloping into the ocean. Frequency of boundary display was negatively correlated with geographical separation. Like northern fur seals and unlike California sea lions, the boundaries for the Steller bulls are well defined and extremely stable (Gentry, 1970; Sandegren, 1970). Gentry (1970) observed 2094 threat displays and only 43 fights among males in a given area. The number of days of consecutive territory maintenance ranged from 20 to 68 with a mean of 43 days. Mean territory size was 225 m². Selection of territorial sites and locations of threat displays were related to the location of females. Establishment and maintenance of territories occurred, however, considerably before the female population peaked. Sandegren (1970) found that of 105 copulations during the 1968 breeding season on Lewis Island, Alaska, bulls with "terrestrial" territories accounted for only 11, "semi-aquatic" bulls accounted for 88, and bulls with aquatic territories copulated only six times (see Thermoregulation).

Steller bulls generally remain on their territories during the entire breeding season and thus do not feed for about two months. Gentry (1970) found some evidence to suggest that bulls tend to defend the same territorial site in successive years. The most successful male copulated 32 times (mostly with different females). Although Sandegren (1970) claims males never established territories in areas not visited by females, Gentry (1970) saw a few such territories established. However, if a male's territory was originally not used by females, the animal sometimes extended or moved his territorial boundaries to include areas that were frequented by females.

Perinatal, maternal and pup behaviour

Perinatal and maternal behaviour of *Eumetopias* females has been most thoroughly studied by Gentry (1970) on a California population and by Sandegren (1970) on an Alaskan population. Gentry notes that premature births occurred at Año Nuevo Island as early as February and continued until live births began in mid-May. The highest frequency of births in both the northern and the southern populations occurred in mid-June and in both populations the birth rate at night was approximately half of the daytime rate, with a midday decline. Gentry saw one case of albinism and one case of twinning in his three-year study. Females probably arrived approximately three days *pre partum* on Año Nuevo Island. Sandegren (1970) found that females most favoured birthplaces just above high-tide level which were

protected from high waves and solar radiation, easily defensible and some distance from territorial boundaries. Such locations were competed for *pre partum* and the most aggressive females acquired such birthplaces (see Calloway, 1972, for a discussion of population differences in aggression in *Eumetopias* females). Aggression in females was sometimes manifested, as in males, by head nodding (with the rate of nodding increasing with greater aggression), and other threats, including belly clapping, and a variety of open mouth threats and vocalizations. The most intense aggression among females occurred just before parturition and, according to Sandegren, lasted 3-10 days in the Alaskan population. These displays by females cleared an area of 5 m in diameter of other animals (Gentry, 1970) and helped to protect the neonate from other females. Both Gentry and Sandegren note that the nearest male will interpose himself between fighting females.

Sandegren (1970) gives an extremely thorough account of the birth of a *Eumetopias* pup. In general, there is a "twisting, bending, pressing, lifting and hunching of the hind body" and a spreading of the hind flippers during all stages of labour. Like *Zalophus*, the labouring female moves in a circle, the body bent laterally in a U-shape, sometimes nuzzling the perineal region while staring and vocalizing towards the perineum. Gentry (1970) saw 66 foetal presentations, of which 61% were caudal and 39% cephalic, while Sandegren (1970) saw 17 presentations of which 41% were caudal and 59% cephalic. It seems likely that the probability of cephalic or breech deliveries in *Eumetopias* is 0.50. Timed from the bursting of the amnion, delivery had a mean duration of 16 min for cephalic presentations and 20 min for caudal (Gentry, 1970). Sandegren (1970) reports deliveries lasting 5-70 min with a mean of 30 min. Usually, the umbilical cord was spontaneously broken and the placenta normally remained with the female for 30 min or more. Almost immediately following delivery (on the average, within 44 s), the female lifted the pup by the neck and placed it in suckling position, thus preventing the pup from slipping down a crevice or into the water and protecting it from attack by other females. A vocal exchange between mother and pup usually took place shortly after parturition (on the average, with 75 s). Vocal and olfactory recognition right after birth are probably significant in the maintenance of the mother-offspring bond, particularly following periods of separation.

In the California population, Gentry (1970) rarely saw pups lifted by their mothers except right after birth. However, in the Alaskan population, Sandegren (1970) saw a great deal of "lift-drop-activation" by the mother of the pup following birth until two days of

age. These and other activations soon initiate coughing of mucus, vocalization, and crawling movements by the pup. In 17 instances, Sandegren observed crawling on an average of 2.4 min following delivery. Within a few minutes after birth there is a good deal of vocal communication and nose-rubbing between mother and pup. According to Gentry, suckling began, on the average, 31 min postpartum. The retractable nipples may vary in number from two to six and young sucked equally from each nipple. Suckling during the first day of life averaged 230 min. Sandegren (1970) describes suckling in great detail. It is not clear when weaning occurred in the California population; most likely it occurred sometime between September and June of the next year. At the Año Nuevo Island rookery in California only 2% of the pups continue sucking beyond the first year, while a bond of longer than one year between mother and offspring is frequent (about 80% of the pups are unweaned into their second year) in the Lewis Island rookery in Alaska. Although the reasons for these differences are currently unknown, the consequences on reproductive rates as well as pup mortality rates could be very significant, particularly if differential sex ratios are involved.

Females leave for sea from five to 13 days (mean of nine days) *post partum*, spending 9-40 hours at sea on each occasion. Reunification of mother and offspring are probably dependent on a wide variety of perceptual cues including temporal and spatial memory as well as auditory, olfactory and visual recognition. Females accept only their own pup and are highly aggressive toward alien pups (Sandegren, 1970). Final recognition of the pup by the mother is probably by olfaction since female nosing of the pup preceded suckling in 98% of the contacts in which suckling occurred (Ono, 1972).

At approximately 10-14 days of age pups collect in "pods" a safe distance away from adults while their mothers are foraging at sea. The most conspicuous activity within these groups is play-fighting or social play and individual play with objects such as rocks and kelp, as well as playful swimming and playful body manipulation. Play in *Eumetopias* pups, as well as subadults and non-territorial adult males, has been studied in the field (Farentinos, 1971; Gentry, 1974). Motor components in social play were similar to male aggressive behaviour and were clearly separable into fighting bouts versus boundary defence bouts (Gentry, 1974). Sexual dimorphism was clear along several dimensions including the duration of play bouts and the types and numbers of motor components used (males used a greater number of different components as well as more injurious components than females).

Copulatory behaviour

As discussed under thermoregulation, location of the territory was the most important factor in a male's reproductive success. On the basis of his observations in Alaska and California, Sandegren (1972) believes that the courtship display of *Eumetopias* females plays a significant role in initiating precopulatory encounters with males as well as stimulating territorial maintenance behaviour in the male. Gentry (1970) also observed female-initiated encounters but suggests that these are infrequent and that some "precopulatory" behaviour was actually appeasement behaviour associated with attenuating the herding tendency of territorial males. Rather, Gentry found that most copulations were initiated by males. Despite some conflict regarding the role and significance of female courtship displays, both Gentry (1970) and Sandegren (1970) agree on some of the basic behavioural parameters of copulatory behaviour in *Eumetopias*. Females were most likely to copulate 11-12 days *post partum* and they usually only copulated once. Copulation took place on land or in shallow tide pools. Females almost always terminated the copulation which had a mean duration of 16.6 minutes (Sandegren, 1970). Thrusting phases were usually 3-4 min in duration. In a rigid territorial system, such as that shown by *Eumetopias*, each territorial male respects his neighbour's border. Thus, males do not interrupt copulatory behaviour of rival males in the adjoining territories. Non-territorial or younger males were never observed copulating in another male's territory.

Vocalizations

In a typical boundary display a territorial male usually roars before going prone, and while in a prone position emits a hissing vocalization (Gentry, 1970). General characteristics of the sound structure as well as some notion of the social function of airborne calls by territorial males, females and pups are given by Orr and Poulter (1967). Descriptions of the structure and function of *Eumetopias* phonations await much more detailed research in the field. Underwater vocalizations of captive animals have been studied by Schusterman *et al.* (1970) and Poulter and DelCarlo (1971). The function of underwater phonations by *Eumetopias* is not well understood.

Sensory perception

Schusterman (1972) has suggested that in sea lions no single set of internal or external receptor mechanisms is relied on exclusively for

sensory orientation. In *Eumetopias*, descriptions of social, migratory and feeding behaviour in the field, as well as in captivity, indicate that auditory, visual, olfactory and tactual cues all play important roles in these basic behavioural functions.

The notion that an active sonar system is used for purposes of feeding orientation by Steller sea lions has been suggested (Poulter and DelCarlo, 1971). However, the evidence of the operation of a similar sonar system for feeding orientation in the California sea lion (Poulter, 1966) has been called into question (see Schusterman, 1968).

Feeding sea lions have been known to approach some prey from below, thus silhouetting them against the ambient surface light above (Hobson, 1966). Laboratory experiments under relatively well-controlled conditions have shown that when the ambient light was approximately 10^2 mL a three-year-old male *Eumetopias* could visually resolve black and white stripes underwater which subtended a visual angle of $6.4'$ of arc (Schusterman and Balliet, 1970). Schusterman (1968) has demonstrated the visual pattern discrimination skills of *Eumetopias*. A review of recent research on visual acuity in pinnipeds is given by Schusterman (1972). Jamieson and Fisher (1972) have reviewed the functional anatomy of vision in pinnipeds and Lavigne (1973) has studied the visual sensitivity of pinnipeds.

Hearing in air and under water in the California sea lion and the northern fur seal has been investigated by Schusterman (1974) Schusterman *et al.* (1972) Schusterman and Moore (1978, 1980) but no comparable work has been done on any other otariid including *Eumetopias*. If the hearing of *Eumetopias* is similar to that of *Zalophus*, then under water its best hearing sensitivity would be between 1 and 28 kHz and its conventional upper frequency of hearing would be about 40 kHz. Airborne sounds between 2 and 16 kHz would be most likely to be heard by *Eumetopias* and frequencies in air above 32 kHz are not likely to be responded to. Sounds made under water can be readily localized by pinnipeds (see Moore, 1975).

There have been no formal investigations of the temperature, tactual or olfactory sensitivity of *Eumetopias* and very few such studies on any other pinnipeds (see Dykes, 1972, for research on the tactile sensitivity of the harbour seal's whiskers).

Reproduction

Relatively little is known about the reproductive biology of *Eumetopias*, particularly the age of spermatogenesis in the males and the physiology

of reproduction in the female. Some males begin arriving at the breeding grounds during the first or second week of May throughout the breeding range of *Eumetopias* and most are gone by September. Generally the females show a peak in their numbers in June. Day length may be the stimulus which triggers the arrival of females (Gentry, 1970). At Lewis Island, Alaska, copulation begins at the end of May and continues to the beginning of July with a peak during the second week of June which generally also coincides with the greatest number of births (Sandegren, 1970). The pupping season at Año Nuevo Island, California, covers about a 58-60 day period (Gentry, 1970). In a review of the reproductive physiology and anatomy of marine mammals Harrison (1969) gives an estimate of the gestation period as 11 months and implantation of zygote in the uterine wall is estimated to occur within 3.5 months after fertilization. At Año Nuevo Island, California, still births were commonly seen as early as February (Gentry, 1970) and in Oregon still-births were seen as early as March (Mate, 1973). Premature births in Oregon were estimated to represent about 4% of the total births (Mate, 1973). Lactation in the Alaskan population of *Eumetopias* frequently lasts for more than a year. Lactation in female *Eumetopias* occurs during oestrus as it does in several other pinniped species.

Captivity

A relatively large number of *Eumetopias* pups had been brought into captivity at ages varying from a few days to a few months (Hubbard, 1968; Poulter *et al.*, 1965). Most of the young pups died soon after coming into captivity, but the stronger animals managed to survive for over one year (Hubbard, 1968; Schusterman, unpublished observations). Hubbard (1968) reviewed the laboratory care and husbandry techniques involved in raising these sea lions. The activity patterns of two yearlings were quantified by Schusterman (1968) who gives the percentage of time that each animal spent in play-fighting, grooming, basking, environmental manipulations, orientating, aggregate and individual rest and non-nutritive social sucking. Schusterman (1968) discusses the problems in training captive sea lions on visual discrimination tasks.

Diseases and Therapy

Ridgway (1972) lists of some of the major diseases found in pinnipeds as well as various approaches to their diagnosis and treatment. Hubbard (1968) discusses pinniped diseases in general and also specific diseases related to orphaned *Eumetopias* pups brought into captivity.

Acknowledgement

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

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