BREEDING AND MATERNAL BEHAVIOR OF THE STELLER SEA LION (EUMETOPIAS JUBATA) IN ALASKA

A

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BREEDING AND MATERNAL BEHAVIOR OF THE STELLER SEA LION

(*EUMETOPIAS JUBATA*) IN ALASKA

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ABSTRACT

Breeding and maternal behavior were studied in a population of the Steller sea lion (Eumetopias jubata, Steller) off Montague Island, Alaska, in the summers of 1967 and 1968. Three categories of territorial bulls were distinguished: terrestrial, semiaquatic, and aquatic. Of these the semiaquatic have significantly more females in their territories, are more consistent in the maintenance of their territories and breed more frequently than other bulls. Bulls may maintain territories continuously from 40 to 60 days.

Females deliver their young within limited areas of the rookery and may be territorial for several days after the delivery. Births are evenly distributed throughout a month-long period. Between 4 and 17 days after parturition females perform elaborate courtship displays which are directed toward the bulls. Quantitative assessment of this display indicates that its function is to trigger territorial behavior in bulls. Females are bred 10 to 14 days after delivery. The mean length of 102 copulations was 16.3 minutes.

Females reinforce certain activities in their young. Mutual recognition through vocalization between mother and young is established in the first week after parturition, and females appear to know their young by smell shortly after delivery. Females go to sea for the first time between 5 and 12 days after delivery. After that, periods on land or at sea rarely exceed 24 hours. Two to three weeks after birth pups start to swim spontaneously and when the pup is four to five weeks old the mother induces it to follow her to sea. Pup mortality was 12.5 per cent in 1967 and 14 per cent in 1968.

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INTRODUCTION

The Steller sea lion Eumetopias jubata (Schreber) has an estimated world population of 250,000 animals and breeds on islands in the northeastern Bering Sea, throughout the Aleutian Islands, and south along the west coast of North America to southern California (Kenyon and Rice 1961:232). Off the Asiatic continent it breeds on the Kurile Islands, Kamchatka, and on islands in the Okhotsk Sea. In spite of its large numbers, wide distribution, and often close proximity to human populations, the behavior of this species is practically unknown.

Investigations on the life history and behavior of Eumetopias have been few and brief, possibly because of the species' low commercial value. Information regarding habits and life history of Eumetopias appears in early travel reports from the Pribilof and Aleutian Islands and in other reports based on observations of rookeries (areas where animals aggregate to breed) along the Pacific coast (Scammon 1874, Allen 1880, Starks 1918, Newcombe et al. 1918, and Bonnot 1928).

More recently, some aspects of Eumetopias feeding behavior have been described by Fiscus and Baines (1966); growth and behavior of young sea lions is noted by Scheffer (1945); census methods, numbers and distribution in Alaska are described by Mathisen and Lopp (1963); and general abundance in its whole range by Kenyon and Rice (1961). The breeding behavior of Eumetopias has been described in a general way by Mathisen, Baade and Lopp (1962), Thorsteinson and Lensink (1962), and Orr and Poulter (1967).

The social behavior of pinnipeds has been widely investigated. Most derived knowledge, however, is based on the fur seals, Callorhinus ursinus and Arctocephalus spp, the elephant seals, Mirounga spp, and the California sea lion, Zalophus californianus. Data on other pinnipeds are needed to make an orderwide comparative behavioral analysis possible, and also to acquire more knowledge on which to base sound management.

After a preparatory study on Marmot Island in the Kodiak area of Alaska during July and August in 1966, the main study emphasizing breeding and maternal behavior was done on Lewis Island during six months in the summers of 1967 and 1968.

The sea lions on Lewis Island have previously been studied by Brooks in the summers of 1956 to 1958 (pers. comm.).

STUDY AREA

Location and Description

Lewis Island, 147° 20.5' West and 59° 53' North, is the most exposed of the Wooded Islands off the southeastern coast of Montague Island, located in the Prince William Sound area on the south coast of Alaska.

The island is about 500 m long and 150 m wide at its widest point, and is surrounded by boulder-strewn beaches and rocky points. A high plateau surrounded by steep cliffs rises in the center to an elevation of 70 m (Fig. 1). Rock specimens representative of the island substrate are gray wacke and argillaceous siltstone (Swainbank, pers. comm.).

The vegetation, which is restricted to the high plateau, is dominated by rye grass Elymus mollis, salmonberry Rubus spectabilis and members of the family Umbelliferae. A few Sitka spruce Picea sitchensis grow in the higher elevations. Apparently, spruce covered the island not too long ago as evidenced by the large number of dead trees and stumps which remain.

The following birds nest on the island: tufted puffin Lunda cirrhata, pigeon guillemot Cepphus columba, fork-tailed petrel Oceanodroma furcata, bald eagle Haliaeetus leucocephalus, rufous hummingbird Selasphorus rufus, common raven Corvus corax, black billed magpie Pica pica, and song sparrow Melospiza melodia.

Harbor seals Phoca vitulina and sea otters Enhydra lutris are

frequently seen in the surrounding waters. Once a flock of killer whales Grampus rectipinna was sighted less than one mile from the island. Shrews of unknown species are common on the island. Two river otters Lutra canadensis were once sighted on the beach.

The Rookery

In the two years of study all breeding activity occurred on the most rocky parts of the island which were exposed to the sea, in the two areas called The Rookery and East Point (Fig. 1). These irregularly-shaped areas are about 120 x 30 and 25 x 20 m large, respectively. Ninety to ninety-five per cent of the breeding population occupied the former, and five to ten per cent the latter of these areas.

The rock substrate within the breeding areas is very irregular, but without sharp edges, and ranges from loose, round rocks of a few dm in diameter to bedrock covering an area of about 30 x 20 m. Cracks, rifts, sheltered niches, overhanging ledges and caves are abundant in both areas and are of utmost importance for animals seeking protection against solar radiation. An 80 m strip of boulder beach between the two areas was never utilized by breeding animals.

Earthquake

In the Alaskan earthquake of 1964, Lewis Island rose about 5 m and the shore line was completely changed. Prior to the earthquake the East Point (Fig. 1) was separated from the island by water

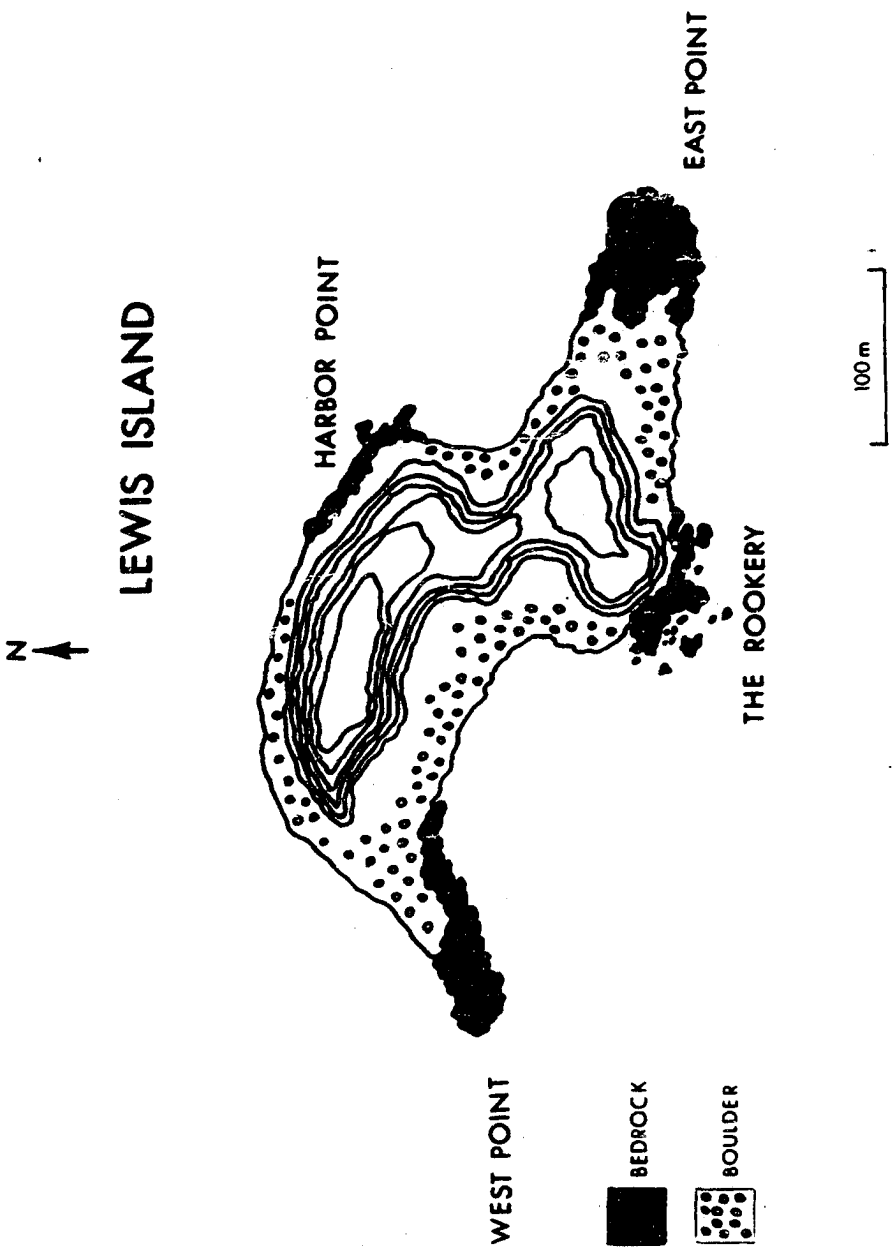


Figure 1. Lewis Island, showing areas described in text.

(Brooks, pers. comm.). Due to the land rise, it is now connected to the island. The beach now leading to the West Point was also completely submerged and the steep cliffs descending from the west part of the high plateau slipped down into the ocean. Before the earthquake, the main pupping and breeding area was on the north side of the island from Harbor Point, west. This area is now partially covered with fallen rock and no breeding took place there during the study. What is now the main breeding and pupping area was formerly freestanding rocks in the ocean, frequented by approximately 100 cows and their yearlings.

METHODS

In 1967, the study began on May 13 and ended on July 29. No observations were made on May 15-17, 23-24, June 25 and July 10-19. On May 13-14, June 14-17, 24, and 26-27, the observation time averaged 5 hours per day; during the remaining time about 18 hours were spent observing the animals each day, yielding approximately 900 observation hours in all.

In 1968, the study was initiated on May 14 and was ended on July 4. No observations were made on May 19-20, June 19-20, and 29. On May 17-18, 28-29, June 6-7, 9, 14, 21, 27-28, and July 2, six hours of observations were made each day. During the rest of the time (30 days), observation hours averaged 20 per day. Due to unusually good weather conditions on June 15-18, 22-27, and June 30-July 1, observations were made around the clock. Thus, the total number of observation hours in the two seasons totals between 1,500 and 1,600.

To provide continuity through the various phases of the breeding activity, observation periods were uninterrupted throughout each day and extended over the greatest number of consecutive days possible. For recording purposes, and to facilitate changing observers, each day was divided into 3 or 4 six-hour observation periods.

To avoid disturbing the animals and to provide shelter from rain and wind, blinds were built of driftwood. Observations in 1967 were made from two different blinds which were set up at distances of 40 and 90 m from the animals. In 1968, one blind located about

40 m from the animals was used. Eight-power field glasses and a 16 to 60 power spotting telescope were used to observe the animals.

Observations were recorded on a portable tape recorder and drawings used for individual identification of animals were done in a waterproof field notebook.

Census photographs were taken throughout the day and throughout the season using a 2-1/4 x 2-1/4 Rolleiflex camera. In 1968, censusing was done by direct counts on discrete areas and the values summed to obtain the total population. Detailed photography was done with a 35 mm Pentax equipped with a 240 mm tele-lens. A 16 mm Paillard movie camera with a 75 mm tele-lens was used to photograph behavioral events.

The characteristics of each cow were recorded by sketches as soon as observations on it were begun. Scars, parasite patches, color, plus size and shape, were the most valuable criteria used for identification. This technique made it possible to identify and follow the activities of 56 cows in 1967 and 30 in 1968, for various times after delivery of young. In 1967, 15 of the cows were followed throughout a two month period.

Thirty-one easily identifiable places within the rookery were marked with red paint to assist in recording locations and movements of animals throughout the rookery. This was done before the breeding season and no visible reaction by the animals was observed.

During the observation periods from May 21 to July 2 in 1967, and from May 14 to July 4 in 1968, the animals were not disturbed by the observers. This was made possible by locating camps out of view

of the rookery, and by having concealed access to the blinds.

Only by individual identification of animals under study is it possible to interpret the many facets of the behavior of an animal species. Because of the still unsatisfactory techniques available for marking large pinnipeds, it was necessary that the animals be recognized and learned individually.

All drawings in the thesis were done from photographs by wildlife artist, William D. Berry.

NONREPRODUCTIVE BEHAVIOR

The seasonal nature of Eumetopias breeding activity divides the yearly cycle into reproductive and nonreproductive periods. The social interactions associated with these two periods are by no means independent. Elements of behavior that outside the breeding season might appear insignificant can be of utmost importance in connection with breeding. Consequently, an understanding of the pattern of nonreproductive behavior can provide a valuable background for the interpretation of the more complex breeding behavior.

Gregariousness

Sea lions are gregarious animals and are, with the exception of sick animals or an occasional bull, never seen on land alone. They are also sociable and seem to search out places providing optimal social stimulation.

Almost every day during high tide (but rarely, or never, during low tide), the breeding season excepted, many animals may be seen in the water outside the rookery. There may be hundreds of them lying quite motionless, packed closely together. The animals in these raft-like formations usually lie on their side with one frontflipper stretched up in the air waving slowly back and forth, as if to keep their balance. Although most animals in these so-called "rafts" seem to be quite inactive, and only occasionally lift up their heads to breathe, there is constant activity and

interchange of animals, primarily in the periphery of the raft. Rafting is not seen very often in the breeding season, which, at least in part, is due to the animals' reluctance to go into the water at this time. Behavior similar to rafting is described for Zalophus californianus (Peterson and Bartholomew 1967:6).

Aquatophilic Behavior

Eumetopias are aquatophiles and are rarely seen hauled out more than 20 m away from the sea. This is more noticeable outside of the breeding season, when the animals primarily haul out in the intertidal zone. This, together with their reluctance to move to higher elevations when the tide comes in, causes strong fluctuations in the number of animals on shore, with a peak during early afternoon hours and a minimum from late evening to early morning. Their strong reluctance to allow great distances between themselves and the water can be observed on days with strong tide fluctuations. Repeatedly, the animals can be seen stampeding down to the water's edge or into the water when the outgoing tide leaves them too far from the sea. The tendency for stampeding appears to be inversely proportional to breeding status and directly proportional to distance to the water and temperature. Sea lions invariably react to overheating by searching for shady, low moist places, or by moving into the water. The behavior of estrous cows, cows with young pups, and territorial bulls (who are reluctant to move at all), however, minimizes the daily downward movement of animals, so typical under non-breeding conditions.

During storms and strong rain, the animals tend to go to sea. During the two summers of study, however, a few animals always remained even under the most severe weather conditions. On two occasions, the whole rookery was stimulated into activity by hail storms and a majority of the animals stampeded into the water.

Interspecific Relations and Reaction to Foreign Objects

Ravens and magpies, and in a few cases gulls, scavenge on placentas. If sea lions are close to the object of a bird's attention they usually react with curiosity, but sometimes with indifference and sometimes with aggressiveness. Cows with young pups are very aggressive and chase an approaching bird away immediately.

Bald eagles, always present on the island, were frequently seen flying low over the animals. Only on two occasions, however, were they seen to dive in an attempt to obtain placentas, and in both cases without success. This caused much alarm among the animals.

Although harbor seals occur in abundance on rocks and islands in the vicinity, they have never been seen to interact with the sea lions.

On two occasions sea otters, frequently seen in the general area, were seen feeding only 10 m from shore, just outside the rookery. In spite of sea lions swimming all around them, they showed no fear and both species seemed to pay little attention to each other.

In general, Eumetopias are very easily frightened and react strongly to the sudden appearance of any foreign object or animal.

The whole rookery has been seen to stampede upon the sound of a falling rock or the appearance of a low-flying eagle, magpie, gull, or raven. Two playing otter pups once caused a panic, as did a dead tree, with its roots sticking up, that drifted towards the hauled-out animals. It is noteworthy that the animals are extremely frightened by the sound of propeller aircraft, even when heard from altitudes of several thousand meters.

From a distance of 40 m the sight of a man can cause the entire rookery to stampede into the water, especially if silhouetted against the sky above the animals. Needless to say, in a study of the behavior of mammals with a complicated social system, disturbance may well introduce errors that cannot be compensated for.

THE POPULATION

As the differences in behavior of animals in different populations have to be judged in view of numbers, composition and density (among other things), attempts were made to evaluate these parameters.

Several factors made it difficult to obtain counts of the population:

1) Animal numbers on shore tended to fluctuate strongly throughout the day. On May 21, 1968, 380 animals were counted at 04:00, 730 at 12:00, and 210 at 21:30. The corresponding figures on June 22 were 210, 900 and 230. These and similar data, combined with figures on 185 arrivals and departures of marked females (Fig. 2), show that animals at this time of the year go to sea in the evening with highest frequency at around 21:00, and come back in the morning with a peak at around 05:00.

2) The number of animals hauled out during a given time of day varies considerably with the weather and tide. Figures as different as 550 and 980 on two consecutive days were obtained. During stormy weather, especially in combination with high tide in the day, more animals tend to stay at sea, as they do also if solar radiation is intensive.

3) Cows that are about to give birth or have recently given birth, as well as estrous cows, are reluctant to go to sea. They attract bulls and stimulate them to intensified territorial activity. Thus, the highest numbers of animals hauled out at one time are to be expected during the breeding season.

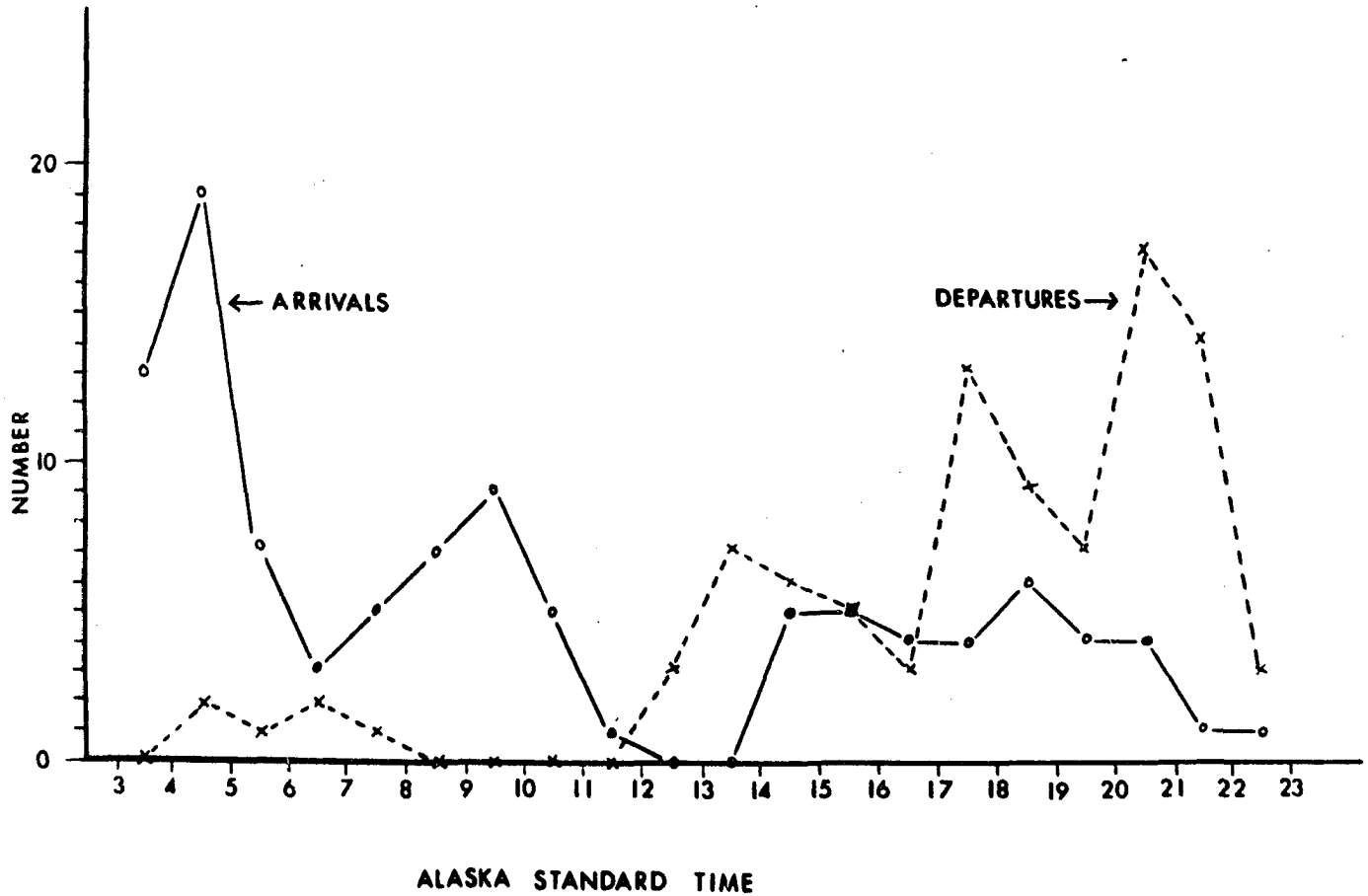


Figure 2. Hourly distribution throughout the day of 99 arrivals from and 86 departures to the sea among individually known females with pups.

With these facts in mind, 30 direct counts of all animals on the island were made between May 21 and June 30 in 1968. Thirteen of these counts were made at the time of day when the numbers were expected to be high (Fig. 3). Eight counts were made in the evening and nine in the morning. The peak counts ranged from 1,500 to 480, with an average of 930. The morning figures ran from 400 to 180, with a mean of 340, and the evening figures from 400 to 110, with a mean of 250.

Unfortunately, there is no way of telling how close the highest obtained counts (1,500, 1,400, and 1,300 animals) are to the actual total breeding population, and the figures are, therefore, suggested minima. It should be noted that the highest counts were obtained on May 25, 27, and 31, at the very onset of the breeding season. Figures as high as 980 and 880, however, were obtained late in the season on June 25 and 30. In 1956-58, Brooks (pers. comm.) estimated the population at 2,400 animals.

Although satisfactory data on population composition are lacking, it should be noted that the majority of cows (maximum count 430) were accompanied by nursing subadults of at least two year classes; this is based on the assumption that yearlings can be recognized by their puppish appearance and brown (somewhat curly) fur. Also, the size differences between the nursing subadults were remarkable, and frequently subadults almost as large as their mothers were seen nursing. In 1956-58, Brooks (pers. comm.) estimated that 800 cows with nursing yearlings were present, probably assuming that all nursing subadults were yearlings.

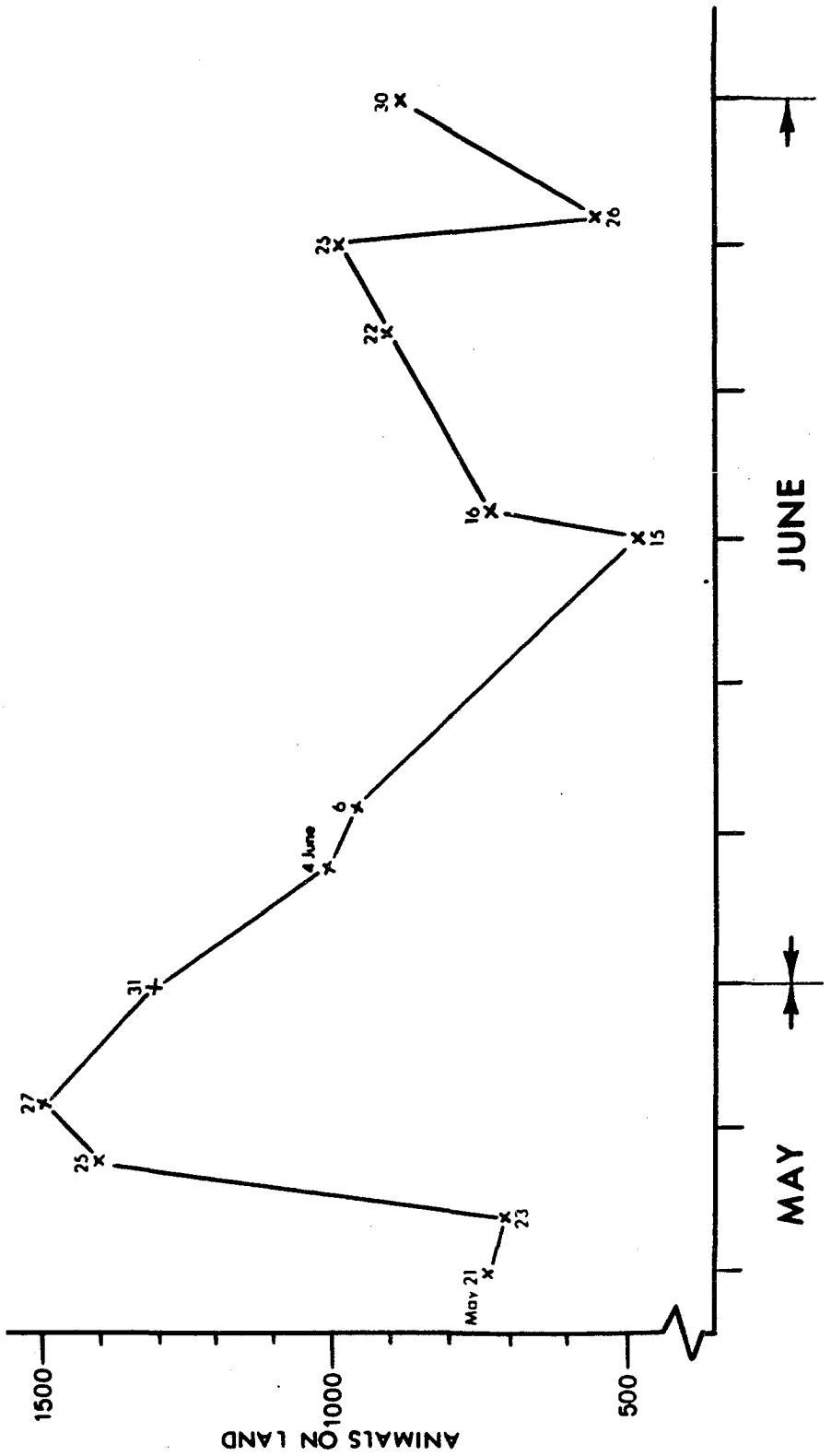


Figure 3. Total number of animals on land from 13 consecutive counts in the summer of 1968.

ONSET OF BREEDING SEASON: CHARACTERISTICS

With the onset of the breeding season, the sea lions tended to concentrate in the two breeding areas, in contrast to their previous distribution around the island.

In 1967 it was noted that shortly before the breeding started, cows showed with increasing intensity a type of display which has a strongly stimulating effect on the bulls; it was later recognized as characteristic of cows around estrus. In 1967 this "courtship display" first became apparent on May 26. In 1968 the number of these displays, directed to a total of 11 bulls, was counted daily for a one-hour period when the evening high tide came in (which is the time of day that this type of behavior occurs with highest frequency). The displays increased from 2 on May 23 to 28 on May 30 (Fig. 4). As cows start to show this type of behavior, they spend more time ashore, and instead of frequenting the intertidal area, they search out places just above the high tide line. Probably as a result of this, the number of bulls continuously maintaining territories increases. On May 21, 1968, 11 territorial bulls were counted; on May 25, 22, and on June 1 and June 6, 33 and 35 stationary territorial bulls were counted in The Rookery, respectively.

On May 29 in 1967, and May 30 in 1968, the first copulations occurred. It seems likely that the courtship display (which will be discussed later on p. 54) performed by cows is of fundamental importance in triggering the breeding functions of the bulls.

On May 30 in 1967, and May 28 in 1968, the first pups were born.

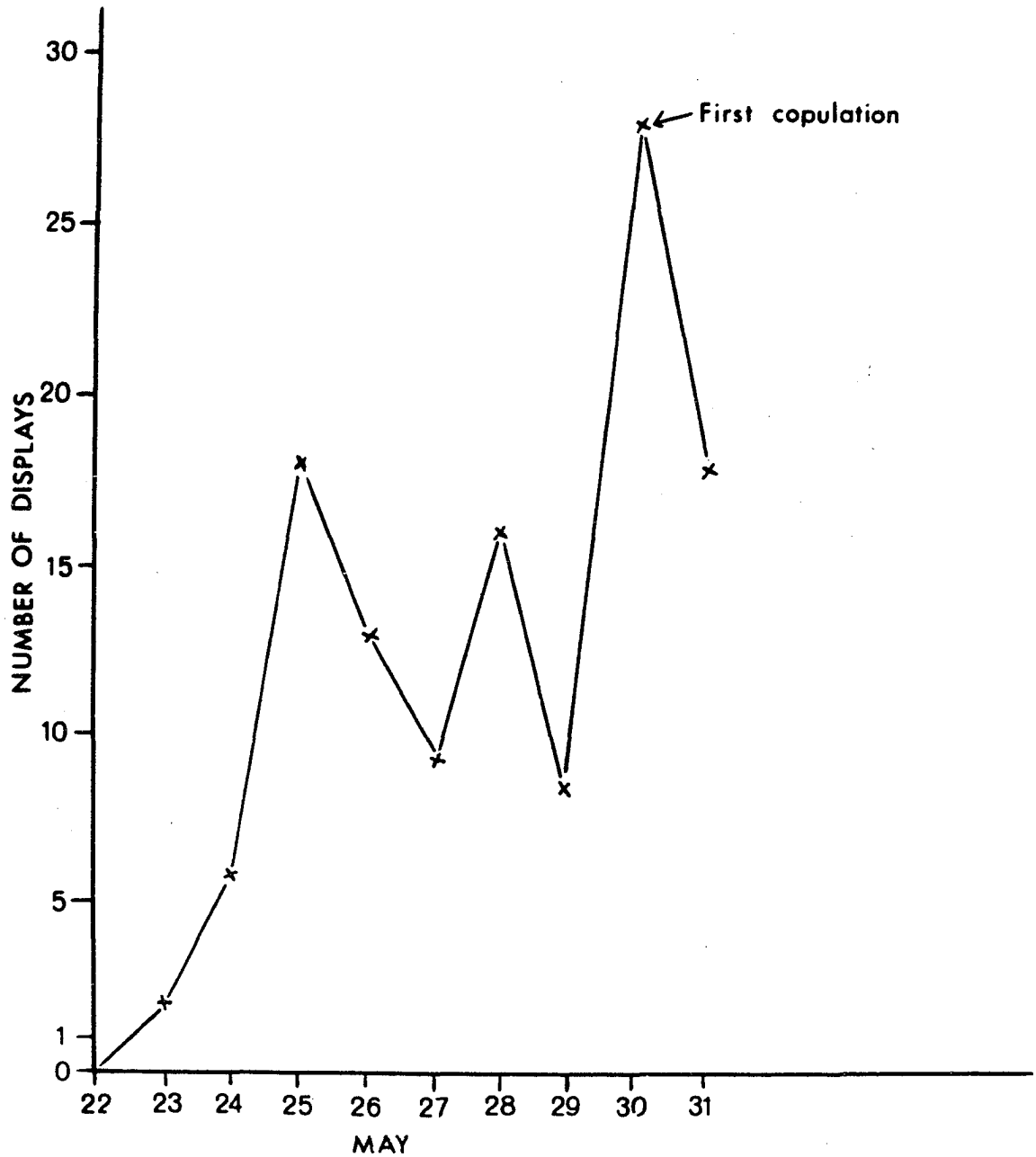


Figure 4. The cumulative number of courtship displays to which 11 territorial bulls were subjected during one-hour sampling periods on each consecutive day between May 22 and May 31 in 1968.

BEHAVIOR OF TERRITORIAL BULLS

Because of the intricate interrelations between bulls and cows in a breeding society, a few aspects of the behavior of the territorial bulls should be mentioned.

Three different types of bulls were distinguished on the basis of the location of their territories in relation to the high tide line. These were:

1) terrestrial bulls with territories above the high tide line;
2) semiaquatic bulls with territories partially above and partially below the high tide line;
3) aquatic bulls with territories below the high tide line.

In 1968, 23 bulls in the heart of the rookery were followed continuously from May 14 to July 4. Of these, 7 were classified as terrestrial, 9 as semiaquatic, and 7 as aquatic.

Of 105 copulations performed by the 23 bulls, the distribution among the three categories was as follows: the terrestrial bulls performed 11 of the copulations, the semiaquatic 88, and the aquatic 6. The difference in number of copulations performed by the three categories of bulls is significant ($p < 0.001$). Three of the bulls referred to as aquatic were of the semiaquatic type during periods with lower than average high tides. These bulls together copulated a total of four times during such periods when their territories were utilized by more cows than usual. Most copulations within the terrestrial territories were performed during periods with high tides when

cows utilized these areas with higher frequency. In summary, 56 (53 per cent) of the observed copulations were performed by the four leading semiaquatic bulls, i.e., 4 per cent of the bulls under observation.

To determine the distribution of females in relation to the three types of territories, the numbers of females in the territories under observation were counted as frequently as possible during June in 1968. The numbers in terrestrial territories (from 27 counts) varied between 0 to 14, with a mean of 3.1 cows; the numbers in semiaquatic territories (from 43 counts) varied between 6 and 28, with a mean of 14.7; and the numbers in the aquatic territories (from 22 counts) varied from 0 to 7, with a mean of 2.3. The difference between the numbers of females in the three categories of territories is significant ($p < 0.001$). Furthermore, observations of individual cows show that females around the time of delivery and estrus prefer the zone just above the high tide line which coincides with the semiaquatic territories. Thus, semiaquatic bulls have more estrous females in their territories and therefore have more opportunities to copulate.

Although idle bulls were always scattered around the periphery of the rookery, they never established territories in areas not visited by cows. The duration of territorial maintenance seems to be closely related to the frequency and duration of cows in the area of the territory. Although the mere presence of a cow on land seems to be enough for a bull to establish a territory, numerous observations indicate that unless subjected to a certain amount of courtship display, they do not copulate or show other types of behavior which are typical of breeding bulls.

Bulls were observed to maintain territories from a few to over 60 days. In 1967 six semiaquatic bulls maintained their territories from 40 to 60 days without leaving them. In 1968 the 23 bulls under regular observation maintained territories from 12 to 50 days. Several that were present on May 14, when observations began, were still present on July 4, when observations were discontinued. Semiaquatic bulls were never observed to leave their territories during the breeding season while terrestrial and aquatic bulls left on occasion, sometimes for more than 24 hours.

The daily activity rhythm of the breeding bulls reflects the general activity pattern in the rookery being high in the late evening, the night, and during the day's high tide; and low during the low tide periods (Fig. 5).

In the strong competition between cows for space within the limited areas where breeding and deliveries take place, bulls intervene and discriminate against nonestrous cows. This discriminatory behavior creates a "conveyer-belt" type of breeding and delivery pattern, in which cows ready for delivery and estrous cows gain a place if space and their status permit. When past estrus, they are forced by the bull to leave if aggressive interaction with an estrous cow in competition for the limited space arises. This type of behavior of bulls gives cows maximum safety during the short period between delivery and estrus when rearing of the young is most important.

The pattern described above is best illustrated by one of several observed examples. On the evening of June 5, 1967, two days after cow D had given birth, high tide and strong wind produced huge

waves that almost washed her pup away. Cow D started to lift her pup in small stages towards a more sheltered place, but was vigorously threatened by three other cows and had to stop. She then did what cows frequently do in a stressful situation--she left the pup behind and tried to gain a place on a protected ledge. Attempting to find a place for herself and the pup seemed to take priority over the actual caretaking of the pup. The pup was washed into the water. She managed to retrieve it and again moved into a safe position, but was again threatened by above mentioned cows. When the situation became very critical, the territorial bull appeared and drove the three cows away. Cow D and her pup were then protected from the storm under the safest possible conditions.

If space is limited, bulls do not allow subadults without mothers inside of their boundaries and wild chasing of subadults often initiates an activity period. Breeding bulls intervene in aggressive encounters among cows by moving between the aggressors and separating them. At least on some occasions, this task seems to have highest priority. Thus, bulls in territories containing many cows with young pups (such cows being especially aggressive) can be busy for hours in such activity. Overly aggressive cows are sometimes subjected to hard blows from the bull's head or are pushed away. On three occasions bulls have left cows during a copulation only to return after quieting aggressive cows.

Breeding bulls sometimes try to prevent cows from leaving their territories. In this sense, the female aggregation within a territory may be called a "harem." The herding response in the bulls is weak,

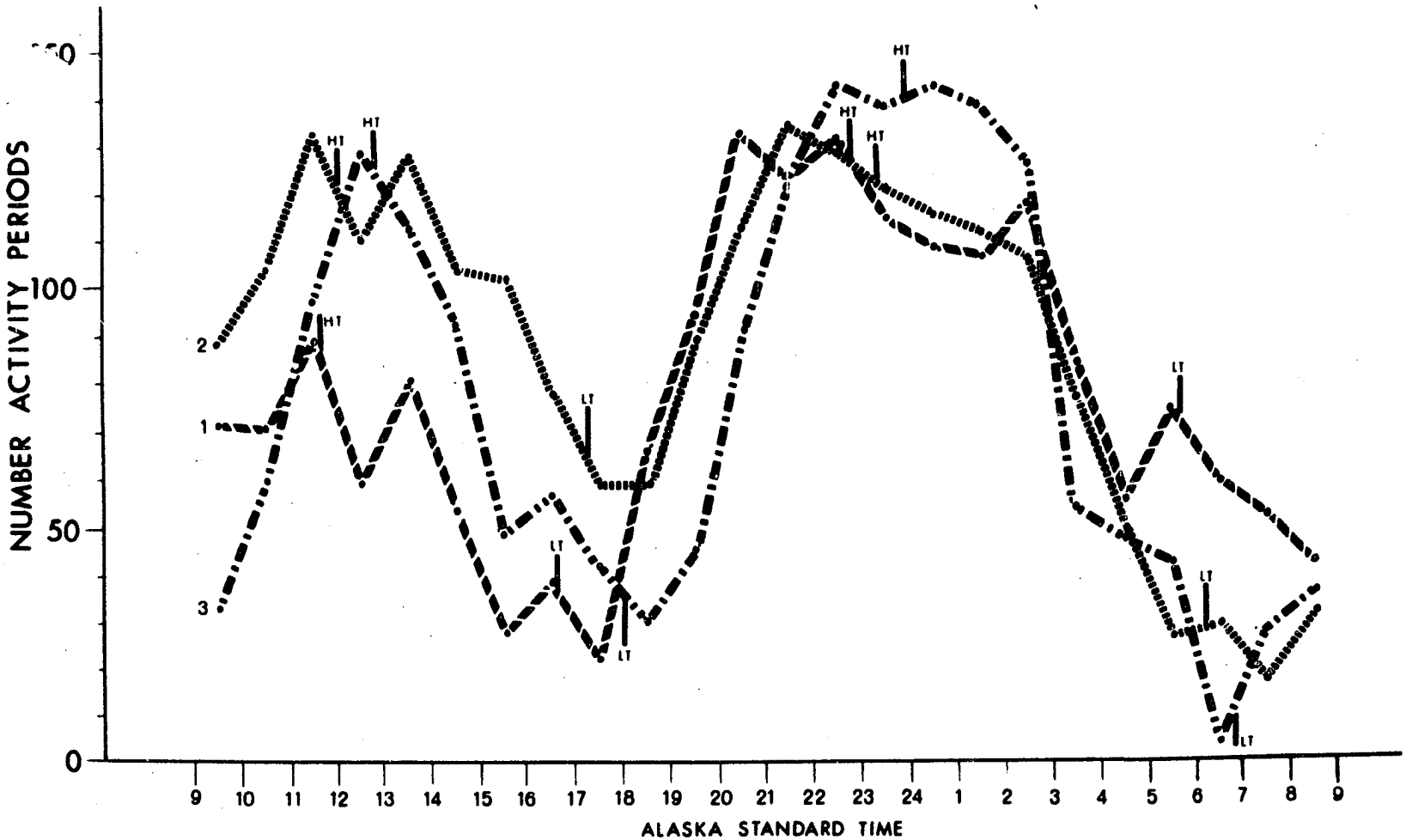


Figure 5. Variation in activity among 13 territorial bulls, measured by cumulative number of five-minute periods of activity per hour, during three consecutive 24-hour periods (1,2,3) beginning 09:00 on June 23 in 1968. High tide (H.T.) and low tide (L.T.) are indicated in the figure.

however, and seems to be directed exclusively towards cows with young pups or estrous cows. In many cases, the herding behavior of the bulls seems to be initiated by the cows (see "Courtship Display of Females and the Occurrence of Estrus").

In general, territorial boundaries among bulls are well defined. This is in contrast to the lack of definite boundaries suggested by Mathison, Baade and Lopp (1962:470) and also by Orr and Poulter (1967:201). Boundaries do shift, however, with highest frequency at the beginning and the end of the breeding season. After each shift, new, well-defined boundaries are established. In the periphery of the rookery, boundary lines may be less stationary and tend to change. This may be attributable to the absence of mutual territorial marking and also to the generally nonstatic conditions in these areas.

After a short period of observations, it became apparent that Eumetopias cows differ not only in size and color, but also in physiognomy, temperament, and aggressiveness. The aggressiveness appears to change in daily, seasonal, and social patterns. The daily pattern coincides with the general activity rhythm of the rookery with peaks during high tide when room is limited. The seasonal pattern shows peaks around the time of delivery when the cows, in most cases, are territorial and vigorously defend a place. This aggressiveness lasts from 3 to 10 days after delivery, and the period increases in length with increased crowding. The social stratification of aggression follows a dominance order, and aggression increases with the status of the cow. My observations indicate that a well-stratified social order exists which, at least in part, is related to the size of the animals. That this order is of fundamental importance in the organization of the complicated social structure of sea lions is evident from the material that follows.

Threats and Aggressivity

Although an Eumetopias rookery, for short daily periods, may appear peaceful with animals packed close together, aggression is the rule because there is a constant struggle for the acquisition of places within the framework of the society.

Aggression has two main manifestations--fighting and threats.

Fighting between bulls and between cows occurs, but is rare, and aggression is usually channeled into less energy-consuming and non-injurious activities such as threats.

Several different aggressive displays occur during encounters among cows. The most common are described in the following hypothetical example of the interactions between cow 1 and cow 2 when the former approaches the latter in a presumed attempt to gain her place.

1) Vocal Threat. Cow 1 approaches cow 2, strongly vocalizing. Cow 2 either moves away or answers the threat by turning her head towards cow 1 and vocalizing in return. Vocal threats are probably part of all aggressive interactions and are intricately associated with movements and postures.
2) Lateral Open-mouthed Threat. Cow 1 remains where she is or moves closer to cow 2. She turns her head laterally, as does cow 2. The cows may end up breast to breast, heads parallel, only a few cm apart, pointing in opposite directions. The cows vocalize while displaying their facial profiles with canines and long (usually erected) vibrissae in a lateral open-mouthed threat (Fig. 6), as described for Zalophus cows (Peterson and Bartholomew, 1967:29). Then, either cow might move off.
3) Frontal Open-mouthed Threat. Cow 1 moves closer, stretches her neck and head straight towards cow 2, opens her mouth wide and keeps it open while vocalizing (Fig. 7). Cow 2 moves away or answers with the same threat. The cows may also separate. A similar threat is described by Peterson

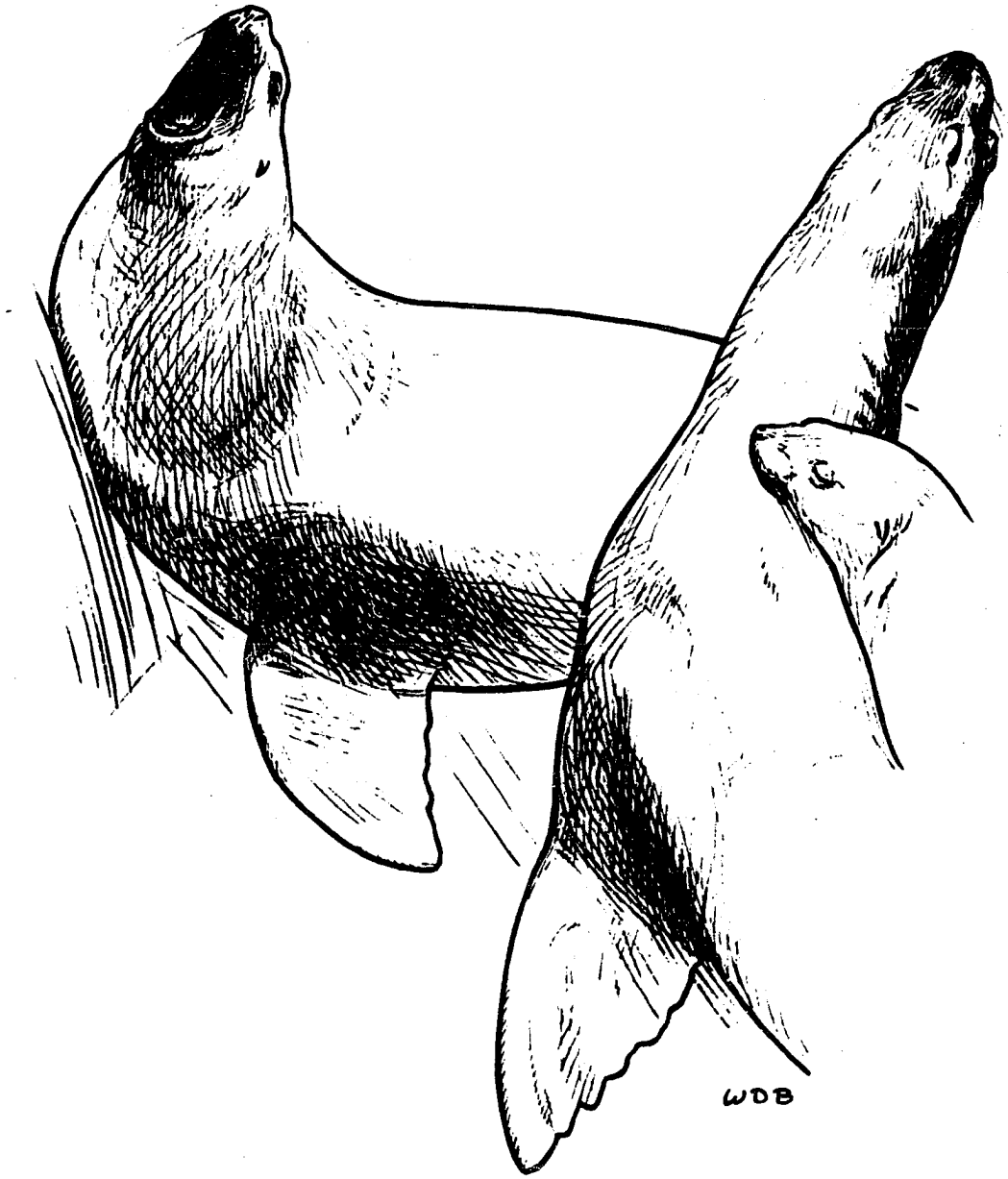


Figure 6. Lateral open-mouthed threat between females. Aggressor to the right.

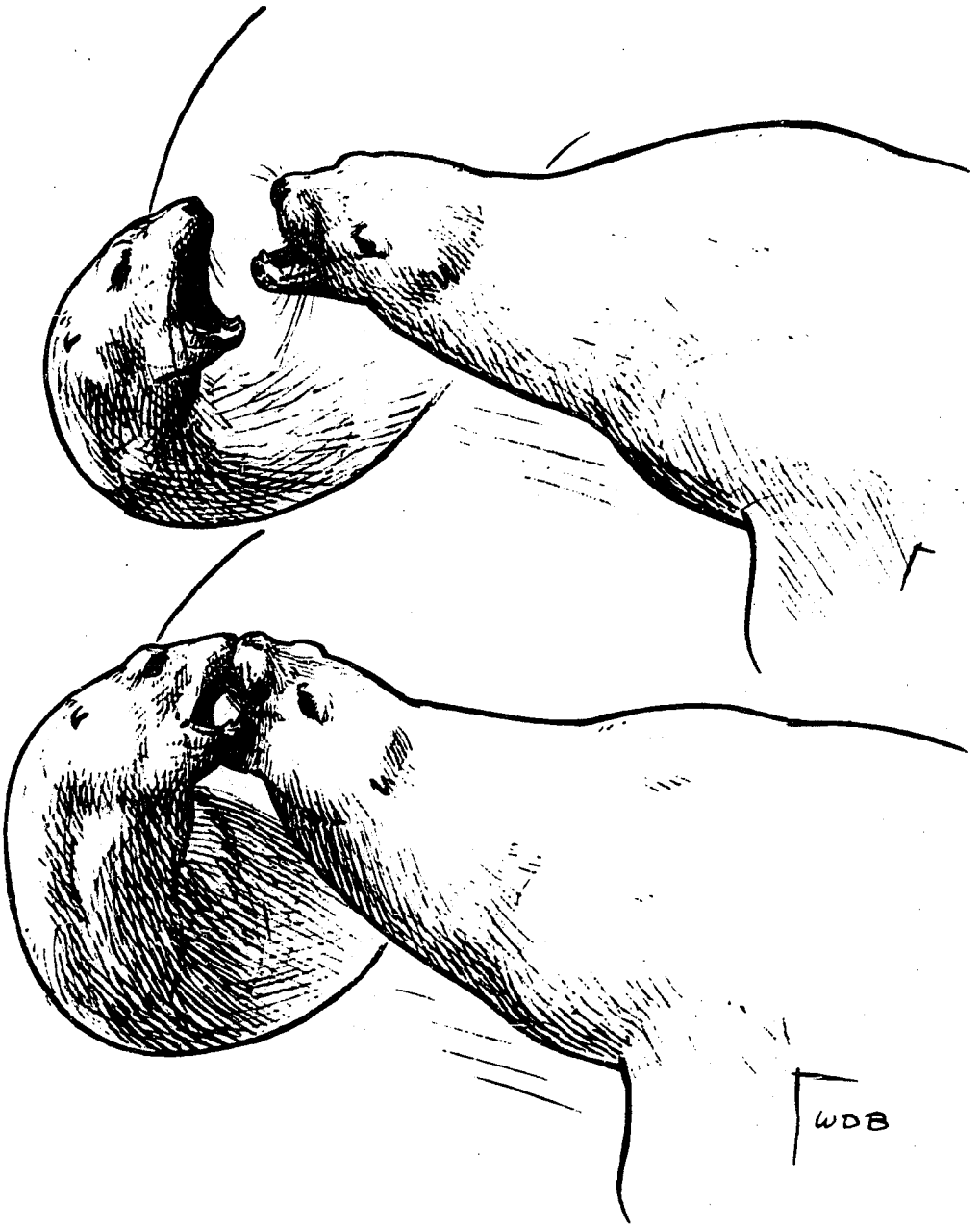


Figure 7. Frontal open-mouthed threat between females. Aggressor to the right.

Figure 8. Crossed-mouth threat between females. Aggressor to the right.

(1965:152) for Callorhinus cows and by Peterson and Bartholomew (1967:29) for Zalophus cows.

4) Crossed-mouth Threat. Rapidly, cows 1 and 2 cross their mouths as if in a "hand-shake," so close that the tongues, teeth, and whiskers of each seem to touch those of the other (Fig. 8), and in this position they make very fast lateral shakes. While so doing, the cows usually try to push each other out of position, breast against breast. In 63 similar cases followed up to this point, cow 1 drove cow 2 away 46 times, cow 1 retreated 7 times, and a bull intervened and separated the cows 10 times.

5) Fight. This is only observed among cows around the time of delivery. The fight is often vicious and bites are usually directed towards the upper part of the neck of the opponent, or towards the pup of the opponent; in fact, on occasion the aggressor may throw the opponent's pup away before attacking the cow herself.

Although this sequence of aggressive elements is often followed, certain elements may be omitted entirely or may occur so close together that they are hard to separate. Also, this chain of events may occur in an uninterrupted sequence of very short duration.

6) Belly-clapping. From a standing position, the cow making the threat leans slightly to the side and supports her body with the frontflipper on that side. With her free front-flipper she claps her wet belly, producing a loud sound that can be heard a long distance (Fig. 9).

The belly-clapping threat can be directed towards one animal or in a general way to surrounding animals. The flight-reaction of the recipient (or recipients) is usually strong. Thus, cows have been seen to gain the most attractive places in the rookery merely by moving towards a cow already lying in such a place and making this threat. Also, cows have been seen to move into an area and then to perform the threat in order to select a place after most of the animals have fled.

The belly-clapping threat occurs among a small number of cows, and the same females have made the threats repeatedly throughout the season as has also been observed among Eumetopias cows in California (Gentry, pers. comm.).

Never was a cow observed to respond to this threat by making the same threat and never was a cow with a pup observed to make the threat. On three occasions, young bulls were seen slapping the wet rock with their frontflipper, producing a very similar sound which also caused a flight reaction in the surrounding animals.

7) Head-nodding. During aggressive interactions among cows, certain individuals were frequently seen performing fast nodding movements of the head. As noted earlier, this is one of the most common behavioral elements among bulls and is constantly seen when a bull is fighting, marking boundaries, or chasing young animals out of his territory. The rate of nodding appears to increase with increased aggression.

Figure 9. Female making belly-clapping threat. Left flipper is hidden behind the animal.

Description of Birth Areas

In 1967 two limited areas, about 8 x 10 and 5 x 8 m in size, were used by females for delivery. These areas, A and B, were located in the central part of The Rookery (Fig. 1). Daily records of deliveries show that all but 6 of 56 pups were born within these two areas. Three births were never localized and the remaining three took place in an area, C, about 7 x 6 m in size, also located in The Rookery. In 1968 five of the 52 recorded births took place in an additional area, D, about 8 x 9 m in size and located on East Point (Fig. 1). During this year three pups were born in unknown locations, 31 pups in areas A and B, and 13 in area C.

The delivery areas had the following attributes in common, the combination of which was not found elsewhere in the rookery:

1) Sufficient space above high tide line, and so located that shelter was provided during storms.
2) Easy access to protected shallow water (which seems to be of importance for the early swimming development of the pups).
3) Gentle slopes around the area such that pups could make their way up if they fell, or were pushed, washed, or thrown down.
4) Locations which provided protection against strong solar radiation.

Cows ready for delivery also seemed to be strongly attracted to areas where other cows had recently given birth.

In summary, over 90 per cent of the deliveries occurred within three

territories in 1967, and within four in 1968, showing that the areas utilized were very limited. The areas were located in the central parts of the rookery where the most stable territorial conditions exist.

Description of Birthplaces

From the exact locations of 30 births observed in 1967 and 23 in 1968, it is apparent that special sites within the birth areas described above were selected for delivery. At least 12 births in 1967 took place in practically the same spot, within an area of 2 x 4 m, and 9 other births occurred within a similar sized area. The case was the same in 1968, with the deliveries clustered in certain spots.

The most favored locations were just above high tide level, and were gently-sloping niches, protected from high waves and solar radiation, and easy to defend from other animals. Also, these niches were located at a distance from the boundaries of the territory, where the activities of the bull would not present an extra danger. No birth occurred more than 1.5 m above the highest tide plane nor more than 10 m away from the high tide line. This is in accordance with the aquatophilic nature of the animals.

Seasonal and Daily Distribution of Births

The frequency distribution of 53 births in 1967 and 43 in 1968 contain no marked peaks (Table 1 and Fig. 10). It is noteworthy,

however, that the highest frequency of births in both 1967 and 1968 occurred in the period from June 10 to June 12, coinciding with the peak in copulations observed in 1968. Investigations in California by Peterson and Gentry (1967) indicate that this is not the case for Eumetopias in its southern range where the number of pups increases rapidly to a maximum in the middle of June.

In the two seasons, the time spans between the first and last deliveries were similar--33 days in 1967 and 32 days in 1968. Scheffer (1945:390) estimated the season of parturition for Eumetopias on St. Paul Island to be 31 days.

The distribution of 35 births through the day (Fig. 11) shows a sharp decline in intensity between 06:00 and 12:00 and a peak in the afternoon hours. The distribution of 12 births through the night is hypothetical and is based on the total births that are known to have occurred between 22:00 and 04:00. Only three of these were observed; the rest were concluded from newborn young first observed in early morning. The decline in births in the late morning hours could be caused by the animals' sensitivity to solar radiation. Among California sea lions, deliveries seem to occur exclusively in the night (Peterson and Bartholomew, 1967:31).

Factors Influencing Timing of Delivery

The long delivery period and the small variation in the number of pups born each day suggests the existence of effective mechanisms controlling the pattern of births throughout the season. Although severe weather conditions seem to cause occasional declines in number

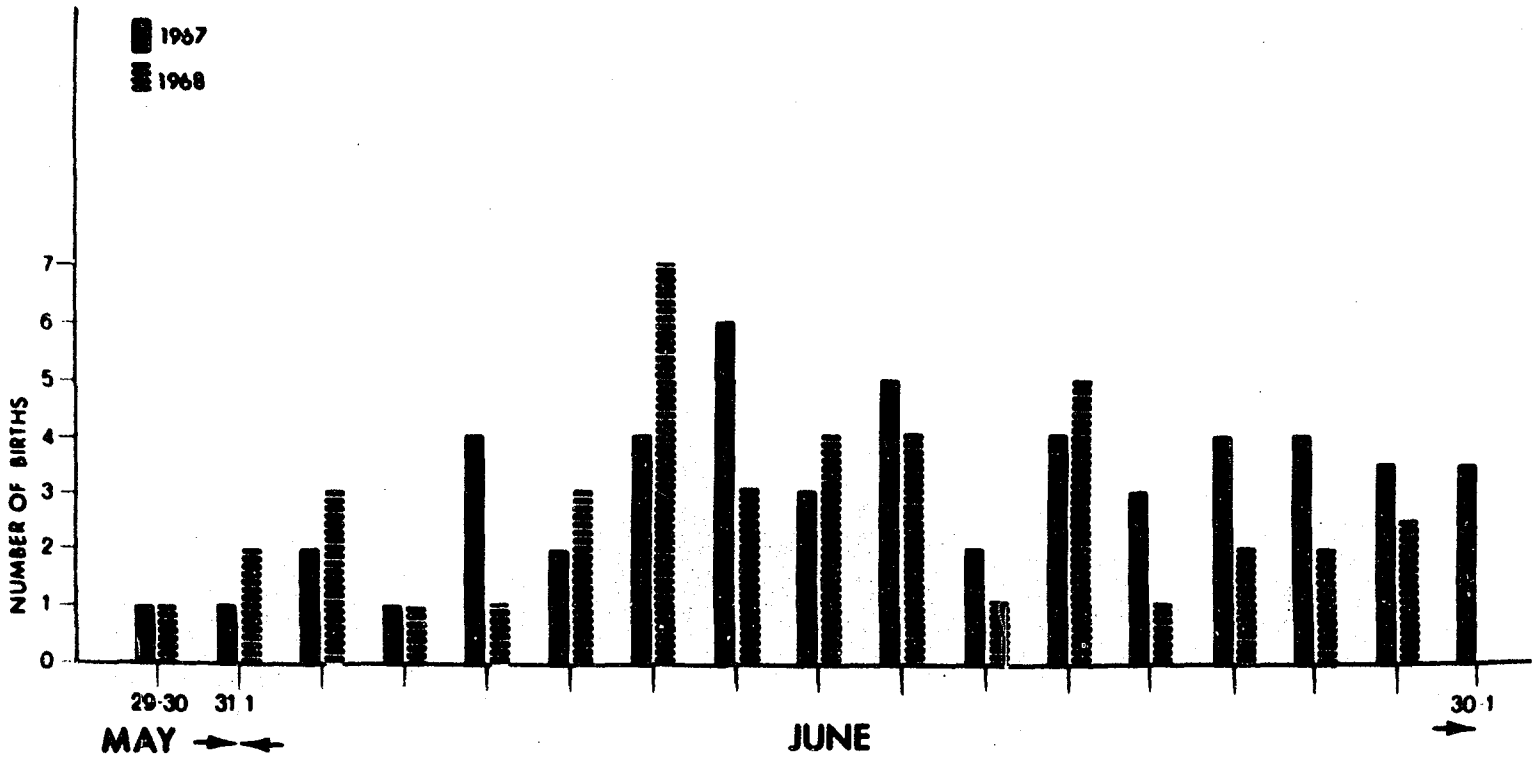


Figure 10. Distribution of number of births in consecutive two-day periods throughout the delivery season in 1967 and 1968.

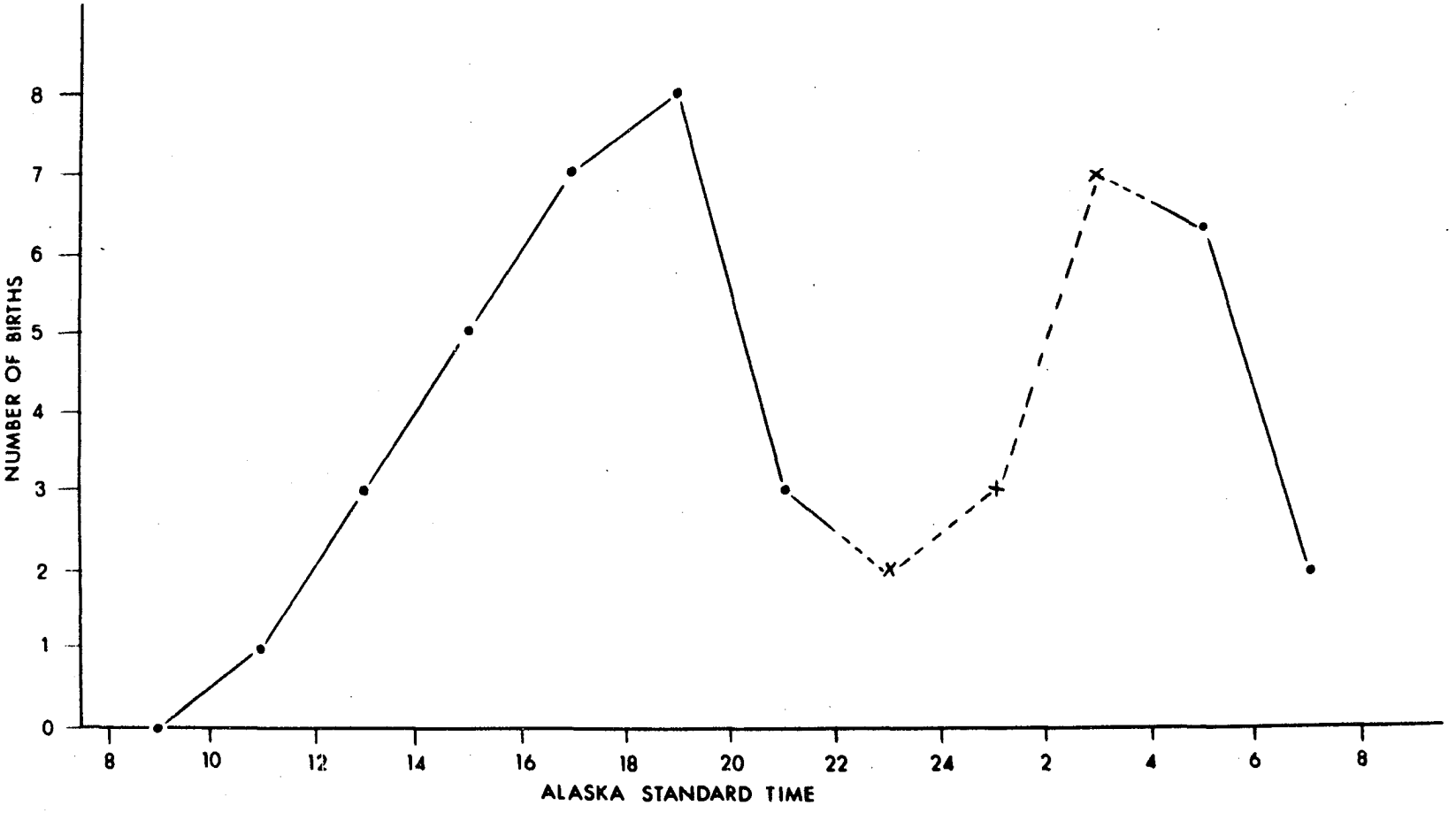


Figure 11. Distribution of 35 births per two-hour period throughout the day shown as points on the curve, plus hypothetical distribution of 12 births known to have taken place in the night shown as crosses.

Table 1. Dates of parturition in 1967 and 1968.

1967			1968		
Code	Date	Number of Births	Code	Date	Number of Births
1	May 29	0	1	May 29	1
2	30	1	2	30	0
3	31	0	3	31	2
4	June 1	1	4	June 1	0
5	2	1	5	2	2
6	3	1	6	3	1
7	4	1	7	4	0
8	5	0	8	5	1
9	6	1	9	6	0
10	7	3	10	7	1
11	8	1	11	8	2
12	9	1	12	9	1
13	10	3	13	10	5
14	11	1	14	11	3
15	12	4	15	12	0
16	13	3	16	13	3
17	14	2	17	14	1
18	15	1	18	15	3
19	16	2	19	16	3
20	17	3	20	17	1
21	18	2	21	18	0
22	19	0	22	19	1
23	20	3	23	20	3
24	21	1	24	21	2
25	22	1	25	22	0
26	23	2	26	23	1
27	24	1	27	24	2
28	25	3	28	25	0
29	26	2	29	26	1
30	27	2	30	27	1
31	28	1	31	28	0
32	29	2	32	29	2
33	30	2			Total 43**
34	July 1	1			
		Total 53*			
Mean 1967:		1033/53 = 19.4 = June 16	Mean 1968:		710/43 = 16.5 = June 14

*In 1967, 3 pups were born at unknown but scattered times, giving a total of 56 pups born in 1967.

**In 1968, 6 pups were born at unknown but scattered times, giving a total of 49 pups born in 1968.

of births per day, weather seems to have little effect on the overall pattern.

It has already been seen that certain areas and certain sites within these areas attract cows ready for delivery. Also, the territorial behavior of the bulls within these areas tends to minimize conflicts among cows. In competition for space within the area, bulls favor cows ready for delivery, cows with young pups (before estrus) and estrous cows.

There are, however, variations among cows in their behavior, social status and relative density per given area at the rookery, which contribute to the pattern of the birth of pups. When a cow approaches the time of delivery she tries to gain access to one of the birth areas. When competing with other cows for access, her chance of success is in proportion to her relative status among all cows competing at the same time, provided that all cows are equally preferred by the bull(s). Cows of low dominance seem to be satisfied with marginal areas where a cow of high dominance would not choose to give birth.

The chance a cow has to gain access is also influenced by the number of cows already occupying the area. The probability of gaining a place is inversely proportional to the number of cows already occupying the area and also to the number of these cows that are about to deliver or have newborn pups. This is due to the peculiar behavior of such cows. Cows with young pups are extremely aggressive towards other cows with young pups, but they are also attracted to them. Thus, a birth area can be occupied exclusively by such cows

spread maximally by the forces of aggression, yet working as a unit to dam the area against intrusion by new cows. The aggressiveness seems to increase with animal density as does the length of the aggressive period.

It is apparent from the foregoing discussion that behavioral and physiological mechanisms exist to prevent an accumulation of deliveries within a short period. Although gestation periods may be timed to fit the broad delivery pattern, the question still remains: what factors regulate the onset of the delivery?

Eight cows were observed for a maximum of four days prior to delivery and the following behavioral trends were noticeable:

1) Six cows were seen, for from one to three days, repeatedly attempting to gain a place in one of the birth areas. They did this by rushing into the area among the cows and vigorously threatening to the left and to the right. They then withdrew rapidly if the resistance was too great. Between these attacks they would lie quietly outside the area. As time progressed, the attacks became more vicious and fights with pup throwing and biting were observed in three cases.
2) Two cows that had gained places in the birth areas were driven away by aggressive females when they showed signs of impending delivery. They returned after about 10 and 25 hours, respectively, and delivered 8 and 11 hours after their return.
3) In two cases, contractions ceased, when, during delivery, cows were involved in strong aggressive interactions.

4) After cows had successfully gained a place, they became very quiet, merely lying for hours without moving.
5) The period between the acquisition of a birthplace and the onset of delivery appeared especially long under crowded, aggressive conditions.
6) Deliveries have mostly occurred after periods of relative inactivity.

According to Naaktgeboren (1963:11) births of mammals usually coincide with the inactivity period. His explanation for this is that during inactivity parasympathetic activity is dominant, while during activity sympathetic activity is dominant. The former stimulates uterine contractions, the latter depresses contractions. Thus, a mechanism is available that could (within limits) delay the delivery until optimal conditions arose. When crowded conditions prevail, overly frequent aggressive encounters would make sympathetic activity dominant until a cow had gained a place and had spent a certain amount of time under peaceful conditions. At that time, parasympathetic activity would take over and initiate delivery.

Delivery

The birth of an Eumetopias pup is one of the more noticeable events in a rookery. This is due to the intricate social interactions involved in the selection and acquisition of a birth place, plus the often protracted, elaborate labor during which the cow's behavior frequently arouses strong reactions from surrounding cows and (consequently) territorial bulls. Similar birth behavior is

indicated for Arctocephalus pusillus (Rand 1967:18). In contrast to this is the rapid and simple delivery of Callorhinus (Bartholomew 1959:164).

The following observations on the delivery of pup B-67 by cow B includes a general description of the typical birth behavior of Eumetopias.

> -210 minutes (before delivery)
>
> Cow B has been lying passively for several hours. Suddenly she starts to move her body, especially her hindbody, restlessly. She stands with shoulder and hindflippers in the usual standing posture and then lies down, repeating this several times. Vaginal dilations and contractions are visible.

The restless movement of the body has also been described for Zalophus (Peterson and Bartholomew 1967:31). Vaginal dilations in the early stages of delivery have been observed for Zalophus (Peterson and Bartholomew 1967:31) and for Callorhinus (Peterson 1965:155). Although they are not always easily observed, contractions may be seen throughout an Eumetopias delivery with increasing intensity towards the end. It is interesting that upon very strong aggressive interactions with surrounding cows, contractions diminish. Also, they appear to decrease in intensity and frequency during the inactivity periods which occur regularly throughout a delivery. The frequency of contractions has been observed to change from 5 to 10 per minute from the early to the late stages of delivery.

> -202 minutes
>
> The cow threatens all animals that approach.

At this stage, cows start to reach their peak in aggressiveness and most cows observed keep open an area around them (3 x 3 m is not unusual). The data are probably biased towards cows of high dominance, however, because low status cows seem merely to select a place lower down, and show less aggression and territoriality, making such cows harder to discover and observe. Considering that the claimed area is kept and defended for several days -- up to 11 days in some cases -- it might well be called a "territory." Territorial activity in the area of delivery has been described for other species, e.g., Arctocephalus (Rand 1967:18).

-198 minutes

Cow B is lying on her belly, frontflippers along her sides, hindflippers and pelvis bent in under her. She stretches the hindflippers straight back so that her body is maximally elongated. Then she stands up and twists her hindbody through 90 degrees, exposing the perineum. In this position she repeatedly bends her hindbody forward like the tail of a crayfish. These bending movements are followed by rigid backward-stretching of the hindflippers and rigid spreading of the digits of the hindflippers (Fig. 12), and, finally, relaxed, flapping movements of the folded hindflippers.

She turns over and lies on her belly with her pelvis bent in under her. She then twists her hindbody again, and extends it over the edge of the ledge on which she lies, swaying it up and down. This is followed by

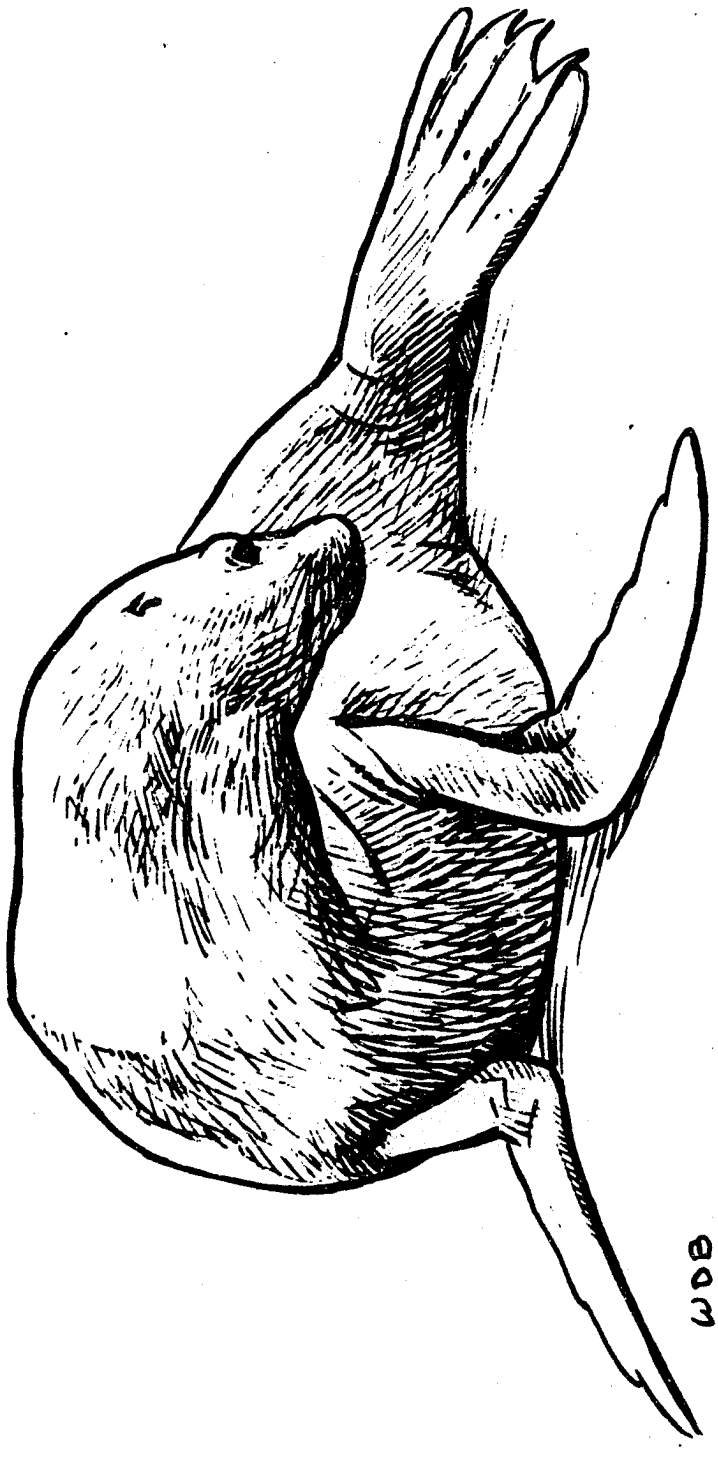


Figure 12. Female in labor staring towards slightly rotated pelvic region. Note the stretching of the hindflippers and spreading of the digits.

twisting, rigid stretching, and spreading, holding the hindflippers straight back; then by pronounced bending forward of her hindbody while pressing the hindflippers on her belly. After this, flapping, relaxed movements of the hindflippers are made.

This pattern of movements is repeated several times. Simultaneously, she hunches her back, makes small lifts of her hindbody, and bends her head and neck backwards, making rolling movements like an athlete softening up his neck muscles.

The twisting, bending, pressing, lifting and hunching of the hindbody and the stretching and spreading of the hindflippers, although varying in frequency and occurrence from case to case, have been seen during all stages of labor. The swaying of the hindbody over a ledge has been observed only twice during the early stages of labor. All of these movements are probably of importance for achieving the fastest possible labor. It is possible that they serve a contraction stimulating function. Frequent change of body position, hunching and pressing are described by Naaktgeboren (1963:8) for the domestic cow. Rotation of the pelvis through 90 degrees is described for Callorhinus (Bartholomew 1959:164).

-185 minutes

Cow B rests on belly for eighteen minutes.

Resting is frequent throughout the early stages of labor and is often of considerable duration. As the birth of the pup approaches, however, these periods become shorter and fewer.

-167 minutes

Cow B stands up and hunches her hindbody.

-162 minutes

Cow B rests for sixteen minutes.

-146 minutes

Cow B stands up and hunches her back several times. She then circles, body laterally bent in the shape of a U, as though she were trying to catch her own tail.

This is described for Zalophus (Peterson and Bartholomew 1967:31) and Callorhinus (Peterson 1965:155).

-144 minutes

Cow B rests quietly for 101 minutes. On two occasions she makes small hunching movements while bending her head back and looking towards her hindbody.

-43 minutes

Cow B raises her hindquarters. While circling, she lifts her hindbody onto the shelf above, so that it rests as high as her shoulder. She goes through the rigid, bending forward, pressing movements of the hindbody, the backward stretching and spreading of the hindflippers, and the relaxed flipping of hindflippers.

-39 minutes

She moves her hindbody down from the shelf. Then she circles, her body bent in the shape of a U. While doing this she looks towards her hindbody and vocalizes twice. She stops after moving approximately 360 degrees.

Prior to this she has been completely quiet.

The circling movement with the body bent laterally in a U shape, head stretched towards, and often touching, the perineal region while vocalizing and staring (Fig. 13) towards the vaginal orifice are the most typical birth behavioral elements and, with two exceptions, have been part of the later stages of all observed deliveries. They usually occur shortly before the onset and continue to the end.

The vocalization, accompanied by bending and staring towards the vaginal orifice, increases in intensity towards the end, and the whole pattern suggests that it is done in anticipation of the pup, but, in addition, it may be a vocal marking of the "birth territory." That the latter explanation is at least partially true is indicated by the strongly aggressive reactions that the sound evokes from nearby cows. On several occasions females several meters away from the cow in labor have been observed to leave their less than four day old young only to threaten a female in labor. In view of the fact that cows with young pups are very reluctant to take their eyes off the pup, much less to separate from them, this behavior indicates that they consider themselves severely threatened. Considering the structure of the birth areas, with sloping, often very slippery ledges and numerous crevices leading to the sea, it can be seen that a helpless newborn pup could easily disappear from its mother's view if not taken care of immediately upon delivery. Moreover, nearby cows react to a newborn pup which comes too close by biting, and throwing it, and can cut a less dominant mother off from her pup as effectively as the strongest fence. In view of the above, the importance of the circling

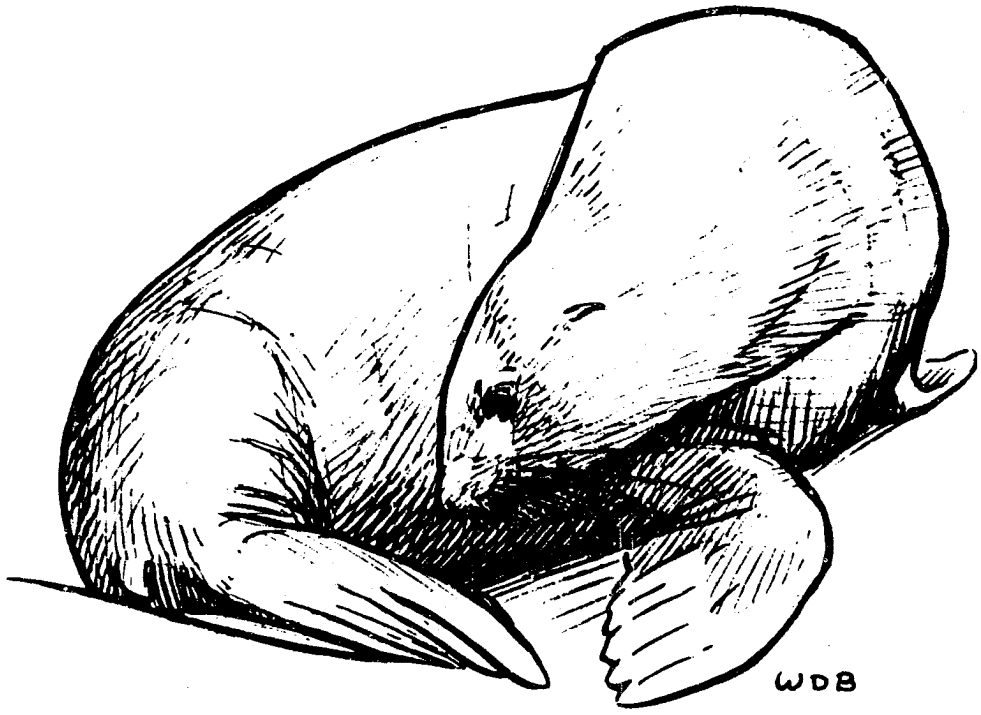


Figure 13. Female in late stage of labor with body bent laterally and staring towards vaginal orifice.

and staring behavior, by which the cow has the best possible chance to observe the progress of the birth, becomes apparent.

-29 minutes

Cow B is still in the same position, circling and staring. She is very aggressive to animals close by.

Although most cows have been described as aggressive throughout delivery, there is, in general, a short period just at the end when they are so absorbed in the progress of the birth that they completely ignore their surroundings.

-25 minutes

Cow B circles, stretches her nose towards her tail, and then lifts the tail with her muzzle.

-22 minutes

From a standing position, cow B lies down almost on her back (Fig. 14), lifts her hindbody, and performs the bending, stretching and spreading movements described above, while staring.

-17 minutes

Cow B is lying still, resting.

-14 minutes

The amniotic membranes are now bulging out. Cow B lifts her hindbody higher up on the ledge. With her hindbody at the same level as her head, she makes hunching, lifting movements and relaxes and stretches her hindflippers.

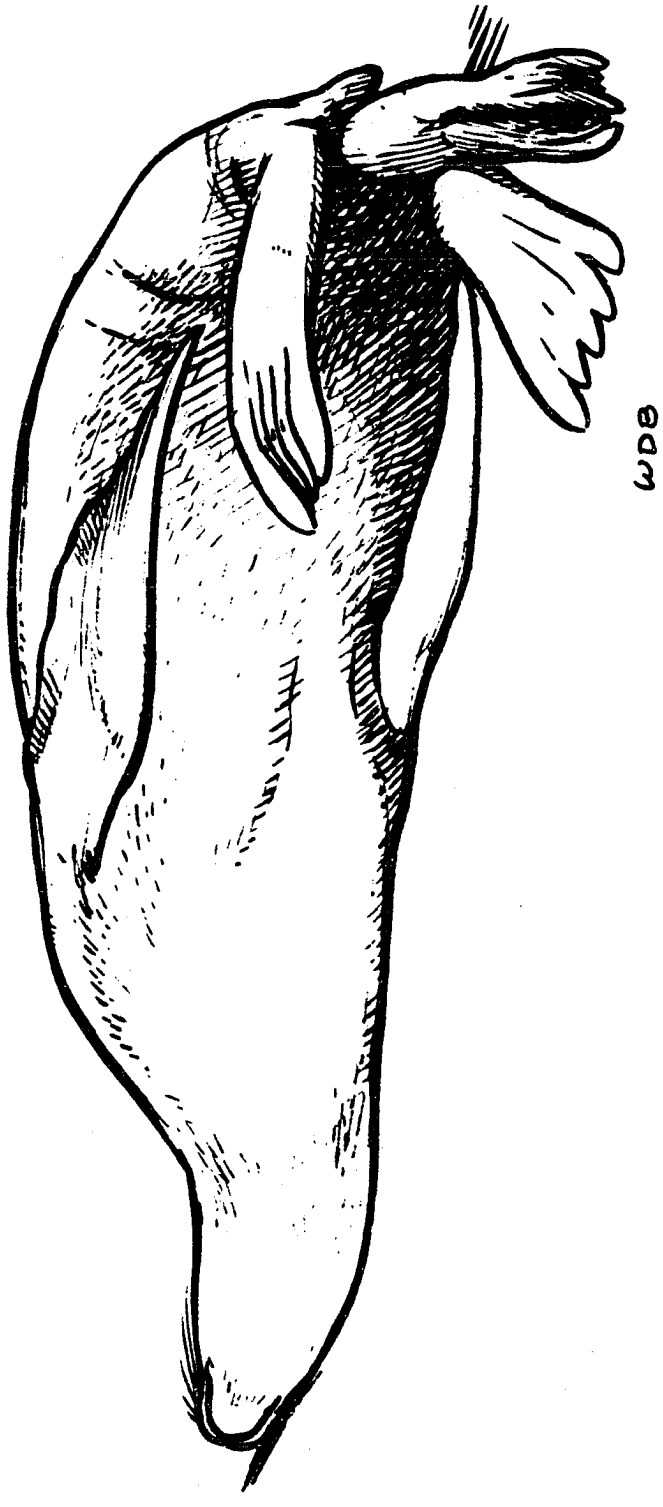


Figure 14. Female in final stage of labor.

-9 minutes

The membranes are now bulging out at nine-second intervals. Cow B is staring intensely.

-8 minutes

The amniotic membranes break and fluid sprays out over the rock. She moves her hindbody down, circles 180 degrees, and carefully nuzzles the rock where the fluid came out, moving her nose back and forth, now and then touching the rock.

In two cases, cows have aided the delivery by tearing the amniotic membranes with their teeth, as described for other mammals by Naaktgeboren (1963:10). In 14 observed cases, the cow has responded to the sudden appearance of amniotic fluid by careful olfactory investigation of the area where it emerged. In view of the importance of early recognition of the pup, it seems likely that this is the first (indirect) olfactory contact with the pup and that it is significant for the fastest possible olfactory recognition.

-5 minutes

Cow B circles and vocalizes strongly. She then becomes quiet, but continues circling and stares at the head of the emerging pup. She circles 360 degrees, dragging the emerging pup behind her.

0 minutes

The pup gradually slides out. When it is halfway out, the cow grabs him by the neck with her mouth and pulls him out. The umbilical cord then breaks. She sets

him down in front of her breast.

The time of delivery has been measured as the period between the breakage of the amniotic membranes and the expulsion of the pup. In 14 cases, delivery lasted from 5 to 70 minutes, with a mean of 30 minutes, in comparison with Callorhinus, where 46 deliveries were observed to last from 1 to 10 minutes, with a mean of 3.2 minutes (Peterson 1965:158).

According to Naaktgeboren (1963:10), uniparous mammals, with the exception of primates, usually do not assist in the delivery of their young. One elephant seal, however, has been observed helping her young out by pushing with her hindflippers (Slijper 1960). In four cases, Eumetopias cows pulled their pups out using their teeth. This is in contrast with Callorhinus, who "...give no oral assistance to the delivery of the pup, umbilical cord, or placenta" (Bartholomew 1959:164).

Of observed presentations of pups at birth, 10 were anterior and 7 posterior, compared to 66 anterior and 44 posterior for Callorhinus (Peterson 1965:158). Slijper (1956:42) suggests a ratio of 1:1 among pinnipeds because there is only slight difference in the overall body shape between the cranial and caudal end of the fetus.

In all cases observed, the pup was separated from the amniotic membranes at birth. In 24 out of 32 cases, the umbilical cord broke spontaneously and the placenta remained in the female for varying lengths of time. In four cases, the placenta was expelled with the pup and in the remaining four cases the umbilical cord was broken when the cow pulled the pup out, leaving the placenta inside her. Thus,

28 umbilical cords were broken on delivery and four were not, compared to 68 and 40, respectively, for Callorhinus (Peterson 1965: 158). In 14 cases, the placenta was expelled 3 to 175 minutes post partum, with a mean of 77 minutes, compared to 1 to 30 minutes, with a mean of 9.2 minutes, in 30 cases for Callorhinus (Peterson 1965:158). In the four cases where the pup was expelled with the placenta and the umbilical cord intact, the pups remained attached for 1, 3, 5 and 20 hours. In these four cases, the cows reacted strongly to the peculiar behavior of the pups who were repeatedly dragged away by the heavy, slippery placentas. In three of these cases, the umbilical cord was broken when the mother lifted the pup by the neck and swung it in an arc in front of her breast. Thus, it is seen that considerable differences exist between Callorhinus, where the placenta in 40 of 108 cases was expelled with the pup attached and frequently remained attached for a week (Peterson 1965:157), and Eumetopias, where the pups were attached in only four of 32 cases and only in one case for more than five hours. It would be hazardous for Eumetopias pups to remain attached to a heavy placenta which constantly tends to pull them down the slippery rocks.

In reference to Callorhinus, Peterson (1965:157) says: "Females usually ignore the placenta entirely, and rarely even sniff it after expulsion." In contrast to this, Eumetopias cows react strongly to the delivery of the placenta and to the placenta itself. The above-mentioned circling and staring behavior usually precedes the placental delivery. One cow was observed trying to pull out the placenta with her teeth. When the placenta is finally expelled, the cow usually

bends down and nuzzles it carefully. Several cows have been observed to interrupt the caretaking of their young in order to bend down over or move to the placenta and sniff and nip at it. Three cows were seen to lift and nip repeatedly at the placenta; two were seen pushing it with their muzzles; and one was seen stroking and slapping it with her frontflipper. All of this behavior is related to the common caretaking procedures directed to the pup immediately after delivery.

Courtship Display of Females and the Occurrence of Estrus

Before onset and during the entire breeding season, Eumetopias cows show a type of display directed to the bulls, in which the bulls take a very active part. This display may occur both in the water and on land. The frequency of occurrence and the vigorous nature of the display makes it a dominant behavioral event in a sea lion rookery.

The display has the following characteristics. Movements and postures of the female are highly exaggerated. A slow-motion, crawling gait, with head and neck swinging almost 180 degrees from side to side, is interspersed with short and long rushes, often through the most crowded areas, and usually to the most visible places in the surroundings. During the rushes the female frequently approaches or crosses territorial boundaries, but usually returns to the general area from which she started. Very soon the displaying female attracts the closest bull; if not, she approaches the bull presumably to catch his attention. While doing this, she vocalizes strongly, mouth wide open, vibrissae erected and salivating strongly.

On the approach of the bull, the cow usually shows a crawling gait. While winding her body around the bull's, she strokes her head and neck against him. She crawls around the bull and over his back while biting him. Bites are usually directed towards the lower jaw and neck, and are also common in the root of the tail. The bites are often hard and vicious, and tufts of hair may be pulled from the bull's fur. Vaginal display, with dragging and lifting of the hindbody to show the dilated vagina and sometimes swollen vulva, has been observed in several cases, and intermittent urination was observed in two of these.

If the bull is not sufficiently attentive to the female's display, as may happen when several females are displaying at once, she usually rushes away and returns shortly later to continue the display. This behavior may be repeated several times until the cow either leaves or calms down.

The bull, in most cases, reacts strongly to the display. He strokes and presses his head on the neck and back of the female. He rubs his nose against hers and, nodding intensively, follows her. Several times during a single display, the bull may investigate the genitalia of the female by inserting his nose in the vagina and licking it. An insertion may last for more than 30 seconds, and may be so intensive that the bull lifts the cow's pelvis high off the ground with his nose (Fig. 15).

Even if the bull does not pay much attention to the female at first, he usually reacts strongly to the combination of display and rushing towards the territorial boundary. He follows her and blocks

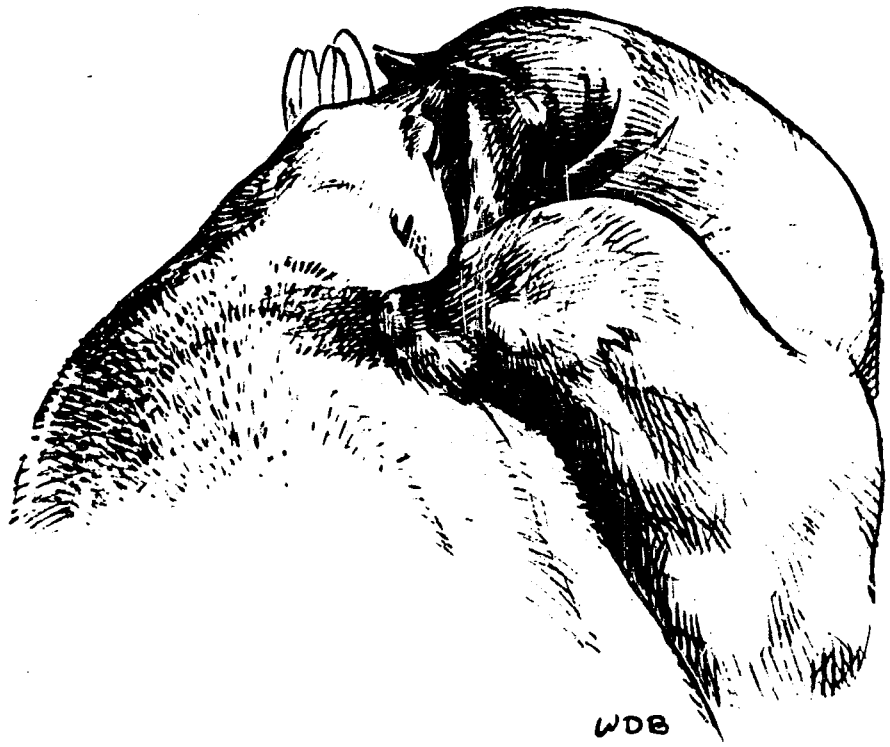


Figure 15. Female in courtship display, biting neck of bull while bull is investigating genitals of the female.

her way, and, by pushing her with his breast and lowered neck, herds her towards the center of his territory. This activates the cow to intensive display and biting. It should be noted that the herding response of the bull is frequently induced by the behavior of the cow when time after time she may rush towards the territorial boundary, trying to stimulate the bull to follow. Once the display is over, the bull shows little interest in a departing female.

When a displaying female repeatedly crosses territorial boundaries (thus causing bulls to pursue her), she stimulates the bulls to intensive marking of these boundaries. In this way, a displaying female in a short while can arouse the bulls in a large area.

The display can continue for as long as 30 minutes without interruption until the female calms down or rushes to the water and rapidly disappears to sea. On the way out she is often stopped by bulls and goes through short displays with them in the water.

According to Peterson and Bartholomew (1967:32), Zalophus females perform a type of display similar to that described above for Eumetopias females. The display among Zalophus generally leads to mounting by the bull within a few minutes. A very similar display is also described for Callorhinus ursinus females (Peterson 1965:161) in which the display "almost always" induces the bull to mount. For both Zalophus and Callorhinus, the authors call the display "estrus display" which should mean that the display is shown during the period when the cows are receptive to impregnation.

That the courtship display among Eumetopias females sometimes is an introduction to copulation, and that certain elements of the display

appear to be important stimuli to the copulation itself, does not mean that the display is a sign of receptiveness. Of 116 displays recorded for approximately 20 individually known cows with pups, only three resulted in mounting. This suggests a wider or different function than the receptiveness-signaling functions attributed to the display for Zalophus and Callorhinus.

As determined from the day of copulation in relation to parturition for 20 Eumetopias cows, estrus occurs between 10 and 14 days after parturition, with a mean of 11.8 days. The courtship display, however, may start as early as four days after parturition, which means that cows start to display five days, and sometimes more, before they copulate (Fig. 16). In both 1967 and 1968, a high frequency of courtship display was observed five days before the breeding season started (Fig. 4). Undoubtedly, this display is initiated by the cow and directed towards the bull. The vigor and length of one display, and the frequency of consecutive displays (one female may display up to four times per day for several days, with a total duration of more than two hours in one day), presumably has a strongly stimulating effect on the bull. Also, the bulls, by nipping, chasing and herding of the cow, and by the intensive licking of her genitalia, could have a strongly stimulating effect on the female.

In the courtship display, we can see one of the means by which the breeding effort of the bull and cow could be synchronized towards that time when the bull is maximally virile and the cow is ovulating. This would explain the time lapse between the high frequency of display and the first copulation at the onset of the breeding season (Fig. 4),

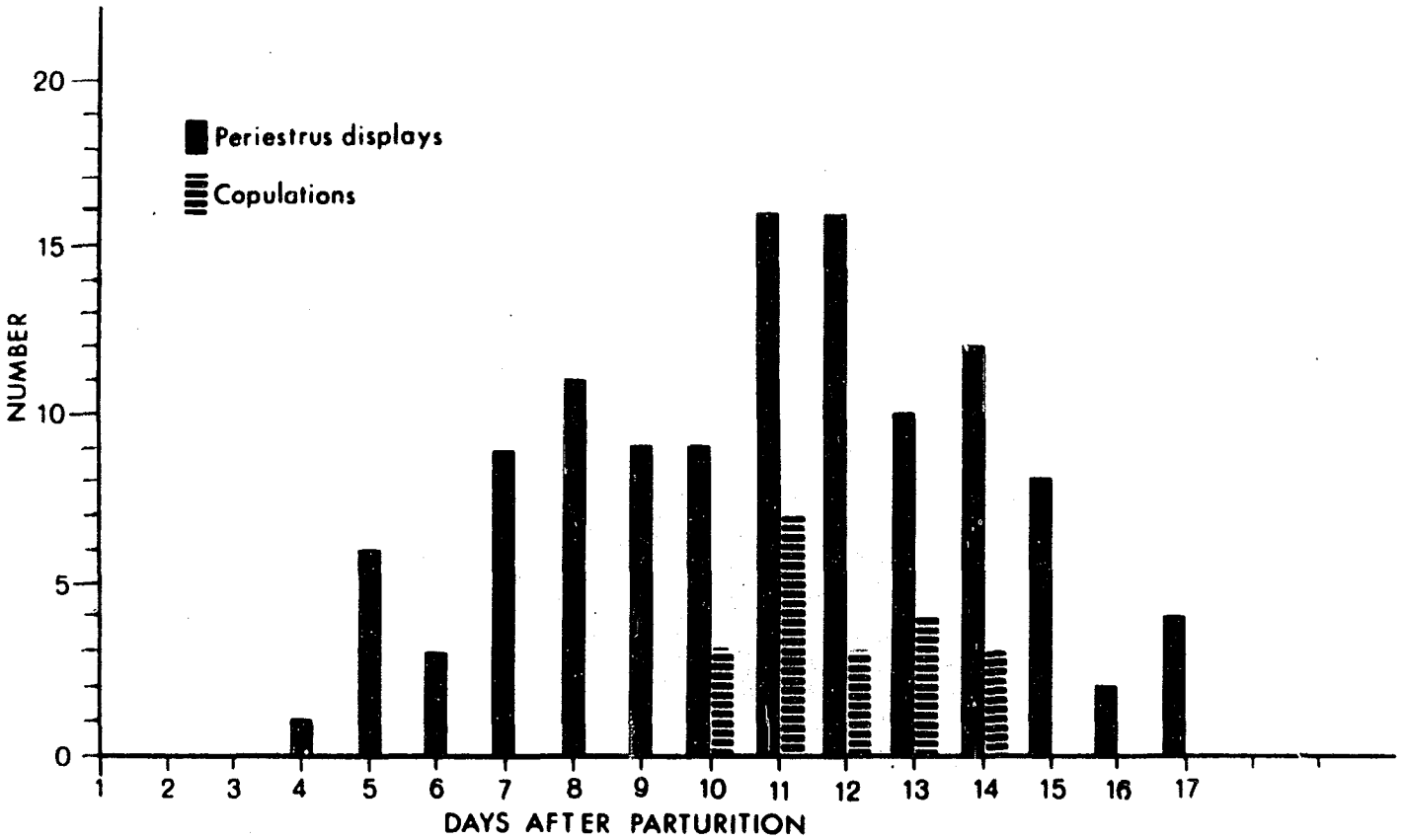


Figure 16. Distribution of 20 copulations and 116 courtship displays for individually known females in relation to day of parturition.

as well as the time lapse between the first display and copulation for an individual cow (Fig. 16).

The function of the courtship display as a means to synchronize the breeding activity of bulls and cows is indicated by the following examples:

1) The frequency and intensity of the display increases prior to copulation. Individual cows have been observed to display as often as four times in a 24-hour period. During each display, the bull may investigate and lick the female's genitalia four to five times (and more), without showing further interest. Six to seven hours after the last display has occurred, the bull may suddenly mount, even though little or no display has taken place.
2) By the end of the breeding season, the intensity and duration of displays by individual cows tends to increase, while the number of displaying cows decreases. This is presumably a reaction by the cows to weakening territorial maintenance activity by the bulls. At the end of the breeding season, extensive display usually precedes mounting.
3) Approximately one-half of the individually known females have gone to sea for short times in the period between parturition and copulation. Before departing they usually perform extensive and lengthy displays. Some of the wildest displays observed, however, occurred when cows went to sea shortly after copulation.

By displaying intensively before departing to sea, the female

presumably stimulates the bull to prolonged territorial activity, which maximizes her chances for future fertilization. Adequate territorial maintenance is also imperative for the welfare of her young, since the bulls keep away subadults and other animals who often harass young pups. This would explain the displays performed by the female when she departs after copulation.

On three occasions, cows have been observed to perform displays under conditions that would suggest an additional function of these displays. In the three cases, a cow with a young pup was driven away from her place and separated from her pup by a cow known to have been nonestrous. The cow that was driven away started to display, and moved towards the nearby bull. When she had caught the bull's attention, she moved towards the cow that had driven her away. As soon as this display began, the intruding cow moved restlessly and vocalized strongly. In all three cases the intruding cow then moved away on approach of the displaying cow and the threatening bull.

Copulation

Like most pinnipeds, Eumetopias is characterized by a post-parturitional estrus. To determine under field conditions the length of the period between parturition and copulation, both events have to be observed for the same individual. This was done for Eumetopias for the first time: for 20 Eumetopias females the period varied between 10 and 14 days, with a mean of 11.8 days (Fig. 16). In five cases among

Callorhinus the same period was from four to seven days (Bartholomew and Hoel 1953:420), and Peterson and Bartholomew (1967:32) suggest about two weeks for Zalophus californianus.

In 1968 the breeding activities of bulls in the central part of the rookery were followed throughout the breeding season. These bulls (constituting about half of the territory-maintaining bulls in the population) were observed to copulate 128 times. The distribution of these copulations throughout the breeding season is shown in Fig. 17. It is apparent that the frequency of copulations increases slowly from May 30 to June 5. In the relatively short period from June 7-10, there is a marked peak. During this four-day period, 40 per cent of the total observed copulations took place (even though some copulations were probably missed on June 7 and 9, due to discontinuity in the observations on these dates). After this, a rapid decline in copulation intensity is noted, and the breeding rate was low throughout the rest of the season. Interestingly enough, the four-day peak in copulation intensity coincides with the small peaks in parturition for both 1967 and 1968.

From the distribution of copulations throughout the day (Fig. 18), we can see that the intensity is irregular and slowly increasing throughout the day, and rapidly increases in the evening. This is in accordance with the overall activity pattern of the animals. Copulations have been observed throughout the night.

The duration of 51 copulations in 1967 ranged from 9 to 34 minutes, with a mean of 16.6 minutes, and for 51 copulations in 1968 the duration ranged from 9 minutes to 32 minutes, with a mean of 16.0

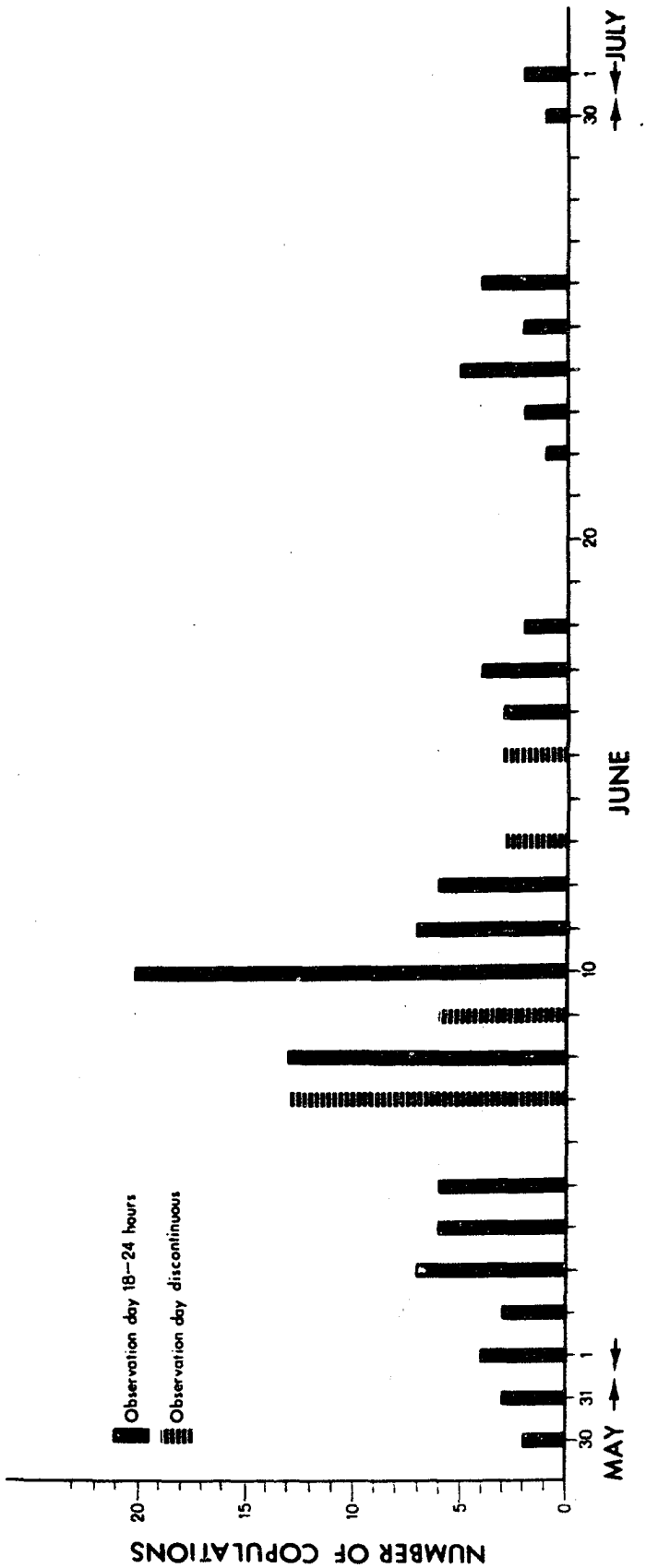


Figure 17. Distribution of 128 copulations during the breeding season in 1968.

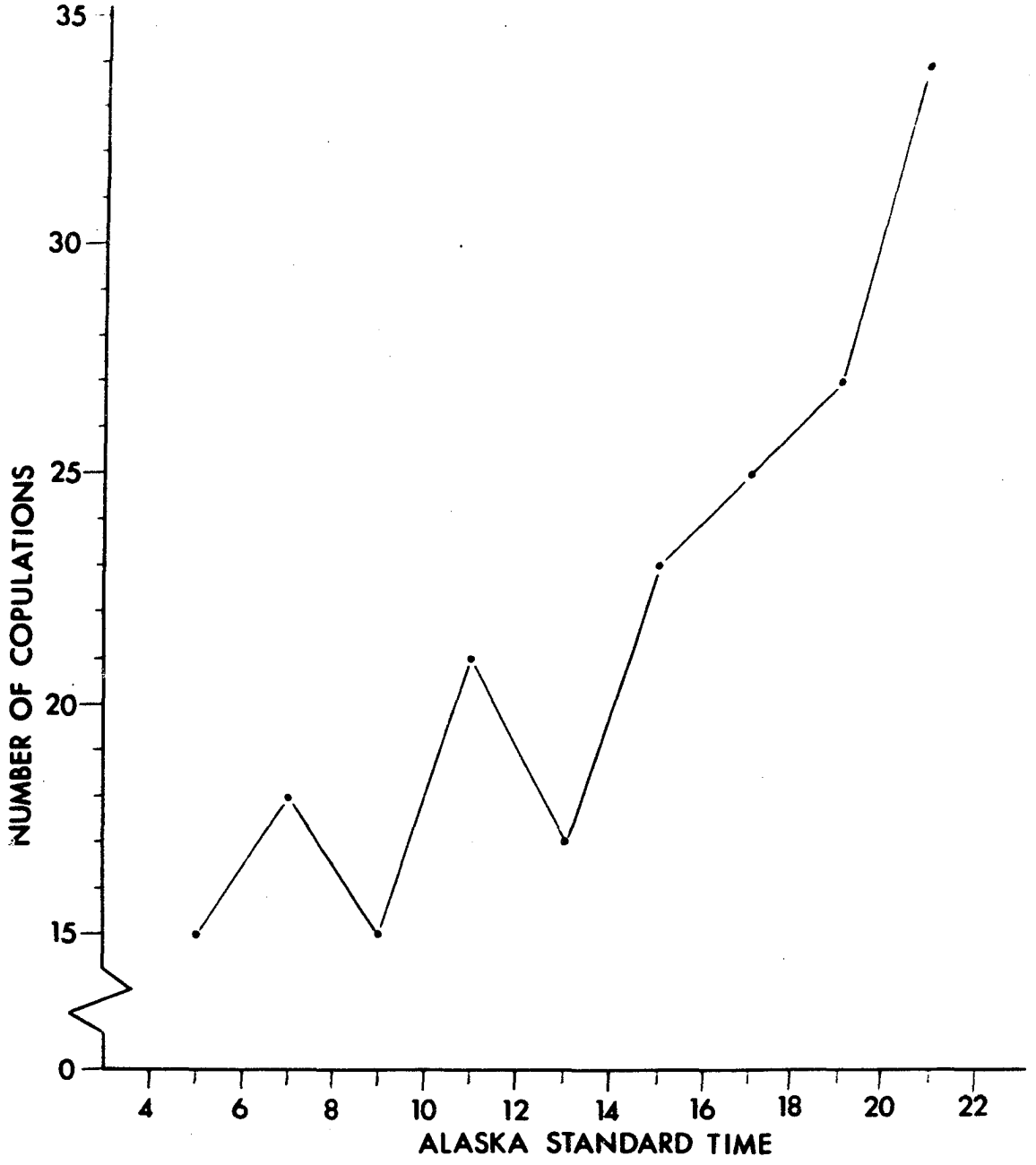


Figure 18. Distribution of 195 copulations throughout the day. Each point shows number per two-hour period. Data from 1967 and 1968.

minutes. Copulations lasting for more than 23 minutes are rare and, judging from the atypical behavior patterns accompanying such copulations, they are abnormal. Four such copulations were recorded, lasting 42, 75, 124 and 80 minutes, respectively. The first three were performed in the same day by one aquatic bull with the same cow, and it is doubtful whether the copulation was ever completed. Among Callorhinus, copulations last from 0.5 to 20 minutes, the mean increasing from 5 to 10 minutes through the breeding season (Peterson 1965:162). The duration of one copulation timed for Arctocephalus pusillus (Paulian 1964:50) was four minutes for the preliminaries and 10 minutes for the copulation itself, while Rand (1955) writes that the copulation for the same species rarely takes more than 10 minutes. Mathison, Baade and Lopp (1962:470) have found an unspecified number of Eumetopias copulations to vary between 11 and 30 minutes in length, with a mean of 20 minutes.

Cows that have experienced a complete copulation have never been seen to trigger a new mounting by the same or another bull, in spite of the fact that several cows have performed intensive courtship displays before their departures to sea shortly thereafter.

In all but 1 of 20 cases, cows have copulated with the bull in the area where they had been in the days preceding copulation, because cows are very stationary during this period. The territory in which they copulate does not necessarily coincide with the territory in which delivery takes place, although this is frequently the case.

No copulation has been observed in water so deep that the animals could not reach bottom and, in general, copulation in the water is

rare. Possibly for thermoregulatory reasons, bulls soon after mounting are sometimes seen trying to maneuver the female from land into a shallow pool.

In the behavior of the cow, as well as the bull, three distinct phases can be observed in a Eumetopias copulation:

1) Mounting Phase -- Although the cow does not have to display in order for the bull to mount, mutual stimulation seems to be an important factor during the early stages of copulation.

As the bull mounts, the cow usually bites his breast and lower jaw vigorously (Fig. 19). At the same time, she struggles and vocalizes strongly, as if trying to escape. The bull responds by rubbing his nose against hers and nipping her neck. He also strokes his neck against hers and often presses her neck backwards with his. Simultaneously, the bull strives to manipulate the cow into such a position that intromission can take place. Sometimes the rugged substrate obliges the couple to maneuver around for a time until they find a suitable spot.

That mutual stimulation may be a necessary factor for completion of the copulation is indicated by five cases in which the cow became absolutely passive after being mounted. In each case the bull dismounted time after time and tried to activate the female. This was done by bending her neck backwards with his, by nipping, stroking, pushing and poking her with his head, and by smelling her genitalia. The bull persisted in this manner until the cow showed the normal

response of bending her head up and biting when she was mounted.

In 60 cases the duration of the first phase, which is characterized by mutual stimulation, has been timed and found to vary from 1 to 17 minutes, with a mean of 3.5 minutes. Ninety per cent of these range from 1 to 6 minutes.

2) Passive Phase -- The cow, who until now has been struggling, becomes very passive and lies quietly with her head resting on the rock. In a few cases, however, cows have lifted their heads, pressing their neck and head against the bull's neck. In still other cases, the cow never became passive but kept on struggling. The latter behavior is exceptional.

During this phase the bull alternates between two body positions: one in which he stands "towering" over the cow (Fig. 20), and one in which he lies with his neck stretched along the cow's (Fig. 21). When in the towering position, which is the most common of the two, the bull usually swings his head from side to side, vocalizing. The posture, movements and sounds of the bull in this position are very similar to those made during intensive territorial maintenance activity, and probably have the same function. Throughout this phase, the bull makes searching thrusts of low intensity and frequency, while lifting and twisting his hindbody from side to side. In the few cases where insertion could be seen, there seemed to be a close relationship between this event and the sudden passivity of the cow, so characteristic of this

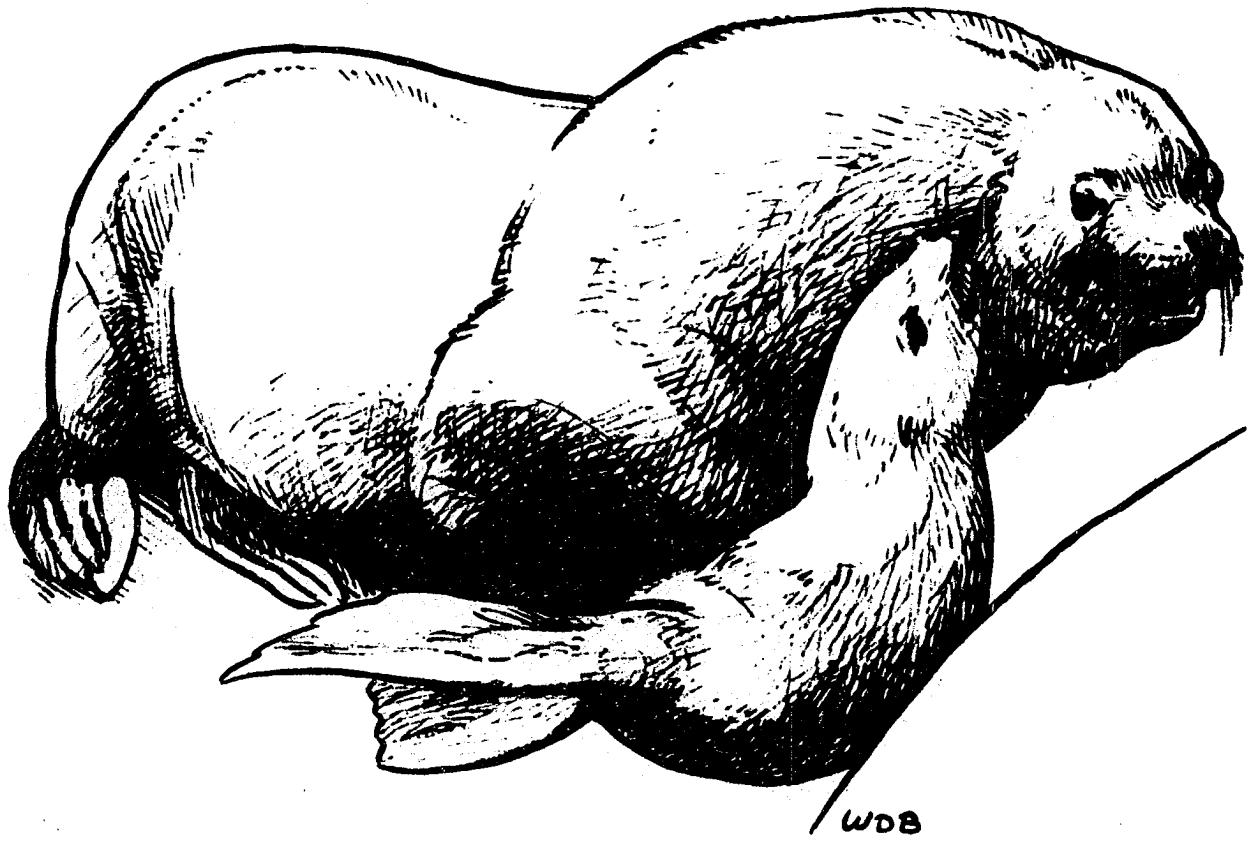


Figure 19. Female biting throat of bull. Characteristic of mounting and climax phases of the copulation.

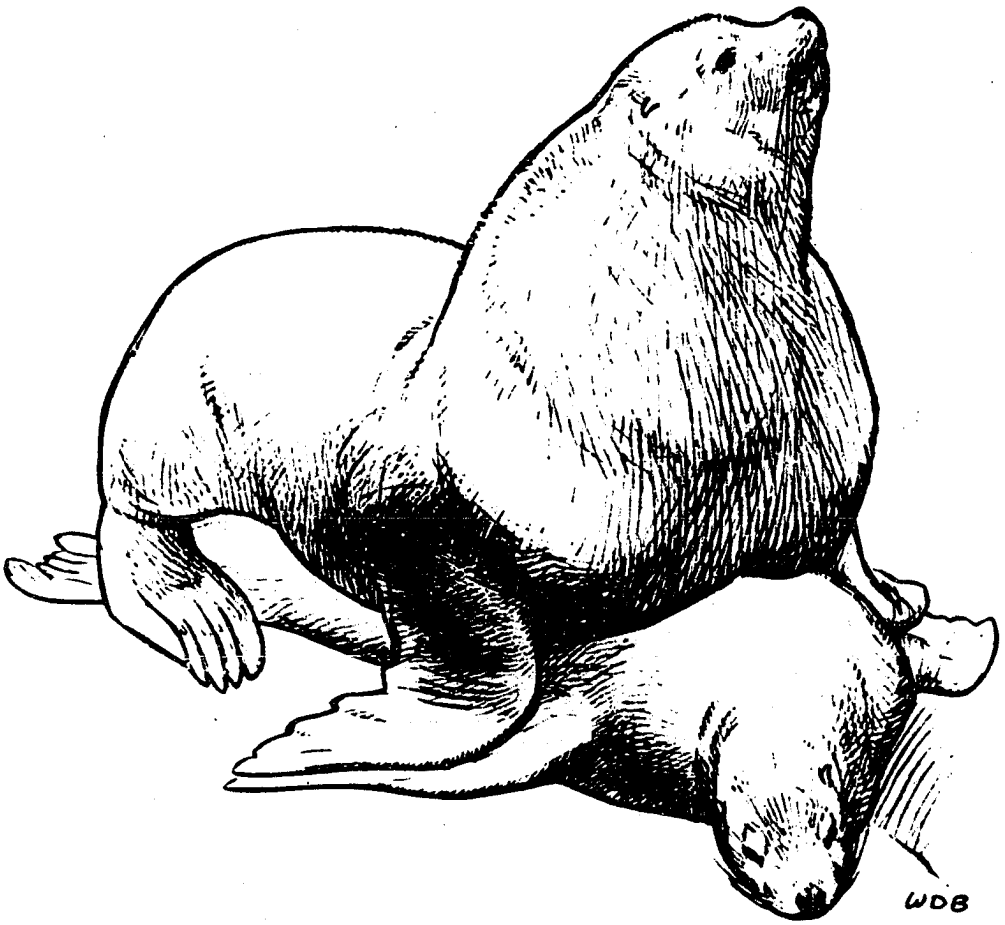


Figure 20. Bull in towering pose and female in passive phase of copulation.

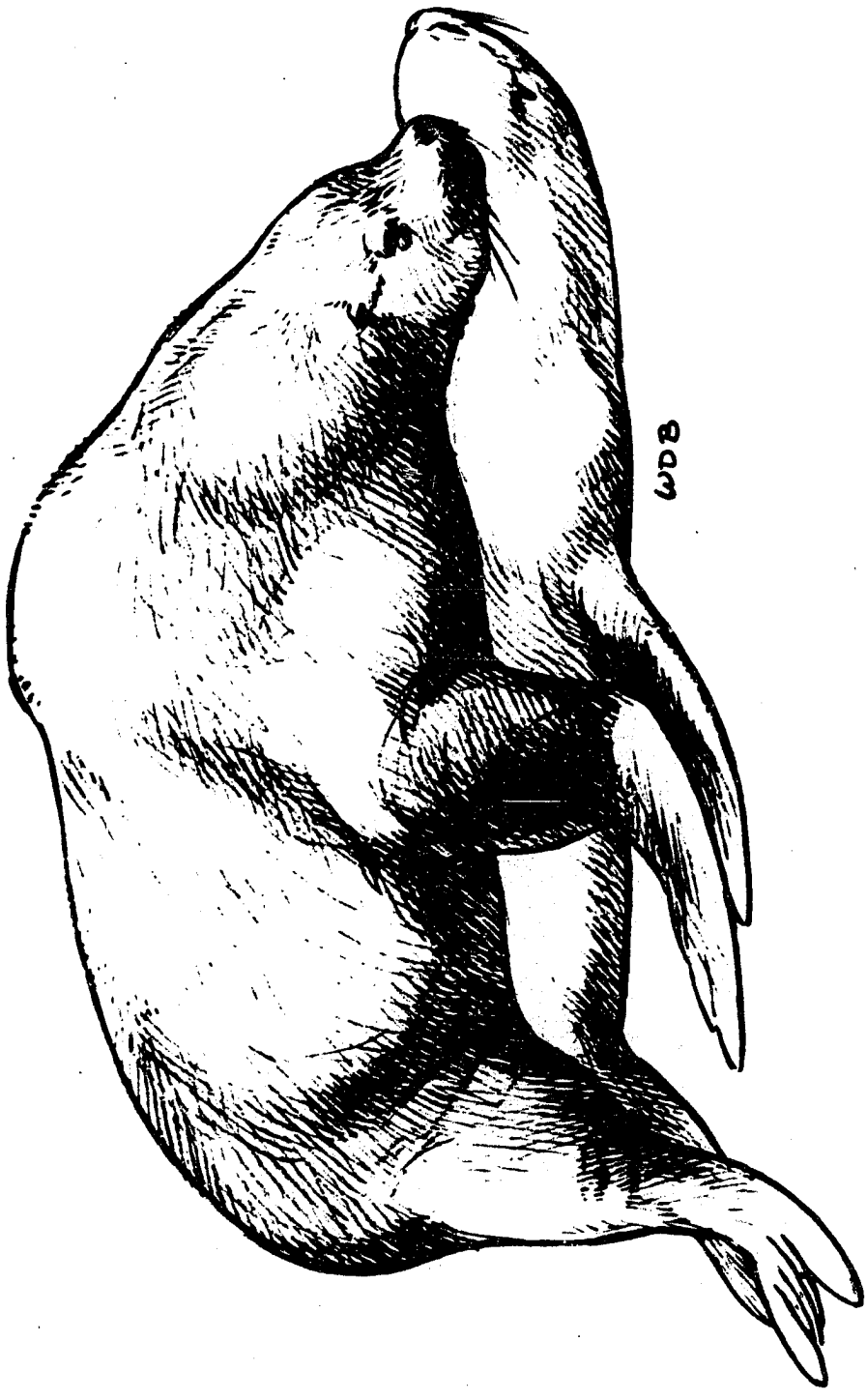


Figure 21. Female in passive phase of copulation; bull lying with head and neck outstretched.

phase. In 61 cases the duration of this phase of copulation ranged from 6 to 18 minutes, with a mean of 9.7 minutes. The distribution of these times is such that 92 per cent fall within the 8-13 minute range.

The position of the bull's pelvis in relation to the cow's, the slow and irregular thrusts, and the constant lifting and lateral movements of the pelvis while making these thrusts, gives the observer the impression that only partial insertion has taken place. It seems possible that a certain amount of stimulation of the cow's genitalia may be necessary to initiate processes allowing intromission, and also that the bull may need this amount of time to achieve complete erection.

3) Climax Phase -- At this point, the pelvic thrusts become longitudinal and regular, and increase several fold in intensity and frequency, indicating that complete intromission has occurred. The bull's pelvis is thrust almost to the vertical, compared to the 30 to 45 degree angle in the previous phase. Often the thrusts are so strong that the female is pushed forward. Shortly after the intensification of the thrusts, usually about one minute later, the cow lifts her head and starts to bite the bull's neck and lower jaw vigorously (Fig. 19). At the same time, she tosses her head from side to side and wiggles her whole body as if trying to get away. Defecation by the female has been observed several times at this stage. The bull responds to the female's biting

> by lowering and pressing his neck against hers, while he continues thrusting. In 64 cases the length of this phase has varied from 1 to 8 minutes, with a mean of 2.4 minutes. The distribution is such that 90 per cent fall within the two-to-five minute range.

In the copulation itself, we can see the end of a chain of appetitive behavior, providing mutual stimulation, and possibly leading to the synchronization of the breeding efforts of the male and female. Quantitative aspects of the behavioral elements providing this mutual stimulation may well determine whether the bull will ejaculate and the female will ovulate.

Duration of Mother-Young Bond

The following observations indicate that a more than one-year-long bond between mother and offspring is so frequent among Eumetopias that it must be considered an important part of their social behavior.

1) High numbers of females in the Lewis Island rookery, both in 1956-58 (Brooks, pers. comm.) and in 1967-68, were accompanied by suckling subadults of at least two year classes.
2) In both years of observations, some cows that gave birth kept both yearling and pup. This has also been observed among Eumetopias cows in California (Gentry, pers. comm.).
3) One cow who lost her pup was soon joined by a subadult and suckling ensued shortly thereafter.

Although a tie of more than one year does exist among some social pinnipeds of other species, this seems to be more the exception than the rule (Rand 1967:8, Peterson 1965:182-183, Peterson and Bartholomew 1967:44, and Paulian 1964:54).

It is important to realize that differences in ontogeny follow from differences in the length of the mother-young tie. This, in turn, results in diversification among individuals and a well-stratified society.

Female-Subadult and Female-Pup-Subadult Bonds

As has been noted, the bond between mother and offspring frequently lasts for more than a year. This can occur in four main ways:

1) Females do not give birth each year and retain the bond with their young into the second year.
2) Females renew the bond with their last young after loss of a pup.
3) Females reject the newborn pup and keep the subadult.
4) Females keep both the pup and the yearling.

Behavior of type 2 has been observed in one case in which a female allowed a subadult to suckle three days after loss of her young.

Behavior of type 3 has been observed in four cases in which the female, immediately or shortly after birth, rejected the pup in favor of the subadult. These cases will be discussed later in connection with pup mortality.

Behavior of type 4 has been observed in three cases. The female maintained the nursing bond with both pup and subadult and the bond in two cases lasted at least two months (and probably more). The relative strengths of the mother-subadult and mother-pup bonds distinguished the three cases from one another.

In the first of these cases, the bond to both young was initially strong, and both suckled. After a few days, however, the mother-pup bond was strengthened to the disadvantage of the mother-subadult bond, and the mother showed increasingly stronger antagonism towards the subadult until it was weaned after about 10 days.

In the second case, the female's bond with the pup and the subadult appeared equally strong. Thus, the motivation for nursing one or the other would change several times in a 10-minute period, with the female shifting to whichever young showed the strongest nursing appetitive behavior at the moment. Sometimes the two nursed side by side. Later in the season, when the female was at sea, pup and subadult often came to the spot where their mother would arrive from sea and lay down together. Sometimes the pup rested on the back of the subadult.

In the third case, the female's bond with the subadult was stronger than with the pup. From an early age, the pup received a minimum of care, and nursing was restricted to one period about each second day. At first the pup appeared to be very weak and emaciated. He was frequently bitten and tossed about, when, vocalizing for his mother, he came too close to foreign cows. The hungry pup could be seen circling about for hours in the spot where his mother customarily joined him. In spite of these hardships, the pup seemed to progress normally throughout the summer.

An interesting bond developed between the subadult and the pup in which the subadult took the role of the pup's protector. The subadult was twice seen guarding the pup and intensively threatening all animals (including the mother) in an attempt to keep them away from the vicinity of the pup. The ever-hungry pup was seen to suckle the penis of the subadult.

It appears quite possible that the bond between mother and subadult continues after weaning. In several cases, cows with young

pups were visited by the same subadults day after day. Not only did the females appear to communicate vocally with these subadults, but they also allowed them to approach much closer than they would a foreigner; on several occasions, these (suspected) young of the mother were permitted to approach the very young pups without arousing any strong aggressiveness from the mother.

The relatively high number of cases--seven per cent of the total number of deliveries--in which the females retained a nursing bond with the subadult after the delivery of a new young might well indicate that this behavior is one of the factors contributing to variability in the social structure. It is apparent that the weaned and unweaned young are subjected to radically different social environments, the former sinking to the bottom of the hierarchical order and the latter indirectly retaining the status of the mother. This variability in environmental influences can, therefore, produce morphological and behavioral differences in the developing young.

Activations

Females subject their young to various types of activating behavior which apparently serve to stimulate or reinforce certain activities in the young. As these "activities" are probably functionally important in the development of the pup, they deserve to be mentioned separately. The following types are those most frequently seen.

Lift-drop Activation -- The mother seizes her pup by the neck or back, lifts it to a height of up to 1 m (Fig. 22), and drops it on

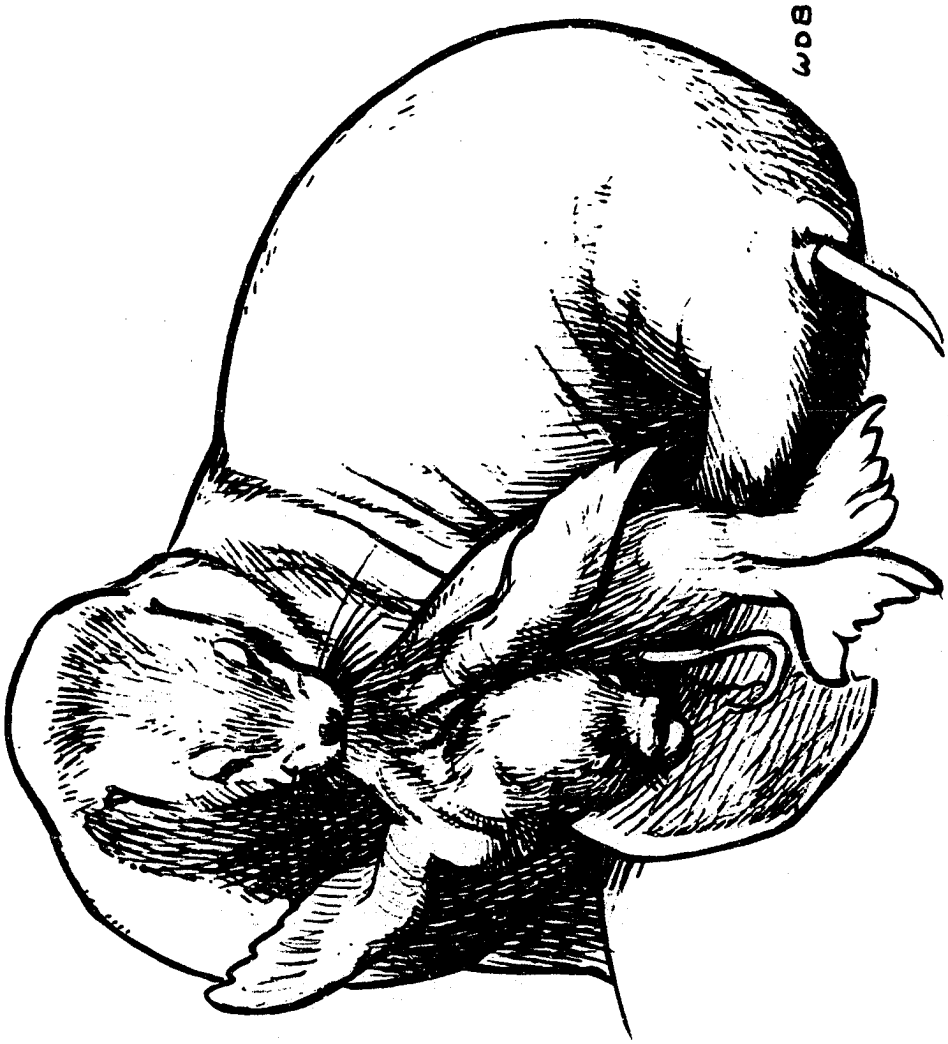


Figure 22. Female lift-drop activating newborn young.

the rock on which they are lying.

This behavior is exhibited by most cows, and occurs with highest frequency in the hours following delivery. Cows have been seen to lift and drop their pups as many as 52 times within a two-hour period. Lift-drop activation ceases quite abruptly and is rarely observed when the pup is more than two days old. In two of the few instances when this type of activation was observed with older pups, one pup had recently died and the other pup was about to die.

The pup's reaction to the lift-drop is intensive and signs of strong irritation are shown -- all movement are accelerated, the head is shaken vigorously, and the normal bleat is transformed into a long, loud scream. After a short time, the mother has only to bend over her young, while vocalizing strongly, and soon only to bend over without vocalizing, to evoke the same reaction as the whole prior sequence of actions (i.e., vocalization, bending over young, and lift-drop) evoked previously. Thus, the lift-drop becomes superfluous and disappears, and is only observed on rare occasions such as those described above.

A type of related behavior has been observed on four occasions. In these instances, in which the females had given birth under very crowded conditions, the females at certain times were subjected to extreme aggression from surrounding cows. They were almost constantly defending their minimally-sized birth areas. Under these conditions the females were seen to lift their pups by the frontflipper (instead of the usual lift by the neck) and hold them high while swinging them from side to side. Each time the lifting of a pup and repeated

swinging could go on for up to a minute before the pup was set down, or the female, with the pup dangling, approached a nearby female. Cows with newborn pups are maximally aggressive. Therefore, it seems possible that a behavioral element which emphasizes this state, such as the dangling pup, could be used as a threat. This is indicated from the strong flight and aggressive reactions this behavior provoked in the approached cows.

Peterson (1965:157), referring to an incident among Callorhinus, where a female lifted her young above the ground and shook it vigorously, says "this form of behavior may only be an extreme form of nipping." Behavior similar to lift-drop activation is not mentioned by Peterson.

Nip Activation -- The mother nips or tugs at the head, back or neck of the pup. In a few cases, this behavior completely replaced the lift-drop activation, which is the most common activation of newborn pups. Nipping is a milder type of activation than lift-drop, and can be seen until the pup is 10 days or older. Nip activation is common among Callorhinus, but only for a short period of time following delivery (Peterson 1965:155).

Slapping with Frontflipper -- This activation has been seen in only a few cases. The mother stimulates her newborn young to activity by rapidly slapping back and forth over the head and body of the pup with her frontflipper.

Frontflipper Pressing and Stroking -- This has been seen in only a few cases. The mother makes pressing and stroking movements with her frontflippers over the body of the newborn pup to initiate activity.

Tooth Activation -- This may occur as an intermediate part of vocalizing, bending and nipping. The mother bends over her newborn pup and rubs her teeth along its back and head, scraping them back and forth.

Nose Pushing -- The mother pushes the muzzle of the newborn pup, as though she were trying to open its mouth. This has only been observed twice when pups appeared unusually immobile after birth.

Nose Rubbing -- The female touches the youngster's nose and they maintain contact, often for several seconds (Fig. 23). This behavior is frequently seen when the female wants to encourage her young in a situation in which he shows fright. It may occur, for example, when a pup tries to get down from a high shelf and is hesitant, when waves hit a young pup not yet accustomed to water, when bulls mark territorial boundaries close by, or when the mother introduces her young to pelagic swimming. Female and young usually rub noses when meeting after a separation, apparently so that the mother may identify her young olfactorily.

Neonatal Cow-Pup Interactions

The mother's primary activity after delivery is to retrieve her young and place it in the most protected place available. Activating behavior ensues shortly thereafter and is most frequently of the lift-drop type (Fig. 22). The amount of activation to which a pup is subjected is influenced by at least two factors:

1) The amount of activation is proportional to the inactivity of the pup. An inactive, flaccid pup receives more activa-

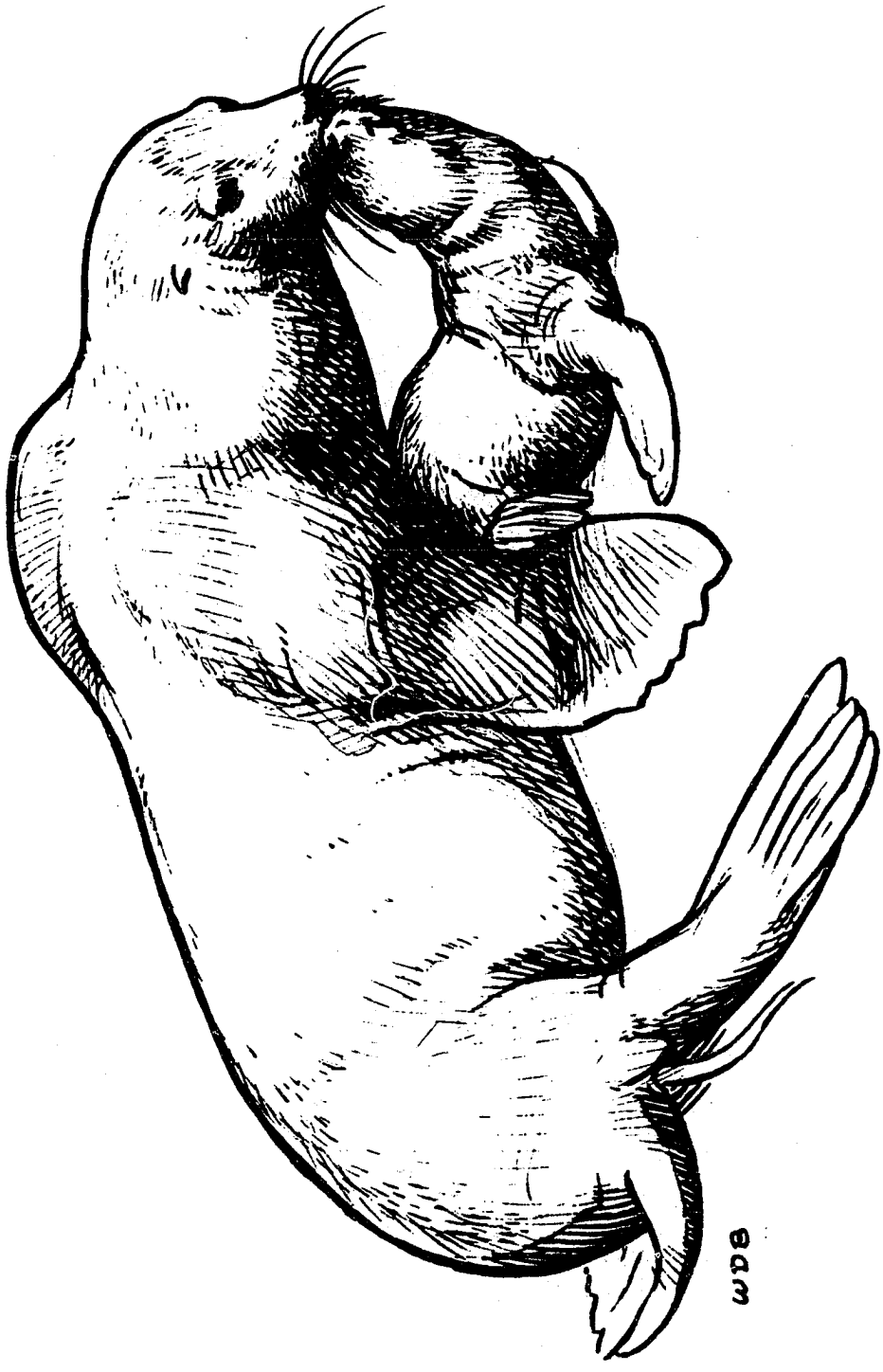


Figure 23. Nose rubbing between mother and young.

tion than an active one.

2) Small cows of low dominance activate their pups much less than large dominant ones. Of 16 cows followed closely after delivery in 1967, four showed very little activating behavior. These four were all small and apparently of low dominance.

The first activations after delivery are usually the most violent the pup will ever receive. The mother may repeatedly lift her young and smash it down on the rock below, sometimes even when the pup appears very active. The intensive activations soon initiate coughing of mucus, vocalization, and crawling movements. The pup starts to vocalize (often intensively), looks around, and tries to lift its head.

In 17 cases, the young made its first visible crawling movements in the interval from the time of delivery to nine minutes after (mean of 2.4 minutes). As soon as the pup becomes noticeably active, the mother lies down and rests for a period ranging from a few minutes to over an hour. In 16 cases, this rest began between 2 and 73 minutes after delivery. While resting, the mother usually lies with her body in the shape of a U around her young, who lies by her neck. She rarely takes her eyes from her young. Vocal communication and nose-rubbing (Fig. 23) occur frequently. If the pup shows the least sign of inactivity, the mother starts to vocalize strongly and to activate it, sometimes moving in a circle around the pup.

Soon the pup can crawl slowly forward, dragging its body along with its well-developed frontflippers. It can lift its head and shake it laterally, sometimes shaking its whole body like a dog. The pup

also starts to show interest in its surroundings, looking at animals close by and sniffing the rocks.

The frontflippers are well developed at birth, and are usually strong enough to keep the pup from sliding down a gentle slope and also to permit slow forward locomotion. Movements of the hindflippers and pelvis, which eventually become important for forward locomotion, are less well developed and are of little help in early locomotion.

Shortly after birth, stereotyped scratching movements, with the hindflippers in the air, are usually observed. Within the first three to five days of the pup's life this "air-scratching" gradually evolves into the most common grooming posture: the animal bends his head and neck backward and to the side and scratches with the claws of the folded hindflipper.

The first lifting of the head off the ground is very shaky. In 13 cases, it first occurred between 1 and 45 minutes after delivery (mean 15 minutes). Soon after delivery, pups often make intensive, lateral, shaking motions of the head. In 12 cases, the first occurrence was between 7 and 111 minutes after delivery (with a mean of 39 minutes). Head shaking later on (and possibly at this time) indicates hunger, and is generally shown by pups when they join their mothers after a long separation. Head-shaking by hungry pups has also been observed for Arctocephalus gazella (Paulian 1964:51).

After her initial rest, the mother's main activity usually is directed toward nursing of her young. Visible lactation, sometimes with milk oozing down the belly, is common, and has been observed in all cases where it was possible to follow the pair closely

before nursing was initiated. In 12 cases, lactation began from 200 minutes before to 180 minutes after delivery, with a mean of 18 minutes after delivery. Several observations indicate that the white milk on the dark abdomen visually directs the pup's searching to a limited area. In addition to this, smell may be a factor of importance to direct the pup's searching.

The pup spontaneously searches for the mother's teats, making small, searching, circular movements with his head while poking his nose against any available part of the cow's body. In 18 cases, searching commenced between 9 and 128 minutes after delivery, with a mean of 45 minutes.

Although searching develops spontaneously, it is, like nursing, usually aided by the mother through intensive activating procedures. While the mother stands with abdomen rotated and teats easily accessible, she repeatedly lifts and drops, or nips her young, who is now lying within easy reach of the teats. Time after time, cows have been observed to pull their young up to the teats in order to localize searching in the right area. When the pup's (still unsteady) head repeatedly drops, new activating behavior is provoked in the mother. In several cases, a cow has been seen supporting her pup's head with folded hindflippers or guiding the pup's head to the teats with her nose.

During the first 15 to 45 minutes of nursing activity, suckling is very sporadic and intermittent. The pup still has difficulty keeping his head up and frequently loses contact with the teat. He is subjected to frequent activation from his alert mother, who does not grow calm until her young nurses easily, without interruption. In 22

cases, the first relatively uninterrupted nursing began within 19 to 240 minutes after delivery, with a mean of 145 minutes. In a few cases this period was much longer. Small cows of low dominance are difficult to observe, and the least well-developed young are found among them. In addition, maternal caretaking is least developed among these nonaggressive cows.

A newborn pup is apt to spend an impressive amount of time nursing. In 1967, four pups that were followed during their first 18 hours of life spent an average of 230 minutes suckling. Data obtained on the suckling activity of several pups during the first 24 hours of life in 1968 show similar, or even greater, values. That a pup can suckle for more than 50 per cent of its waking hours during the first day of life is more a result of the behavior of the cow than of extreme hunger on the part of the pup. Here again, activation of the pup is the dominant factor. The mother actually forces the pup to feed. As long as the pup suckles, she remains calm, but should nursing activity decline, she becomes excited and moves around her young in a circle, while vocalizing loudly, and nips and lifts it. Then she lies down and apparently anticipates the pup's nursing. In combination with this type of activity, cows have been observed to nuzzle the anal region of their young carefully. Possibly the female in so doing perceives whether or not defecation has taken place. She may also induce defecation.

The pup is usually not allowed to have his first rest until it actually falls asleep and its head slides down time after time, while it is in the suckling position. The rest is usually brief,

as the mother soon activates the pup to renewed nursing activity.

Milk-vomiting

During the first days of life, young sea lions frequently vomit milk. As many as 10 to 15 such occurrences within an 18-to-24-hour period are not uncommon, and often such large quantities are regurgitated that the mother, pup and surroundings are smeared white with milk.

That the vomiting is caused by over-feeding which, in turn, is caused by the activating behavior of the mother is indicated in Fig. 24. It is seen that the amount of activation to which eight pups were subjected on each of their first 10 days (measured by the number of nursing periods during which activation occurred) varies directly with the total number of times that milk was vomited per day during the same period.

It is known that over-feeding can cause vomiting among animals (Luick, pers. comm.), but the reason why the mother over-feeds her young is not understood. This pattern of over-feeding followed by regurgitation cannot be regarded as abnormal since it is much more common among large cows who take "good" care of their young than among small cows who sometimes show a minimum of maternal caretaking.

It is quite possible that a large cow produces much more milk than her newborn pup can consume and digest. If this is the case, over-feeding could relieve excessive mammary gland pressure. Cause

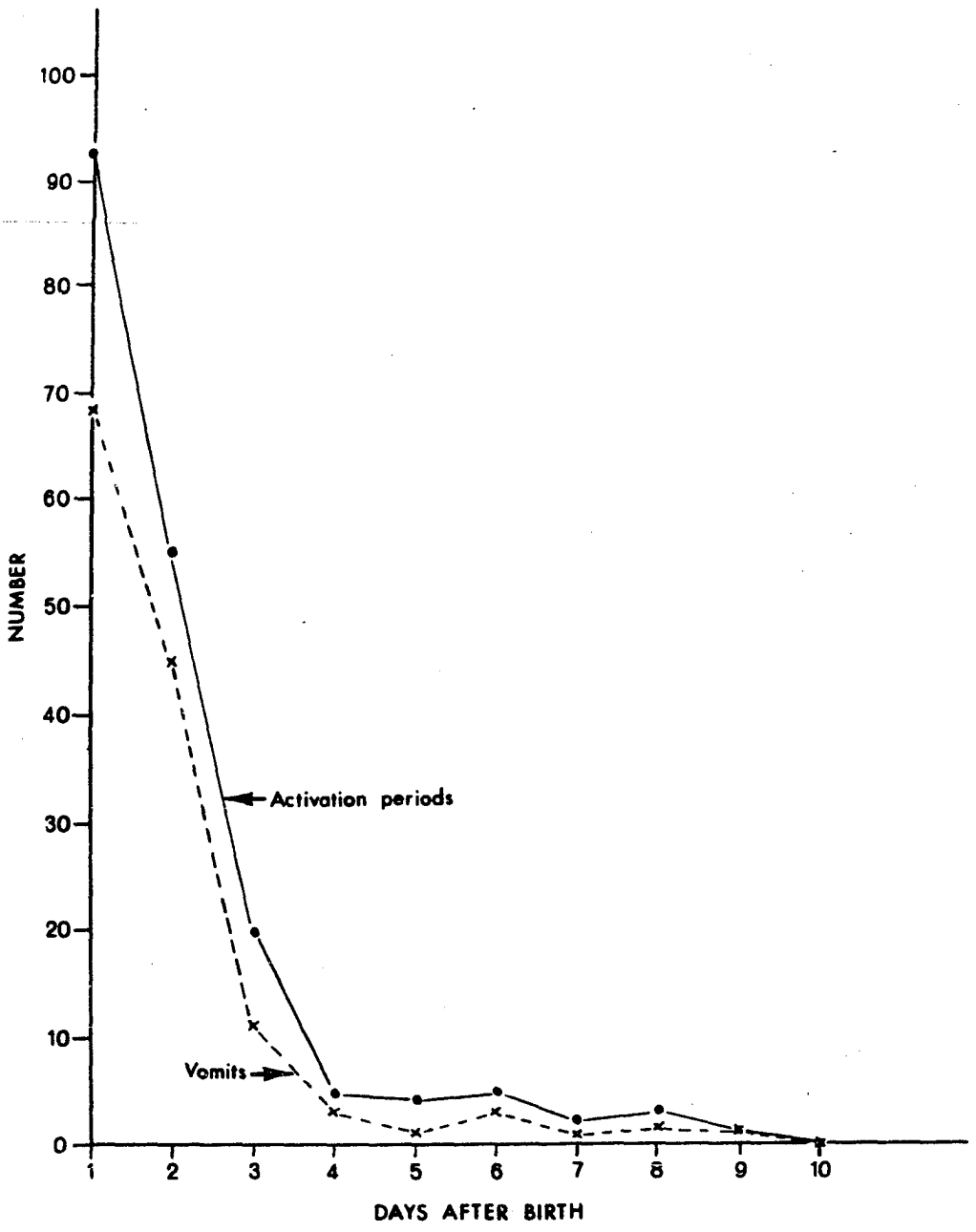


Figure 24. Comparison of the amount of activation (measured by the number of nursing periods during which activation occurred) with the cumulative number of milk-vomits for eight pups in the first 10 days of life.

and effect would then explain the behavior.

Vomiting could also be a signal to the mother that her young has been feeding properly. Although the observations are far from conclusive, cows have been observed to calm down when their pups vomited.

If the over-feeding-vomiting process were to maintain the feeding capacity of the young at a maximum rate, it could promote rapid development of the young and, therefore, be of survival value.

Mother-Young Recognition

Observations of seven individually known pups and their interactions with their mothers during a period of seven weeks after delivery, plus observations of 30 individually known cows and their pups before the first separation, show that means of mutual recognition have developed by about 10 days after delivery and, at least in some cases, are fully developed as early as three days after delivery.

It is obvious that among animals with a long lasting mother-young bond who live in large social herds, the earliest possible development of mutual recognition, and any other means of guiding mother and offspring to each other, is of prime importance. Synchronization of the efforts of pup and female to join might be accomplished on the basis of time and geographic locations, while olfactory, vocal and visual stimuli might be of importance for the final identification.

Geographic Location and Timing -- During the absence of the mother, the pup regularly returns to the place of the last nursing and caretaking. These returns coincide with the periods of high tide at which times pups are active and females are most likely to return

from sea. As the time elapsed from the female's departure increases and, presumably, the hunger of the pup becomes more intense, the pup returns more frequently to the meeting place. On each successive return, the time spent there increases until finally the pup may concentrate all its activities in the area where the mother is expected.

Usually several, and sometimes 10 or more, meetings occur successively in the same place. Individual differences are great, however, and it appears that cows of low dominance tend to change place more frequently than dominant cows. The latter may appear day after day in the same place and drive whomever is in "their" place away, while the former frequently find their old places occupied, and, therefore, have to find a new one. If, after a change of rearing place, a pup does not home to the new one, the mother searches in the place they previously occupied.

For example, after meeting her pup in exactly the same place (place 1) for 11 days, cow C called her young into the intertidal zone to a new place (place 2) about 30 m away from the old one. Mother and young stayed there during the day. When the female left in the evening, the pup made his way to place 1. The next day the mother appeared at place 2, where the young had been attended during the preceding day. She called for a while and then lay down. After spending 40 minutes in this spot, the mother moved, vocalizing, towards place 1, and the pup answered her there. The female immediately turned around and settled down in place 2 and there the pup joined her. During the following six days, mother and pup C were

seen to join in place 2 on four different days.

By the end of the summer, pups each day awaken in their high resting places and then, when the tide comes in, they scatter widely over the intertidal zone. On consecutive days, the mother-young pairs often show up in the same spots at predictable times.

Peculiar behavior on the part of the females, and good homing on the part of the pups, was demonstrated when, during a stampede, pups P12 and P19 were separated from their mothers for the first times in their lives. The females soon returned to the exact places where they had been lying with their young ever since they were born. For a short while after their return, the females moved around an area roughly 5 m in radius, vocalizing and sniffing foreign pups as if searching for their own. They settled down in their places and after 42 and 49 hours, respectively, the pups returned to their mothers who were still lying in the same spot.

Vocal Recognition -- Presumably, mother and young learn to distinguish each other's voices as a consequence of the vocal interchanges which begin almost immediately after delivery and continue with the greatest frequency and persistence for about three days thereafter. During this period, the vocal interchanges between mother and young are characterized by their intensity, and females usually bend closely over their young, vocalizing very strongly and for long periods, as if trying to drown out the voices of the surrounding females. That this is indeed the very function of such behavior is suggested in view of the fact that pups at this time do not know their mother's voices and tend to answer and approach any, or the most strongly, vocalizing

female.

When mutual vocal recognition has developed, the intensity of the vocal interchanges between mother and young decreases rapidly. At this stage, the mother apparently does not have to overpower the voices of surrounding females to awaken a response in her young. The pup soon learns that a strongly vocalizing female other than his mother means danger, and his response is flight.

Conclusive data are lacking as to exactly how long it takes before females and pups can recognize each other's voices. The incident in Case 9 (see "Mortality Among Pups"), however, demonstrated that pup P14 knew his mother's voice when he was four days old. Until his death, he answered his mother by intensive approach, but all other females by escape. Furthermore, pup P17, when three days old, responded to the vocalization of his mother but not to the vocalization of the adoptive mother. Finally, cow P17 constantly answered to the slightest vocalization of her young even when she did not see him. On the other hand, she never showed the slightest reaction to the call of pup P14.

During the study, there were many opportunities to observe how mother and young find each other when the female returns after a period at sea. The general pattern is fairly constant. Almost without exception, the female arrives at the water's edge at a location from which she can approach as directly as possible the place where the pup has been left. She stretches her neck vertically and starts to give the typical attraction call, often when only her front quarters are out of the water. Usually the young answers immediately,

whether or not he can see the female, and starts to move towards her, strongly vocalizing. The female responds to the young's call sometimes by approaching him, sometimes only by staying in her place, calling. Among Callorhinus (Bartholomew 1959:169) and Zalophus (Peterson and Bartholomew 1967:43), several pups frequently responded and approached a female under these circumstances. This, however, is not the case among Eumetopias, where all young but the one belonging to the female are indifferent to the calling female, or, if they are close, respond with fear. Although many complications can arise, especially if the female is of low dominance and aggressive cows lie between her and the young, mother and young normally soon meet.

Olfactory Recognition -- During the delivery, the female intensely sniffs the spot where the amniotic fluids are expelled. Careful olfactory examination of the perineal region, and later of the partially delivered pup, is also general. Furthermore, the marked persistence and frequency with which the female sniffs and nuzzles her pup immediately after delivery, and for a period of about two days thereafter, is noticeable. That the sniffing and nuzzling activity may enable the female (shortly after delivery) to differentiate by smell between her own and other young is indicated in Case 4 (see "Mortality Among Pups"). Female D's pup was stolen immediately after delivery, and half an hour later she reacted to pup E, who slid down in front of her, by throwing him away after careful olfactory investigation. Females with newborn young react in a similar way if they are suddenly faced with two pups (the extra pup having been tossed by a nearby female). After careful olfactory examination of the two, they

toss one away. Presumably, the alien is rejected on the basis of difference in smell.

At the time when female and young start to separate, the vocal preliminaries each time they meet always seem to be followed by the female carefully sniffing the nose and body of the pup before she accepts him. The young, however, usually heads right towards the nipple without showing any apparent interest in the female's smell. Sometimes females are seen to examine the pups in a pod, one by one, and then to awaken one and nurse him.

The function of olfaction as a means of mutual recognition is not well understood. It seems quite clear, however, that olfaction, at all stages after delivery, is of great importance as a means by which the female at a short distance can identify her young. In fact, it seems to complete the recognition process, and at an early stage it is the only means by which the female can identify her young.

Recognition by Vision, Touch and Taste -- Although visual clues are obviously used to orient pup and female to each other, these, together with touch and taste, are probably of little importance for specific individual identification, at least in comparison with sound and smell.

Factors Influencing the First Departure to Sea After Parturition

Among the 20 individually known cows that were observed to copulate, 12 went to sea for the first time before, and the remainder after, copulation. Callorhinus females leave for sea for the first time about one day after copulation (Peterson 1965:166). In the cases

where Eumetopias cows went to sea following copulation, the departure usually took place only a few hours later.

The timing of the first departure to sea in relation to parturition for 39 individual cows with pups ranged from 5 to 13 days after parturition (Fig. 25), with a mean of 9 days. In one case, the mother left her young on the second day after parturition.

In an animal without dependent young, the relationship between time at sea and time on land could ultimately be influenced by two simultaneous forces: the need for rest and social contact, and the need for food. The gross pattern of time spent on land and at sea could be species-specific.

In the case of a female with a newborn young, the normal feeding rhythm is disrupted and, as we have seen, the duration of this disruption varies considerably between animals. The duration and variability of the period when the female uninterruptedly stays with her young after parturition is likely to be closely related to the development of the young and the individual cow's perception of this development. Since the interval between parturition and the female's first departure to sea is probably the most critical period in the life of the pup, some of the factors likely to influence the duration of this period will be mentioned.

The time required for the mother and young to identify each other individually is very likely one of the main determinants of when the cow will leave her young for the first time. Many observations show that the young knows its mother vocally within 10 days after delivery. A young pup responds only to its mother. From a

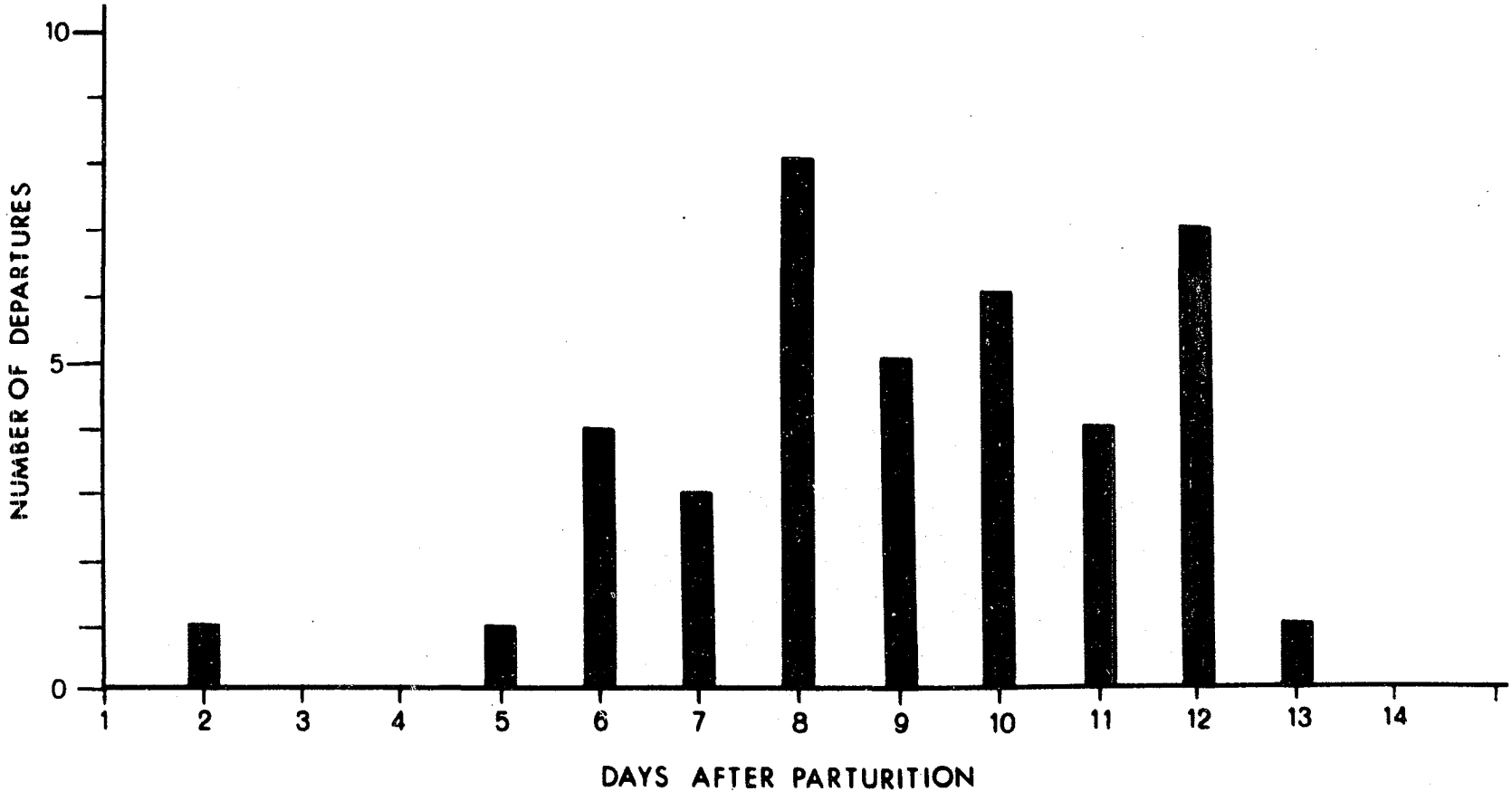


Figure 25. Frequency occurrence of first departure to sea in relation to day of parturition among 40 females.

purely operational point of view, it would be extremely dangerous if the pup were to respond to the pup-attraction call of foreign females, because it would probably soon be bitten so badly that its life would be endangered.

Before his mother departs to sea for the first time, the young must acquire a certain degree of physical development to be able to endure alone the very hostile environment that a sea lion rookery presents to a young pup. Proper food intake is one of the requirements for physical development; exercise is another. It is of fundamental importance for survival that the pup, during the absence of his mother, be able to climb steep, slippery upgrades and quickly scramble to one side on the approach of aggressive cows or heavy bulls. Training to acquire the necessary physical skills is, at least in part, reinforced by the mother who regularly exercises her young in locomotion from an early age. The distribution of 65 such exercises among 10 pups in relation to their age is shown in Fig. 26. Females have been observed to exercise their young as often as three times in one day and over 15 minutes for one exercise period. The exercises are performed in accordance with the principle of punishment and reward. They generally occur in the periods of low activity in the rookery, and usually lead the couple in a circle back to the place from which they started. A purpose other than the exercise itself is difficult to imagine. When the pup is young, the exercise is performed on a surface with little or no upgrade. As the pup develops, the training becomes more advanced until the mother finally activates her young to climb the steepest slopes available.

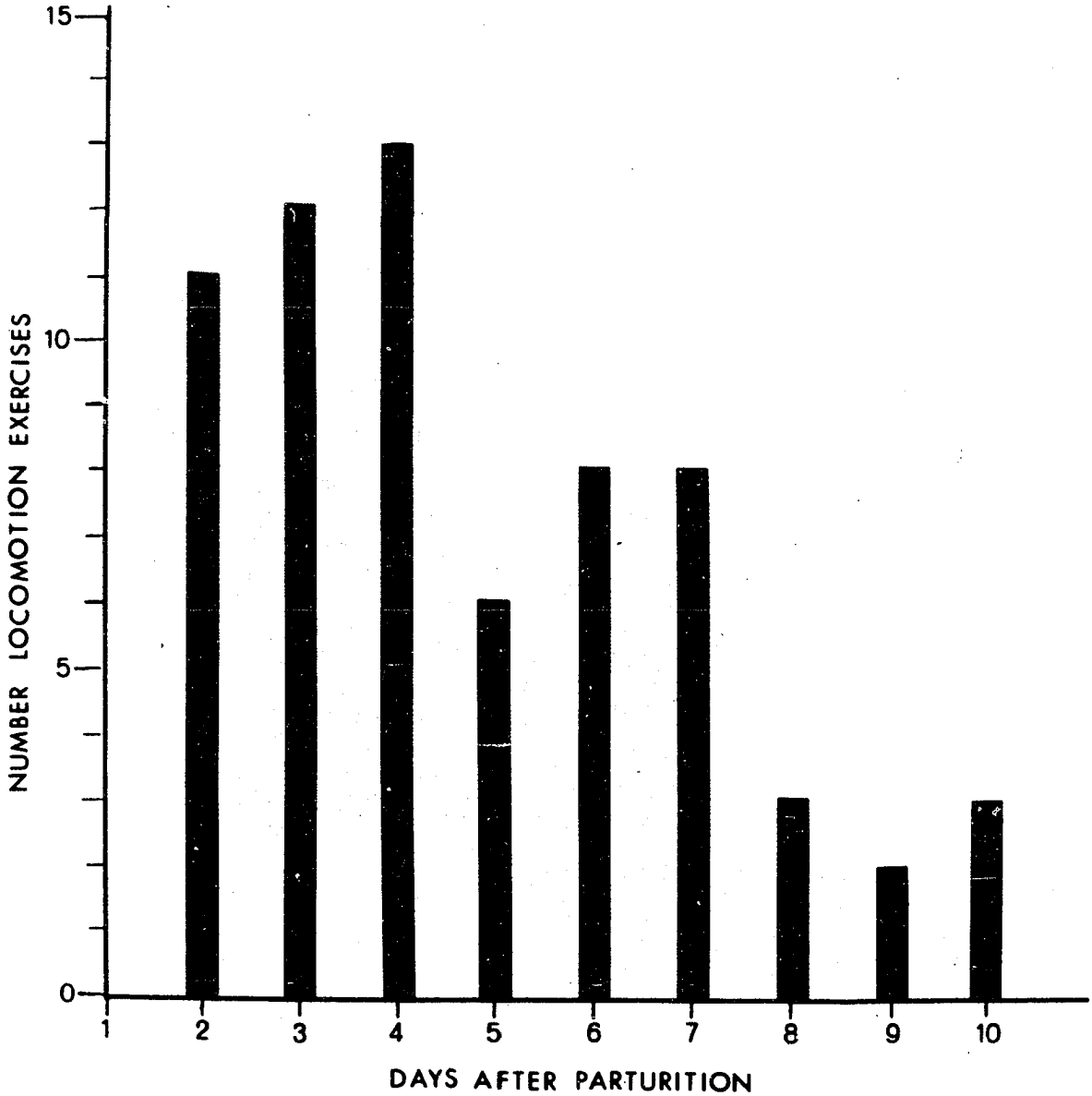
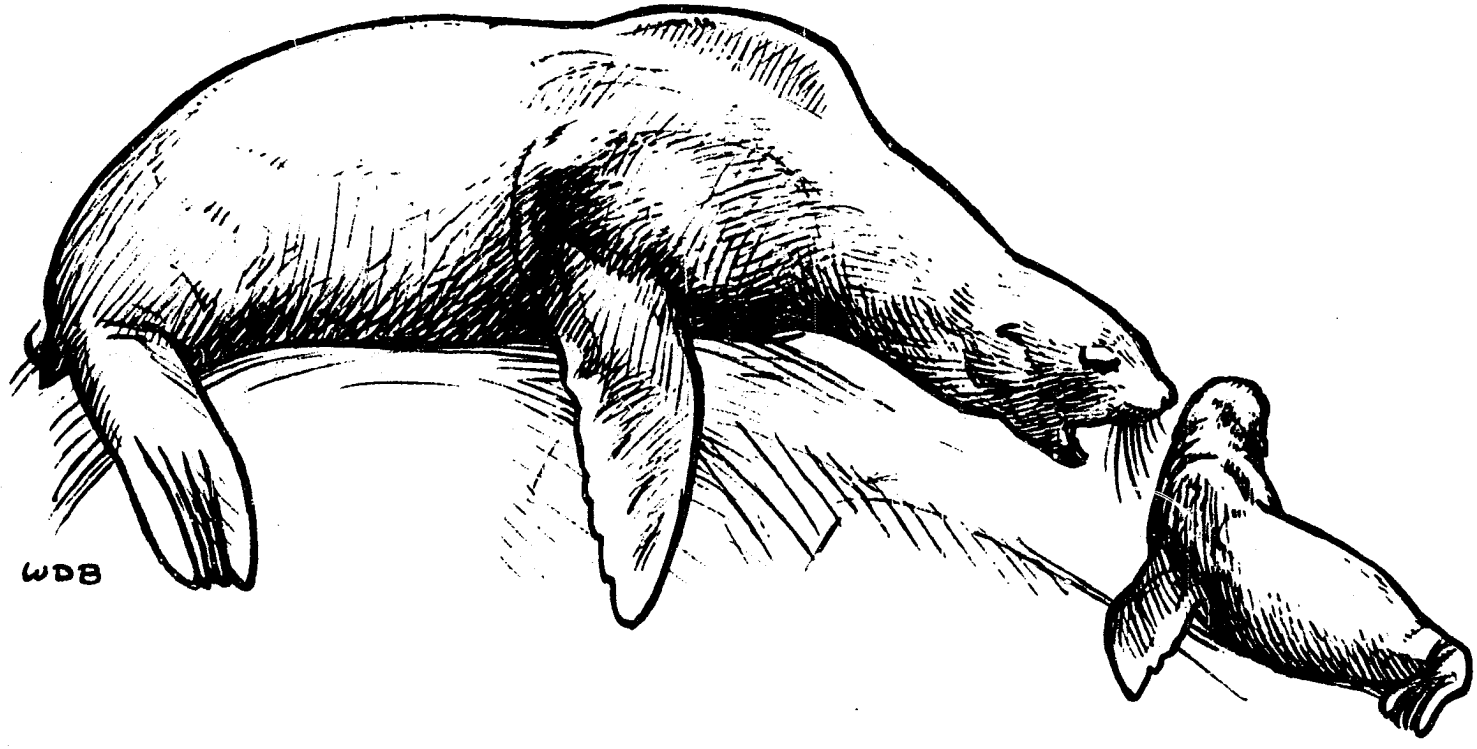


Figure 26. Distribution of 65 female-stimulated locomotion exercises in relation to day of birth of 10 pups.

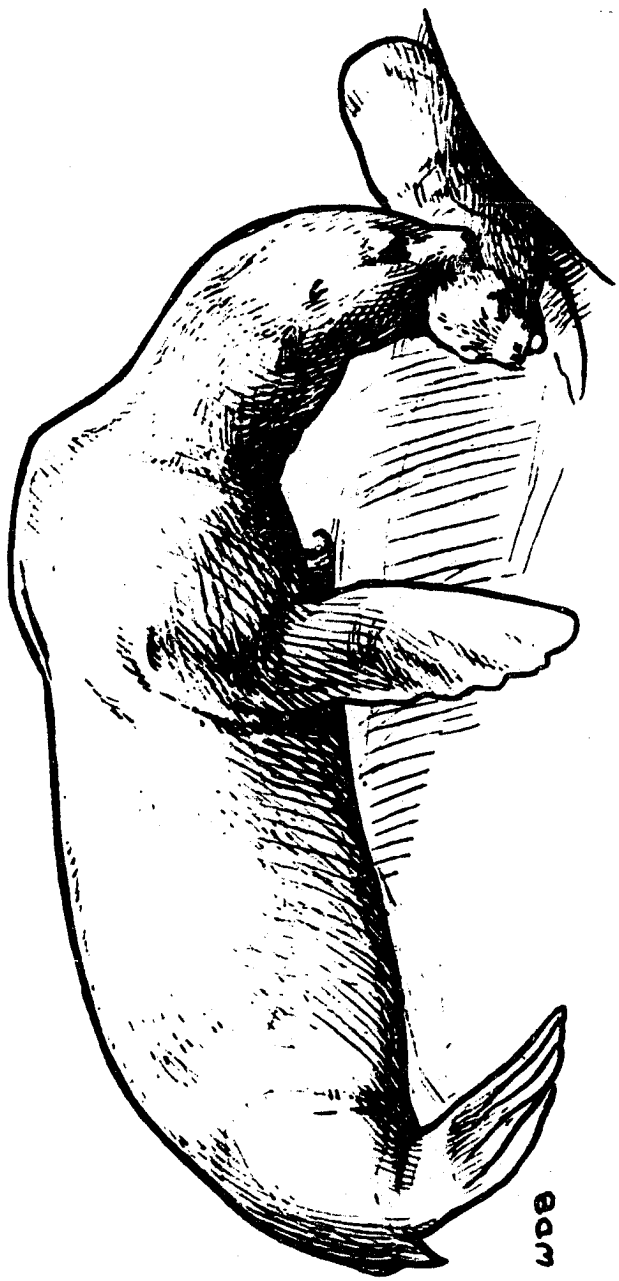
A period of exercise is usually initiated when the pup wants to suckle. The mother moves away and starts to vocalize to the pup. If her young answers and moves towards her, she remains quiet and observant until the young reaches her. Then she may move away again and repeat the process several times. If her young does not show interest, cannot, or has difficulty following, the mother bends over her young and vocalizes strongly at a close distance (Fig. 27a). If this does not accelerate the pup's efforts, she will nip him (Fig. 27b). This usually has a strongly stimulating effect and often enables the young to overcome obstacles that initially seemed great. At the same time as the cow nips, she usually drags her young in small stages towards her. If the pup still does not manage to reach her, she finally drags him slowly to her by the nape of the neck (Fig. 27c). Several times, females have been seen to support their young with neck and breast when the pups had trouble climbing an especially difficult place.

During the period in the pup's development when exercises occur, the females are very stationary, usually lying in one spot day after day. Under these circumstances, it is easy to imagine that exercise is important, not only for physical training, but also to give the female a perception of the stage in the pup's development.

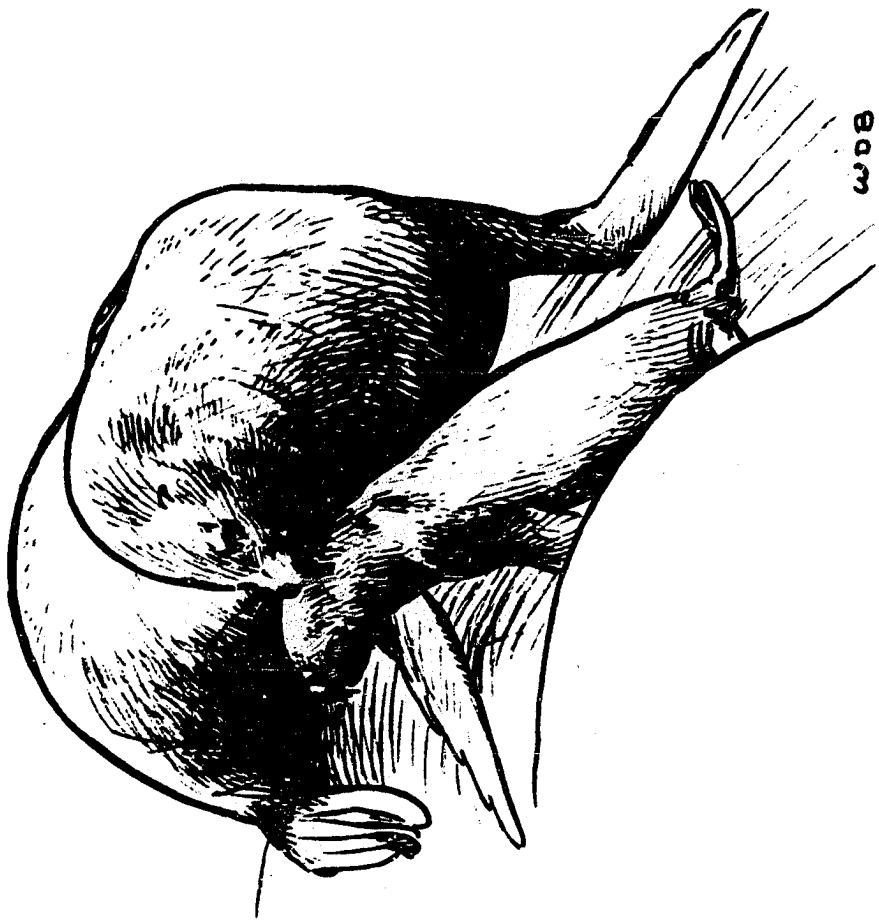
Although the period of development of mutual recognition and physical strength is likely to determine the minimum amount of time that the females spend with their young after parturition, the maximum time spent with the young, at least in part, seems to be a function of the size of the female. Thus, seven of the largest females left their



Figures 27a-c. Female exercising her young by stimulating it to locomotion.
a) Calling.



b) Nipping.



c) Lifting and slowly dragging young towards her.

young for the first time between 8 and 12 days after parturition, with a mean of 10.2 days, while seven of the smallest left 5 to 7 days after parturition, with a mean of 5.4 days. In 40 cases, only two females left their young for the first time sooner than six days after parturition and in both cases the pups met an early death.

It seems likely that a correlation between size and nursing capacity exists, which would enable large females to remain with their young for a longer period than small cows, who would have to feed to restore their energy resources sooner. Also, large dominant females can use their energy reserves more conservatively than small ones, as the latter are involved with frequent and energy-consuming agonistic encounters with surrounding animals.

It should not be forgotten that females are reluctant to go to sea in the period around estrus. Certainly, for late departing females, this could be the overriding factor in the time of departure.

Feeding Rhythm of Females

After the first departure, the feeding habits of *Eumetopias* cows are quite regular and the periods on land and at sea usually do not exceed 24 hours, at least not in the first weeks after the first departure. Although individual differences exist, females usually depart in the evening or afternoon and return the next day. Based on 76 observations of 11 females, the time at sea varies between 9 and 40 hours, with a mean of 16.7 hours, and the time on land between 9 and 42 hours, with a mean of 17.0 hours. In comparison, *Callorhinus* females spend about eight days at sea and two days on land in the

first four to five months after parturition (Peterson 1965:171). Fig. 28 illustrates periods on land and at sea for five females in the first six to seven weeks after delivery.

In 1967, cows F, H, J and A, B, N were followed closely enough to ascertain that the three former were dominant over the three latter in many agonistic encounters. Based on 24 observations of F, H, J and 22 of A, B, N, the three former spent between 9 and 24 hours at sea on each occasion, with a mean of 13.7 hours, while the three latter spent 12 to 40 hours at sea on each occasion, with a mean of 21.2 hours. Although more data are needed to draw any wider conclusions, this shows that considerable differences in time spent at sea exist among cows and that these differences, at least in part, may depend upon differences in size and dominance.

Most data on the time spent in the rookery and at sea among different females were gathered during a period of about 30 days after the first departure. As the summer progresses and the breeding ceases, the habits of the animals change. They tend to haul out in more exposed areas where they are harder to observe and, therefore, exact arrival and departure data are hard to obtain. During the last eight days of continuous observations in 1967, the 10 most easily identified females were sighted on 66 out of 80 possible days. This, combined with the fact that none was missing for more than one day, indicates that no major change took place in the feeding pattern as late as 40-50 days after the first departure to sea.

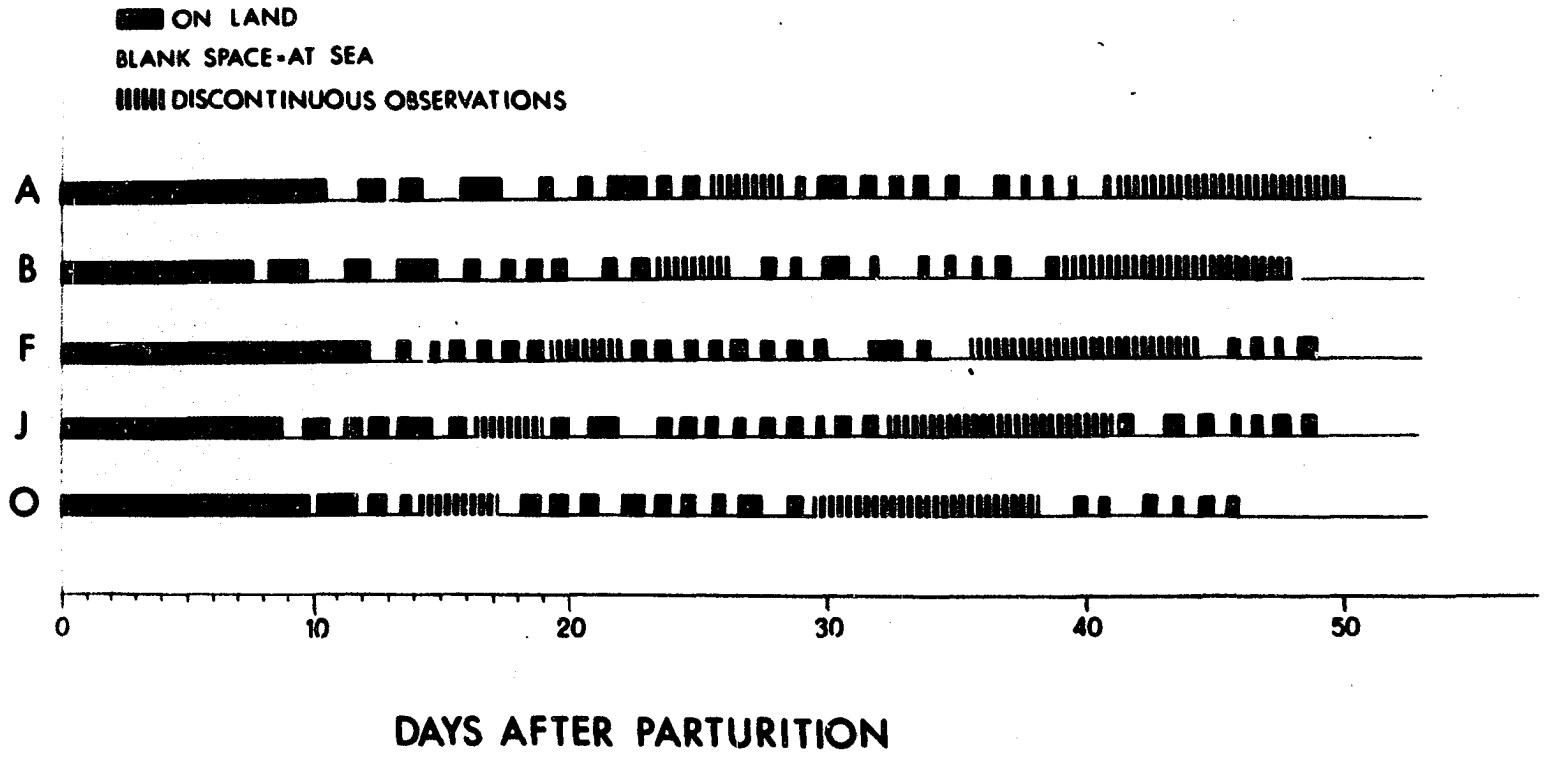


Figure 28. Periods on land and at sea for five females in the first six to seven weeks after parturition.

Nursing

Observations of seven individually known pups and their mothers during a period of seven weeks, and of approximately 30 individually known mother-young pairs in the period before the mother first left for sea, show that females do not normally separate from their young before mutual recognition is developed and that they nurse their young to the exclusion of all others. Pups have never been seen to try to nurse a foreign female. The absence of fosterage is also described for Callorhinus (Bartholomew and Hoel 1953:421) and Zalophus (Peterson and Bartholomew 1967:41), while fosterage frequently occurs among Halichoerus (Smith 1965:73).

In the first few days after delivery, the female initiates suckling. This is done by rotating the hindquarters to make the teats easily available, followed by activation and careful watching of the pup at close range. During this period, the lift-drop and nip activations gradually disappear and from then on the pup initiates nursing by showing various types of appetitive behavior. The most common elements of this behavior are bleating combined with fast lateral head shakes, and repeated nose to nose contact with the mother, interspersed with periods in which the pup pushes with his nose while attempting to reach the nipples.

Teats vary in number from four to six and are either extruded spontaneously or through stimulation by the pup's pushing combined with sucking. The teats may remain extruded as long as the female is lying in nursing position, in contrast to Zalophus where retraction of the teat occurs immediately on release by the young (Peterson and

Bartholomew 1967:40).

Three phases of a nursing period can normally be distinguished in relationship to the physiological mechanisms regulating milk flow and the associated behavior of the pup. These are as follows:

1) The first period commences with the first display of appetitive behavior and continues up to the initiation of consummatory nursing activity.

Milk ejection usually starts within five minutes after initial stimulation of the teat. In some cases, however, the pup may spend 20 minutes or more trying to obtain milk, but without success. The pup's behavior characterizes this period. If the nipples are not extruded, he pushes intensively in the area of the inflated nipple and this stimulation apparently causes erection of the nipple. Upon extrusion of the nipple, he pushes and pulls on it, sucking loudly. He changes nipples frequently, usually alternating between two. If, in spite of his effort, no milk is obtained, he responds by vocalizing strongly and biting the belly of his mother. He repeatedly rubs noses with her and then continues to massage her teats. If the pup is still unable to obtain milk, he may bite the female severely several times in the belly or in the immediate area of the nipples. Apparently, this is often painful, since the female may be seen to jump up and threaten the pup. Apart from this, threats are rarely seen in the interactions between mothers and young.

2) The second period extends from the initiation of consummatory

activity up to the point at which milk flow ceases, or the pup is sated.

When the milk flow starts, the pup becomes very calm, as does the female. The intensive pushing and sucking activity that preceded it disappears almost completely and the massaging of the nipples by the pup's lips seems to be sufficient for maintaining the flow of milk. Throughout this period, the young either swallows continuously or takes short pauses in which he swallows the milk. Towards the end of this period, a pup may fill his mouth with so much milk that his cheeks bulge before he pauses to swallow. As his hunger apparently becomes satisfied, the pauses grow longer and the pup may spend several minutes with his head up, holding milk in his mouth, before gradually swallowing.

3) The last period begins with the cessation of milk flow and ends when the pup changes to another activity or initiates a new nursing period.

If the milk flow ceases before the pup is satiated, the behavior of pup and female is similar to that described above for phase 1. Intensive pushing by the pup may cause the cow to change position so that the young can suckle on the other teats. This may enable the pup to continue suckling for an additional period. Violent hiccuping and belching are often observed during and after a nursing period.

In 1967, 267 nursing periods of pups from newborn to one month old were timed and found to vary in length from 1 to 50 minutes, with

a mean of 15 minutes. The majority of these times are for pups less than 10 days old. In 1968, when the activity pattern of pups was recorded with respect to the main type of activity within consecutive five minute periods, 181 timed nursing periods for pups less than 10 days old varied between 5 and 45 minutes, with a mean of 16 minutes. The distribution of these periods is illustrated in Fig. 29 and shows that the most frequent nursing time is 15 minutes. Additional data from pups of various ages are required as a basis for more accurately relating the length of the nursing period to changes in age of the pups. It is noted, however, that the mean of 103 nursing periods for pups less than two days old was 11 minutes while the mean of 56 periods for pups between 10 and 20 days old was 19 minutes, indicating a lengthening of the nursing period with age. This is also indicated by a mean of 23 minutes for 46 nursing periods of subadults.

The total amount of nursing time (i.e., the summation of nursing periods) within a 24-hour period was measured. For 21 such periods representing 18 pups one-two days old, the time varied between 120 and 295 minutes, with a mean of 205 minutes. In those cases where nursing activity was recorded for only 18 hours, the results were extrapolated to 24 hours. For pups between 3 and 10 days old, total nursing time varied from 25 to 350 minutes, with a mean of 107 minutes, on the basis of twenty-seven 24-hour periods. Pups more than 10 days old are difficult to follow for long periods, but in eleven 24-hour records of pups 11 to 28 days old, the total nursing time varied between 75 and 240 minutes, with a mean of 126 minutes.

The drastic decline in mean nursing time for a 24-hour period a

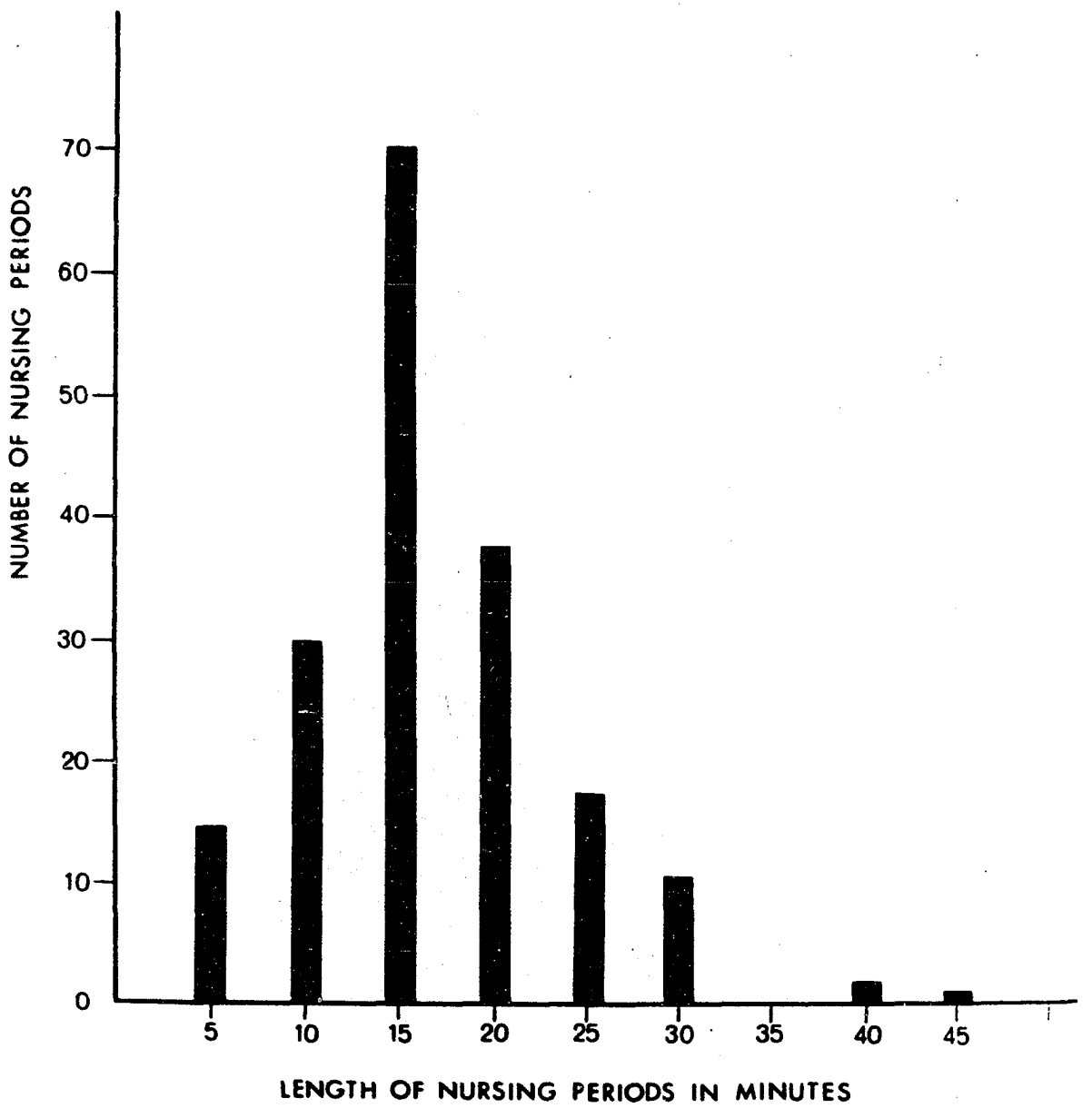


Figure 29. Variation in duration of 181 nursing periods among pups 1 to 10 days old.

few days after delivery might be attributed to several of the following factors:

1) The strong nursing activation to which the pup is normally subjected in the first two days after delivery is likely to produce long nursing times during this period.

2) It is known that milk secretion in domestic cows (Luick, pers. comm.) markedly decreases at the time of ovulation. If the same were true for Eumetopias females, the decrease would occur somewhere between 10 and 14 days after delivery and therefore could contribute to the general decrease in nursing by pups during this time. In several cases, the decrease, however, had been apparent six to eight days before the female copulated, indicating that other factors are at work.

3) Since the average female (mean of 40 cases) stays continuously on land without feeding for nine days after delivery and the net use of energy by her for milk production and her own metabolic demands are great, a decline in milk secretion during this period may be merely a reflection of this energy deficit.

The variations in time spent nursing for pup B during the first eleven 24-hour periods after delivery are shown in Fig. 30. The decline in nursing from 285 minutes on the day of birth, to 25 minutes on the seventh day is noted. On the eighth day, cow B went to sea for 13 hours and during the following day she nursed her young 245 minutes--almost 10 times more than on the seventh day. The decline before and

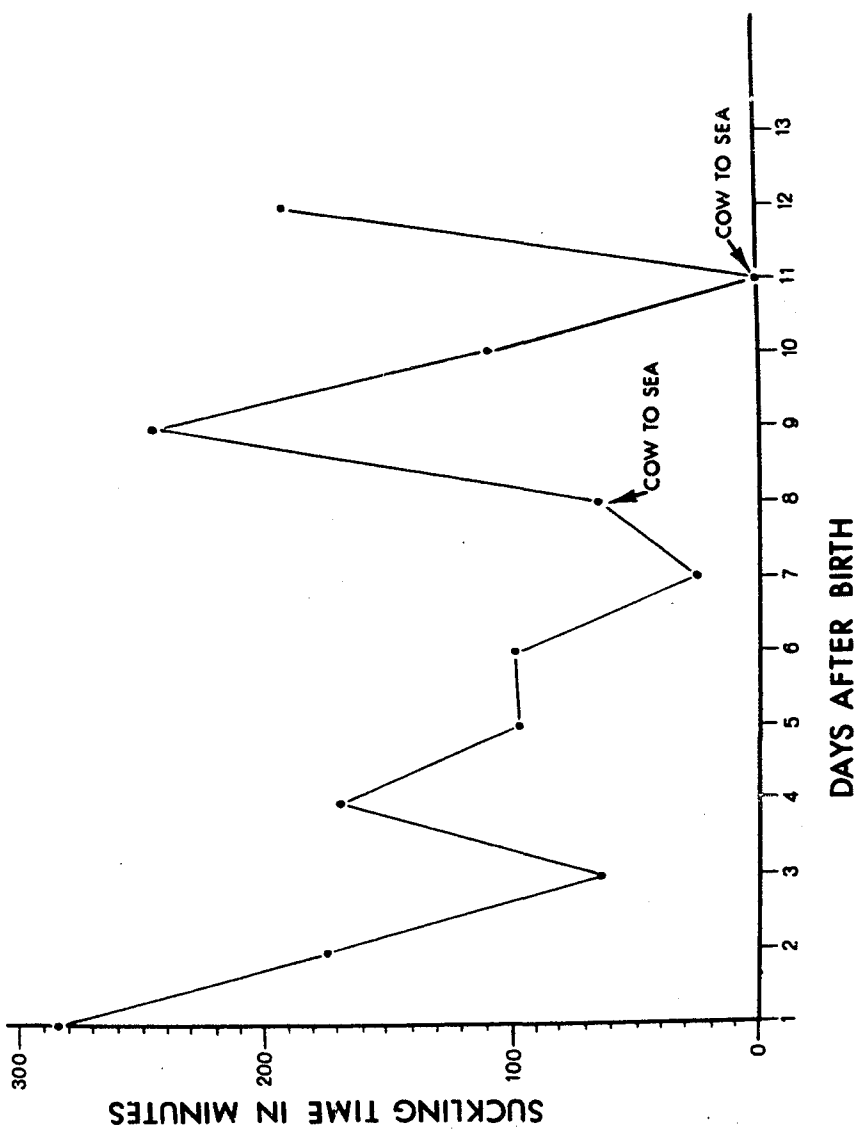


Figure 30. Variation in nursing time per day during the first 12 days of life for pup B.

rise after the next trip to sea, which took place on the eleventh day, is also noteworthy. The similar trend among other females gives strong support to point 3, above, as a main contributing factor in the decline of nursing.

Between June 15 and 18 in 1967, four female-young couples, lying within "pecking" distance of each other, were followed continuously for three 24-hour periods. Their activities were recorded on the basis of the dominant type of activity within each five-minute period. When the study began, the pups belonging to the four females (named Vi, J-67, P, and Di) were six, seven, six and three days old, respectively. Cows Vi and J-67 appeared to be of equal dominance, and both were dominant over P and Di. The cumulative nursing time in each 24-hour period (Fig. 31) for the four pups varied considerably--420, 705 and 360 minutes. The difference in nursing times on the second and third days may be (partially) attributable to the difference in weather. The third day was very warm and the animals were less active than on the previous day, when it was cloudy and cool (Fig. 32). The cumulative nursing times during the three days were 590, 375, 255, and 265 minutes for the pups in the above-mentioned order. Note that cow Vi, who went to sea in the first 24-hour period, nursed her pup more in the following two days than any other female nursed her pup in the entire observation period. It is also noteworthy that pups Vi and J-67, belonging to the two dominant females, together nursed 87 per cent more during the three days than pups P and Di.

Fig. 33 shows the nursing pattern throughout three 24-hour periods for the pups discussed above. Each curve illustrates the

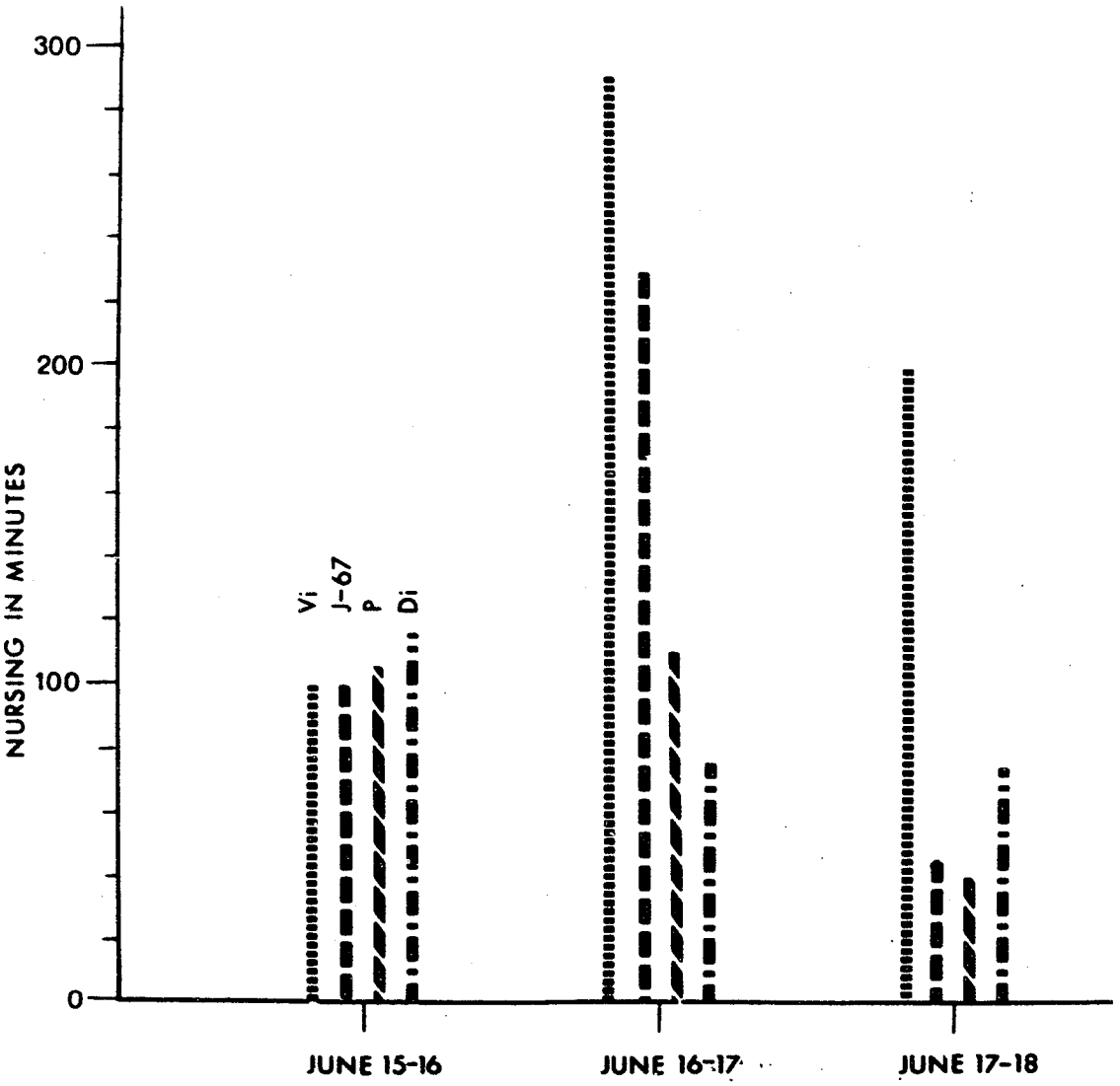


Figure 31. Suckling times for four pups in three consecutive 24-hour periods beginning 19:30 on June 15 in 1968.

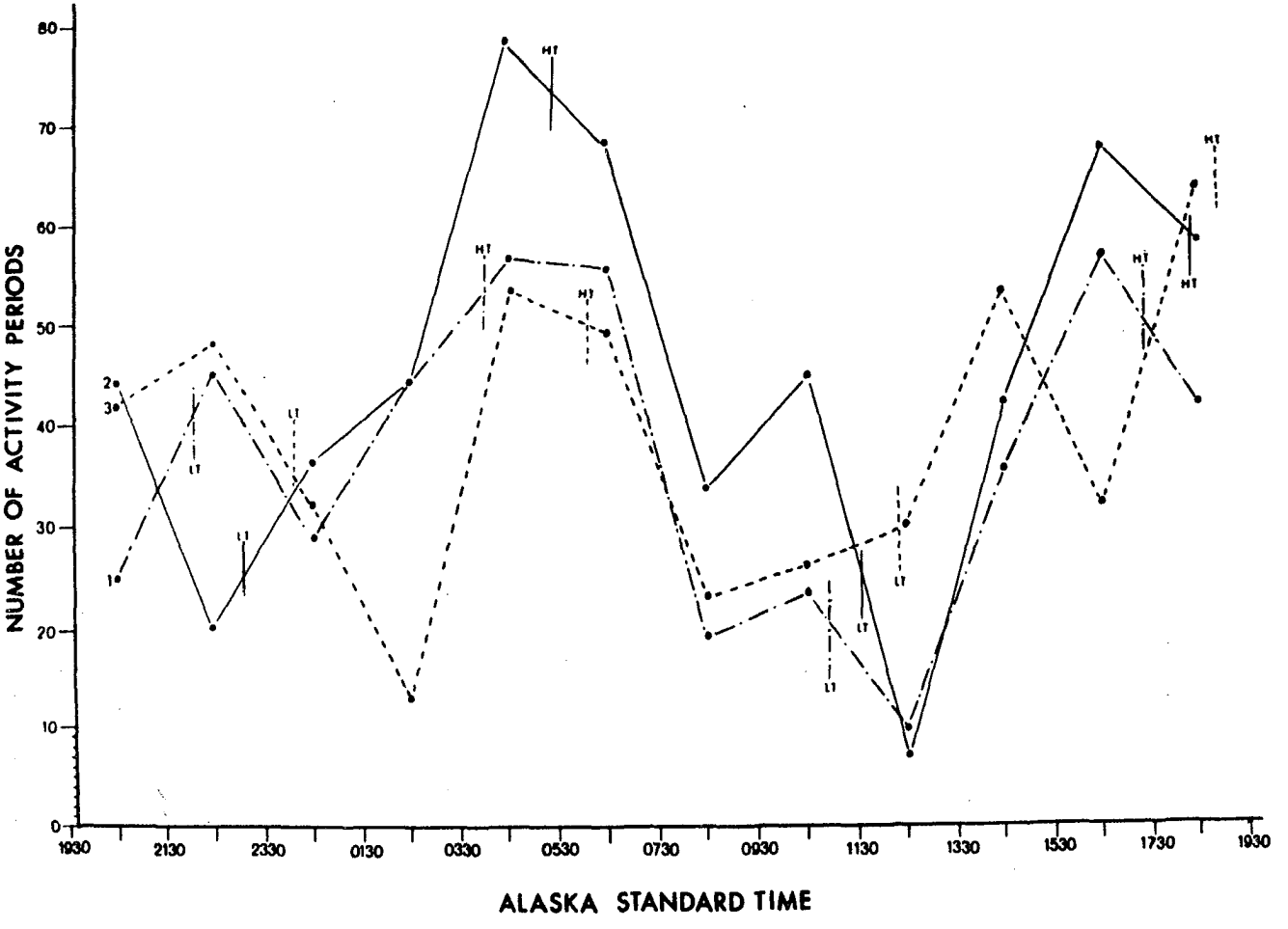


Figure 32. Variation in activity among four pups, measured by cumulative number of five-minute periods of activity per two-hour period of observation, during three consecutive 24-hour periods (1, 2, 3) beginning 19:30 on June 15 in 1968. High tide (H. T.) and low tide (L. T.) are indicated in the figure.

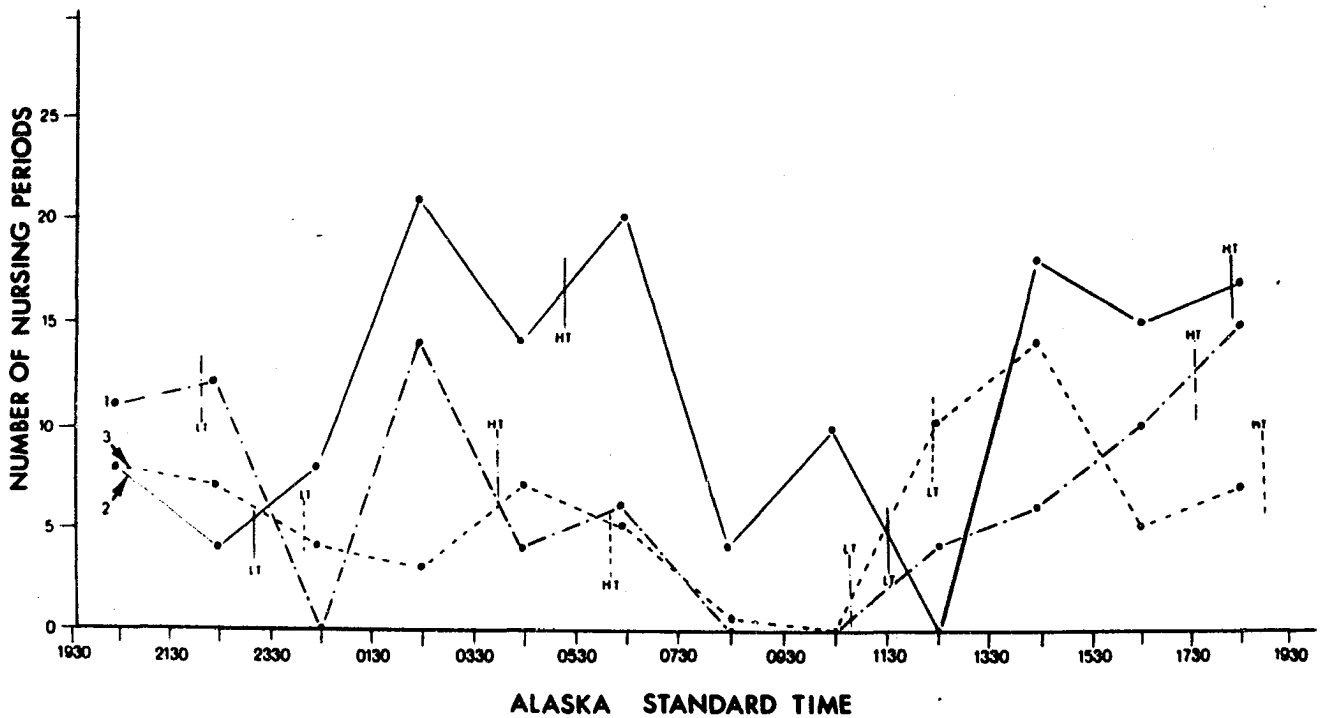


Figure 33. Variation in nursing activity among four pups, measured by cumulative number of five-minute periods of nursing per two-hour period of observation, during three consecutive 24-hour periods (1, 2, 3) beginning 19:30 on June 15 in 1968. High tide (H. T.) and low tide (L. T.) are indicated in the figure.

variation in the cumulative number of five-minute periods of nursing activity per two-hour interval for the four pups. In Fig. 32, the activity patterns of these pups on the same three days are plotted in the same manner. Comparison of the two graphs of nursing activity and general activity shows that periods of high nursing activity coincide with periods of high general activity, in a diurnal rhythm. Furthermore, high general activity on a given day seems to correspond with high nursing activity on the same day.

The diurnal rhythm seems to follow that of the tide, with high activity during high and low activity during low tide. It might have been mere coincidence that the rhythm observed on these days happened to follow a tidal rhythm and the actual cause may have been other factors. To prove or disprove this, similarly collected data from periods of different tidal rhythm would be needed. Assuming that the activity rhythms of all animals in an integrated society are roughly similar, it should be possible to utilize data collected for bulls during a period of different tidal rhythm to make a comparison. In fact, Fig. 5 shows that there is a marked diurnal activity rhythm among bulls following the tidal rhythm, which in this case is about six hours out of phase with the rhythm of the aforementioned pups. Highest activity among the pups was found between 04:00 and 08:00, a period coinciding with the period of lowest activity among the bulls. The data for the bulls was collected five-eight days after the pups were continuously studied.

In the first few days after delivery, most females continuously defend a rearing territory which they try to locate as close above the

high tide line as possible. The aggressiveness in combination with this defense reaches a peak during periods of high tide, when room is limited. Some of the implications of this behavior among females, for the development and survival of their young, will be discussed later.

Within a few days after estrus, females and young start to occupy the intertidal zone. Within this zone, a definite order of preference exists for places suitable for nursing of the young, and aggressive interactions between females in competition for these places are frequent. The most desirable places are flat shelves, as close as possible to the high tide line, and there the dominant females claim and vigorously defend a place during periods when they nurse their young. Between nursing periods, the aggressiveness of the female ceases and the young, if still with the mother, usually rests on her back while other animals are allowed to pack together around the couple. The competition for nursing places is illustrated by the following example. Cow F was dominant over cow A. For five days, F and A were seen to meet their young and nurse them on rock 32 in the intertidal zone. On this rock, there were two nursing places of which one, 1.5 m higher in elevation, was generally favored. Female A usually arrived from sea early in the morning, contacted her young, and then settled down in the upper place, only to be driven away shortly thereafter by F, who usually arrived and contacted her young between 10 and 30 minutes after A. F soon began to nurse her young in the upper place while A, after the tide had dropped, then settled down in the lower place to nurse her young. On two warm days,

F, when she had nursed her young, drove A away from the lower (cooler) place before A had even begun to nurse her young. A then moved to the higher spot. In the evening, when the tide came in and reached F, she moved to the higher place and drove A away, who then left to sea. F then nursed her young and left later, when the tide reached her nursing place. On three days with cool weather, F stayed in the higher location and A in the lower throughout the day.

The number of nursing periods on observation days varying in length from 18 to 24 hours was counted. For pups one to two days old, the number of such periods within each of 21 days varied between 7 and 19, with a mean of 12. For pups 3 to 10 days old, the number in each of 27 days varied between 2 and 14, with a mean of 7; for pups 11 to 28 days old, in each of 11 days the numbers varied between 3 and 9, with a mean of 6. Referring to Zalophus, Peterson and Bartholomew (1967:41) state that pups of this species when more than two or three weeks old seldom were engaged in more than one nursing period in one day, compared to Eumetopias pups who by the same age were never seen engaged in less than three nursing periods in one day. In three cases, subadults have been engaged in 3 to 12 nursing periods in one day.

Fig. 34 shows the distribution and length of the nursing periods for pups Vi, J-67, P and Di during the first two days in which these four pups were followed. The length and distribution of activity and inactivity periods are also given in the diagram. It can be seen that activity and nursing periods of the four pups tend to coincide.

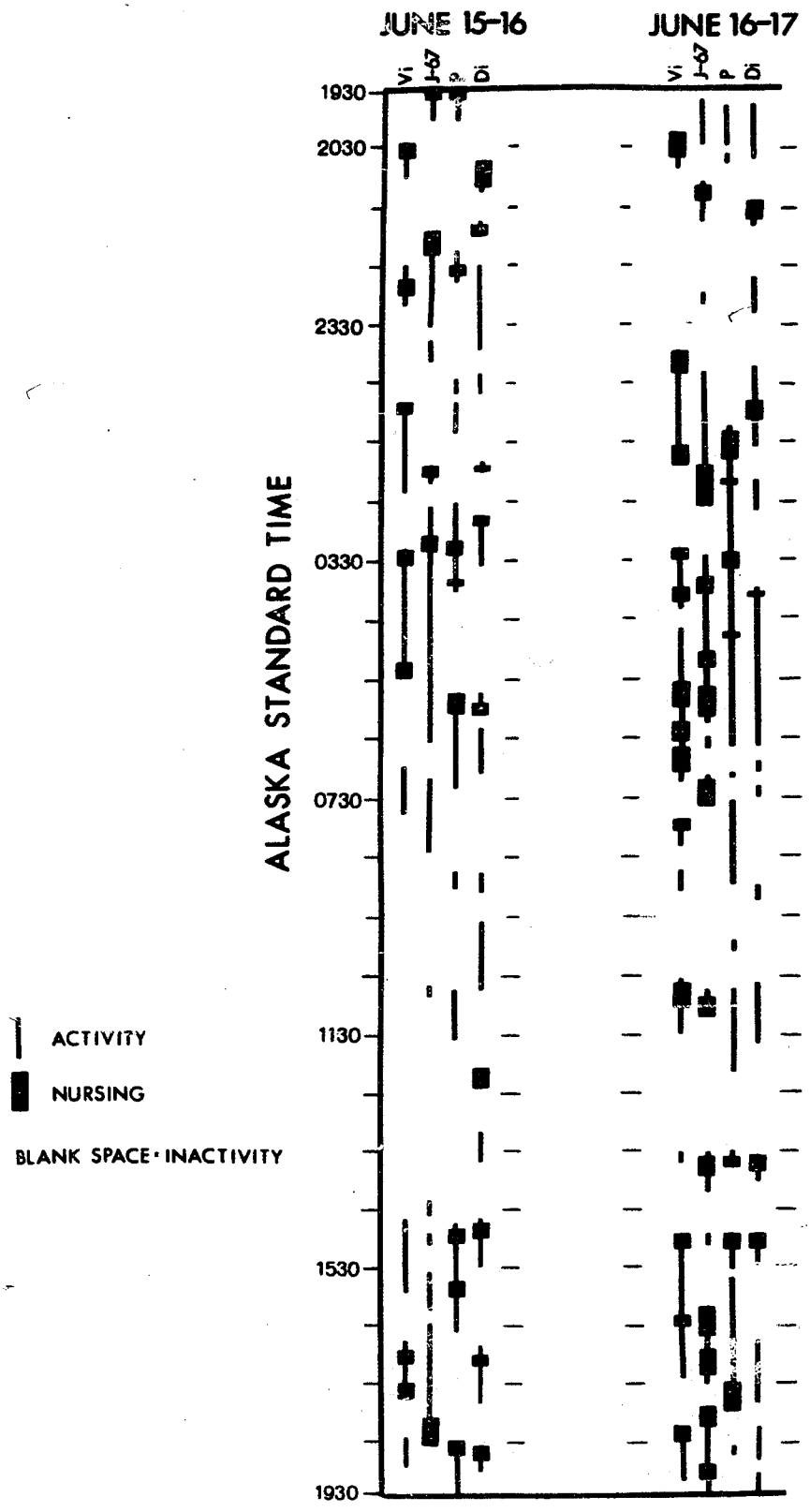


Figure 34. Distribution of periods of activity, nursing, and inactivity for four pups during two consecutive 24-hour periods beginning 19:30 on June 15 in 1968.

Mortality Among Pups

In 1967, a total of seven (12.5 per cent) of the pups born died within the first two weeks after delivery. In 1968, six pups (14 per cent) of the 43 under regular observation died within the same period. Among the cows and pups observed for six to eight weeks after delivery in 1967, no mortality was noted after the first two weeks.

As the numbers and locations of the pups that were observed to die in both years corresponded to the numbers and locations of carcasses found when the rookery was searched after the breeding season ended, the above-mentioned figures are probably close to the actual mortality rates. Furthermore, these observations indicate that the carcasses are not washed to sea. Scavenging birds do not show any interest in dead pups.

No stillbirths were observed, which is noteworthy since these have been quite common among Eumetopias females on Ana Nuevo Island in California in both 1967 and 1968 (Peterson and Gentry, pers. comm.).

In three cases, females remained close to dead pups from one to three days after death occurred. Although these females attempted to activate their inert pups, and one was seen to defend her dead pup against intruding animals, their caretaking behavior soon ceased, and most of the time they simply lay on, or close to, their pups.

Although the reason for the death of one pup is completely unknown, most of the remaining cases have been followed closely enough to suggest the nature of the mortality factors involved.

Cases 1 and 2 -- At an early age, two pups were subjected to injuries that caused complete and partial paralysis of their hindquarters,

respectively. Within four and five days, the pups became emaciated and died. Although the circumstances under which the injuries were acquired (and thus the actual mortality factors) are unknown, the maternal behavior in one of the two cases is worth describing.

The injured pup was lying about 10 m on the inland side of the rookery, separated from the main herd. When the mother came from the sea, she stopped 7 m away from her young and vocalized. The young soon answered and started to move towards her slowly, with dragging hindquarters. When they met, the female nuzzled her young and then turned around and moved into the intertidal zone from which she had come. She turned towards the pup and vocalized strongly. The pup tried to reach her but was unable to do so. After about one half hour, when the female had called to her pup several times, she turned back and nursed it. After a few minutes of nursing, the mother appeared very restless and again moved from the isolated place where they had been lying into the intertidal zone. She visited with her young twice again that day, but both times appeared restless and soon left.

The next day, much of the same activity was repeated and the female did not stay with her young for more than a few minutes. Two days later, in the morning, the mother was seen again. She vocalized several times towards the now dying pup. As she did not get any answer, she did not approach nor give the young further attention.

This occured at the time of the pup's development when mother and young usually join in the intertidal zone. The isolation of the pup--typical for sick or injured animals--combined with the extreme reluc-

tance of the female to separate from the herd, accelerated the death of the pup. A life outside the social community does not appear to exist among Eumetopias females.

Case 3 -- During a stampede, caused by the observers on July 3, 1967, pup P6 was separated from its mother and disappeared. On six of the following seven days, the mother came back to the exact spot of separation. Several times she was seen to call and search among the pups in the immediate vicinity, but never anywhere else.

In the following four cases, the females did not wean the subadults and, probably as a consequence of this, normal caretaking of the newborn pups either did not begin or soon ceased.

Case 4 -- Two females, D and E, were in labor simultaneously and quite close together. While cow D was in labor, she was accompanied by her subadult who tried (apparently successfully) to suckle. Normal birth behavior was never shown by cow D and when her young was presented she merely looked at it without retrieving it.

Cow E caught sight of D's newborn pup and, apparently mistaking it for her own, she attacked D and stole her young. Cow D did not attempt to regain her young and was soon nursing the subadult.

When half an hour later cow E delivered her own young, she appeared more concerned with the stolen pup than with her own delivery; E's young slid down in front of D who nuzzled the pup carefully and then threw it to one side. Neither E nor D paid further attention to E's rejected pup.

Case 5 -- Cow F delivered her young in the presence of her subadult. At first, she showed good caretaking and the young soon suckled.

Interestingly enough, the subadult, as in the previous case, reacted very strongly each time the cow showed caretaking behavior to the pup. On these occasions, the subadult started to run around the mother, crawl on her back and neck, vocalize strongly, seek nose to nose contact, and show nursing appetite. Although the mother showed good caretaking once in awhile, she spent most of the time stretched out with her subadult by her neck, paying little or no attention to her newborn young.

When he was about six hours old, the pup began to crawl away from the mother and was not retrieved. The pup came too close to a nearby cow with pup, received a few bites, and then was thrown about 3 m to one side. As the pup started to vocalize intensively, the mother looked at it and moved over to it. For a while it seemed as if the female would retrieve her young, but instead she merely nuzzled it and turned back to the subadult. The deserted pup continued to vocalize and move about. It was soon thrown by some foreign cows and disappeared from view. The mother and her subadult were observed continuously throughout the next 24 hours during which she showed no further interest in the pup.

Cases 6 and 7 -- These cases were very similar to cases 4 and 5. The female rejected the newborn pup shortly after birth and favored the unweaned subadult.

Case 8 -- Cow X left her young for the first time two days after delivery. A few hours after her departure, the young started to move about, vocalizing. The pup approached several foreign females who threatened it. Instead of retreating, he continued to approach and

was bitten and thrown about. Finally, the pup was thrown down into shallow water. Making stereotype butterfly strokes with frontflippers and lateral strokes with hindflippers and pelvis, the pup made his way to a place where he could crawl out and he disappeared among some large rocks. In the afternoon of the following day, cow X was back from the sea and was observed with her young. The latter was weak and badly scarred from bites in his neck. The next day pup X was dead.

In the first five days or more after delivery, the behavior of a sea lion pup arouses very strong aggression in foreign females with pups, and during this period the young needs the mother's protection. (The various reasons for this have been discussed elsewhere.) Furthermore, young pups are sensitive to exposure to cold and in several cases prolonged cooling has induced intensive shivering and a coma-like sleep in young pups. From this it can be concluded that young Eumetopias pups are poorly insulated, as is the case with Callorhinus pups (Bartholomew and Wilke 1956:331; Irving, et al. 1962: 276) and Zalophus pups (Peterson and Bartholomew 1967:38).

Case 9 -- Under very crowded conditions in one of the birth areas, cow P14 left her four-day old pup when threatened by nearby cows. At the same time, cow P17 was separated from her three-day old pup, when cow P18 drove her away. Cow P18 immediately retreated to her original place. P17 did not return to the place where she had been lying and when she was stretching down to pick up her young, P14 threatened her and moved into P17's former place. At first, P14 did not pay any attention to the foreign pup lying by her, but when P17 bent towards her young, vocalizing strongly, and the pup answered and started to

move towards his mother, P14 retrieved and adopted the pup. Two hours later, P14 nursed P17's pup for the first time. For about 24 hours the situation remained unchanged, with cows P14 and P17 lying less than 2 m apart, P14 with the adopted pup and abandoned pup P14 resting quietly about 7 m away. Suddenly, pup P14 headed towards his mother, strongly vocalizing and shaking his head laterally in the manner of hungry pups. Cow P14 stared intensely at the approaching pup. Cow P17 did not pay any attention to the newcomer, even when it moved by her, touching her breast. She was completely intent on her own pup lying with P14. Pup P14 moved up to his mother (who still had pup P17) and tried to nurse. For the first five minutes, cow P14 behaved as if she were very confused. Then she bit her own young and he responded with strong vocalization and intensive nursing appetitive behavior. In spite of several hard bites, the pup (who responded only with strong appetitive behavior) remained by his mother for about 10 minutes until the mother threw him away. In the general confusion, P17 had nose contact with her pup, but did not retrieve it. During the following two days, pup P14 succeeded in making his way back to his mother more than 30 times, but each time was bitten and thrown away. He was also bitten and thrown by all the other females in the area, including P17. In spite of one punctured eye and a paralyzed hind-flipper, the pup managed to drag himself back to his mother time after time. At the end of the second day, after his first approach to his mother, he was thrown into a nearby pool. When the pup was trying to crawl out of the water, an animal moved over his head and squeezed it into a crevice. Here pup P14 was stuck for about 30 hours

until he died.

This case illustrates several interesting aspects of mother-young recognition as discussed under that topic.

Case 10 -- E, a very small female, gave birth in the morning in a spot below the high tide line, just outside one of the birth areas. When the tide came in that evening, she tried to move her young to a higher and safer position, but was stopped by aggressive females lying above her. She lost control over the situation, and her young slid down into the water inside a triangle formed by three rocks. The mother tried to reach her young, but was prevented from doing so because on each of the rocks lay a female who threatened her on every approach. Forced by the tidal current to the far side of the triangular pool, the newborn young drowned in view of his calling mother.

Case 11 -- Cow U gave birth in a low area similar to cow E's. She made her way to a higher position and all appeared well until, in the third and fourth days, three females delivered in the area just above her and cow U was pushed down to a marginal place. For two nights, she struggled in the waves often washing over her and her young. Each time she tried to move to a higher position she was threatened by the females lying above her and had to remain where she was. The young grew weaker and soon died.

Case 12 -- This case was very similar to cases 10 and 11. The young was born to a small female under very crowded conditions. During the pup's second and third nights, the mother was seen struggling with her young, trying to move it to a safe place away from the big waves. She

protected her young by intercepting the waves with her own body. Several times the pup was washed away from her. When she retrieved it and tried to move to a higher place, she was immediately attacked and her young was thrown back. The mother went to sea for the first time on the fifth day after delivery and when she returned 30 hours later her young was dying.

As has been mentioned before, cows with young pups, in spite of their aggressiveness, are extremely social towards other cows with young pups. These females are also attracted to certain areas in which the order of preference for given locations stratifies the animals. Thus, we have "an organization capable of providing conventional competition" which, according to Wynne-Edwards (1962:14), is the definition of society. Cases 8 through 12 illustrates some of the methods and means by which this competition takes place. The pressure on an individual appears to increase with crowding in inverse proportion to size and dominance.

Swimming Development of Pups

In the development of Eumetopias pups towards the aquatic life and the rhythm of adult animals, three periods have been distinguished. These are the terrestrial, the littoral, and the aquatic periods.

1) Terrestrial period -- Eumetopias pups normally stay on land during a period that in 16 cases lasted between 12 and 20 days after parturition, with a mean of 14 days. The only spontaneous water activity observed in this period occurred among a few pups more than 12 days old and was restricted to short

excursions into shallow, brackish pools in the rocks of the rookery. At this age, pups that were washed, tossed, or pushed into the sea always showed signs of fright and made their way out as fast as they could. The swimming style of these pups was awkward and consisted of rapid downward strokes of both frontflippers simultaneously and lateral strokes of the hindquarters, with the head held high out of the water.

During the first 14 days of life, pups frequently engage in a type of play that I have called "frontflipper exercise." Fig. 35 shows the distribution of 63 periods of this activity in relation to age for 10 pups. The length of such activity periods varies from 5 to 55 minutes. The complete disappearance of this type of play when a pup begins to engage in water activity suggests that its function is the development of flipper coordination important in connection with swimming activity.

While performing frontflipper exercise, the pup lies on his back or side, waving one or both frontflippers in the air. Although much stretching and bending of the flipper occurs, the main element is forward stretching of the flipper accompanied by rigid dorsal bending of the distal phalanges while the pup tries to catch the tip of the flipper in his mouth (Fig. 36).

2) Littoral period -- Within a few days after estrus when the female spontaneously, or in accordance with the "conveyer belt principle," starts to occupy the intertidal zone, she

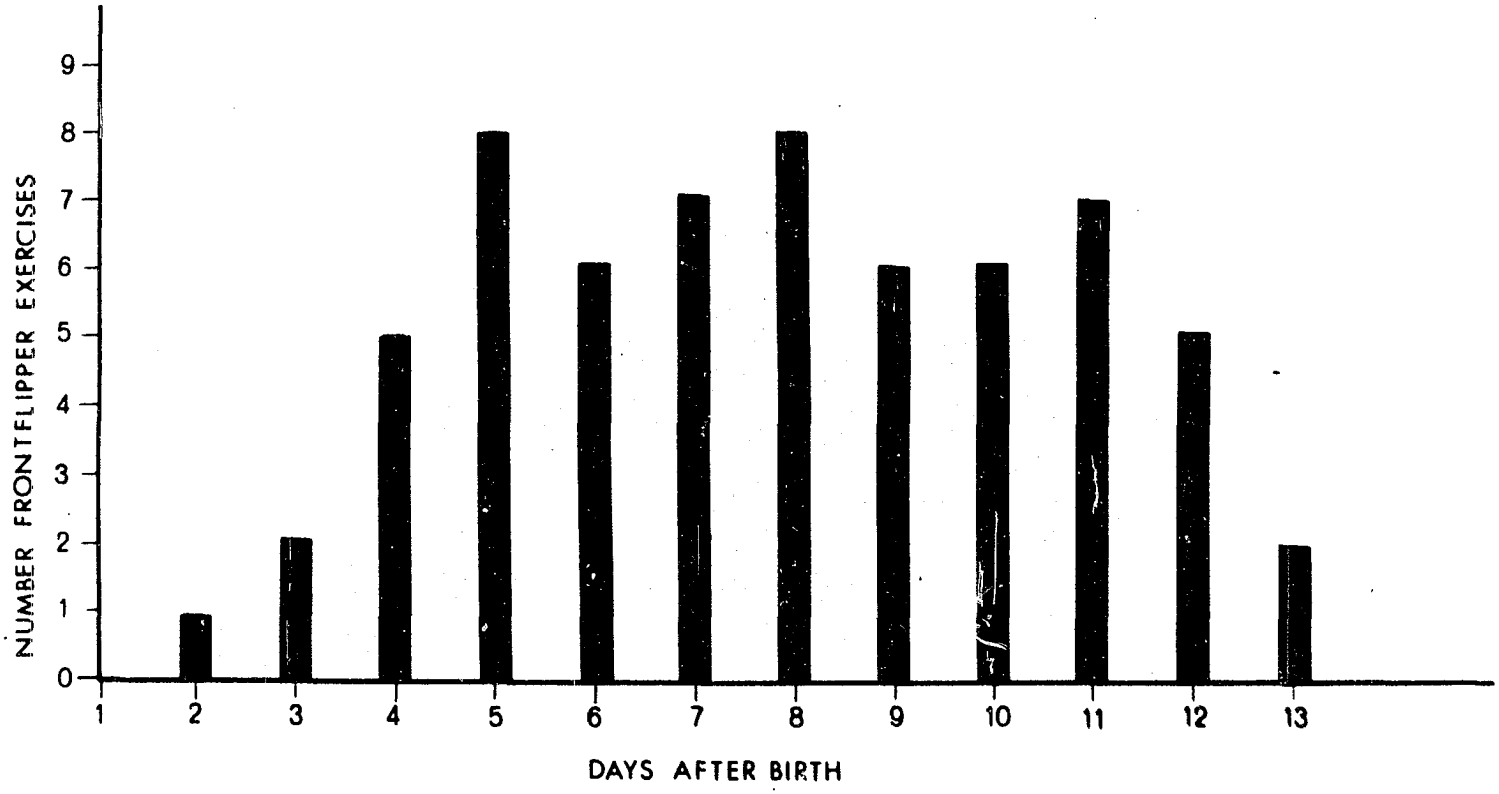


Figure 35. Distribution of 63 periods of frontflipper exercise in relation to age for 10 pups.

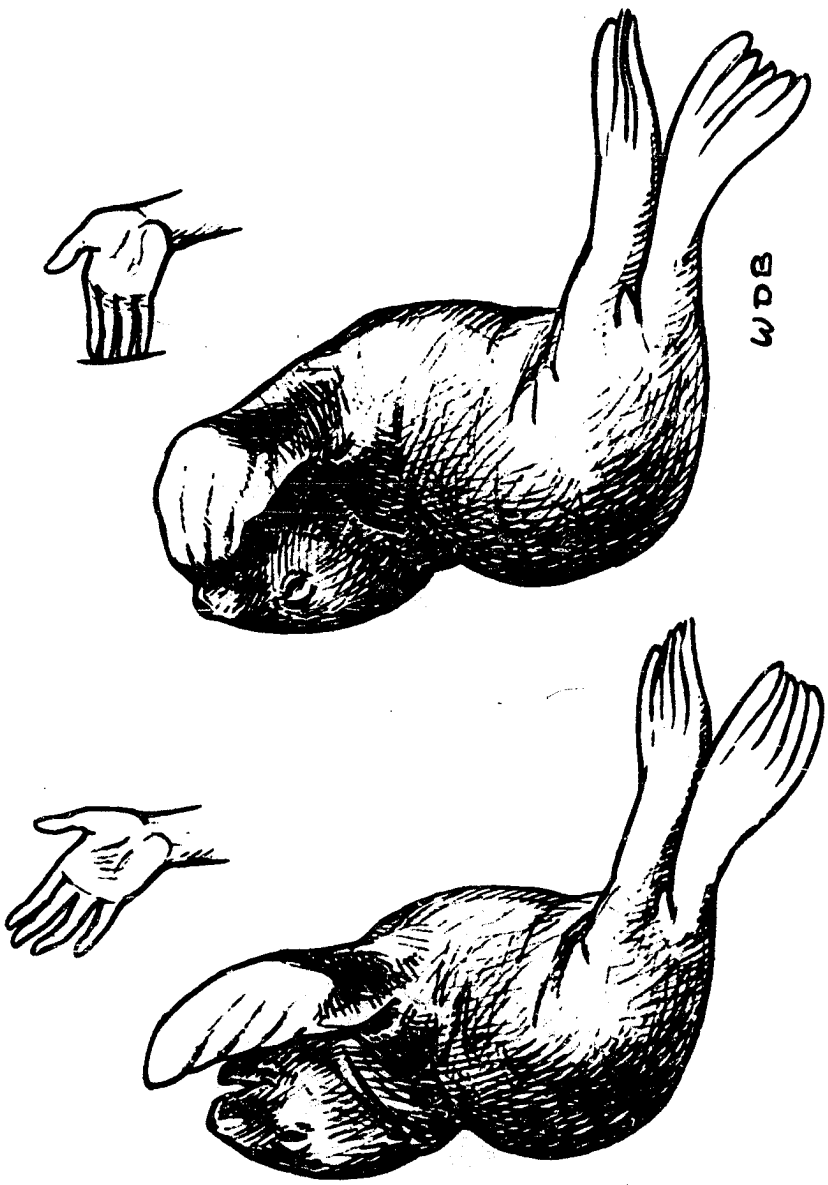


Figure 36. Pup performing frontflipper exercise.

calls her young along and from that time forward, the land activities of the female are, by and large, restricted to this area. Here she tends her young as it gradually becomes accustomed to water life. For example, when pup 0 was 16 days old, he had been in the water only twice as a result of being accidentally washed into the sea by large waves. On both occasions, he showed every sign of fright and climbed out as fast as possible. On the seventeenth day, female 0, shortly after returning from sea, was driven away by a cow when she tried to occupy the place where she had tended her young for the previous seven days. She then called her young to follow her to a nearby place below the high tide line and there she nursed it. In the evening, when the tide came in and reached the couple, the pup showed fear of the water that occasionally splashed over him. When the pup showed signs of leaving, the female nuzzled it frequently and called it back several times. Females have never been seen to introduce their young to the water by force in the manner of Zalophus females (Peterson and Bartholomew 1967:37). After about 20 minutes, when the incoming tide finally splashed about couple 0, the female went to sea and the pup climbed rapidly to a higher, safer place. The next day, cow 0 called the still very hesitant pup to her in small stages through shallow water to an isolated rock in the intertidal zone where the couple settled down for the day. In the evening, when the tide came in and surrounded the rock, the events of

the previous evening were repeated: the female went to sea, and, after some hesitation, the pup went into the water and swam to a place where he could reach high ground. On the following day, the female hauled out on the free standing rock and called for her pup who soon made his way through the water and joined his mother. On this evening, pup O played for a while with a foreign pup in shallow water before he sought higher ground.

When a pup has begun to go into the water spontaneously, swimming and diving ability improve rapidly. As in the case of pup O, water activity is initiated in shallow, protected water where the pup merely splashes about in the manner described above. In a day or two, the pup starts to dip his head while in the water and soon he makes short dives. Coordination of flipper movements and breathing improves rapidly and by the end of the littoral period (10 to 18 days in 16 cases, with a mean of 14 days) pups are seen skillfully tumbling about in water about two meters deep. Here they chase each other rapidly about, jumping almost clear out of the water, and play with pieces of kelp, sticks and pebbles, which they take in their mouths and shake, or throw and catch again. At this time, pups are often seen to play "master of the hill" when they mock fight and try to push each other down from the top of a rock standing out of the water.

Pups were never seen to leave the periphery of the

rookery during the littoral period. All water activity took place during high tide and was restricted to the flooded intertidal zone during these periods.

3) Pelagic period -- This phase in the development of the pup's aquatic abilities is initiated when the mother for the first time calls her young along with her on swimming tours. At first these tours are short and occur in the vicinity of the rookery, but gradually they become longer, until, a few days later, the pup follows his mother for his first long trip to sea. Before this happens, the pup must: a) learn to follow his swimming mother; b) overcome his reluctance to leave the vicinity of the rookery and enter deep water; and c) develop the swimming and correlated breathing rhythm of adult animals in the pelagic swim.

When the female first calls her pup to follow her in the water (24 to 32 days in 16 cases, with a mean of 28 days), the pup shows strong motivation for the group water play described above. Pups are very reluctant to follow their mothers for reasons other than nursing, and the female may spend hour-long periods when she repeatedly attempts to make vocal and olfactory contact with her young. So long as she calls strongly, the pup's following response may be awakened, but as soon as the mother loses interest, he may return to his playmates.

When the young finally follows his swimming mother, she heads for deeper water. Until this time, the pup has never

swum outside the periphery of the rookery and apparently is afraid to do so. As soon as the couple enters deeper, unknown water, the pup shows fright by vocalizing strongly, clinging to his mother's head and swimming in the awkward way of a beginner. He soon dashes back towards shore. Once again, the female must spend much time repeatedly turning back to find her escaped young, calling to him to follow, and then heading out again. When the pup shows fright and hesitation, the female immediately seeks nose contact with him. The high frequency and persistence with which the female and pup rub noses during this phase of the swimming maneuvers characterizes the event.

When the young has overcome his fear of unknown pelagic waters and follows his mother obediently, the swimming pattern of the mother as well as that of the young soon changes. In the previous swimming interactions between mother and young, most activities took place on the surface, but now the female starts to dive and surface in the rhythmic way of sea lions in pelagic swim. The pups initially show much difficulty in adapting to the diving and surfing rhythm of the female, and the sequence is frequently broken. At first, the young often separates from his mother under the water and pops to the surface where he starts to vocalize strongly, swimming in circles with head stretched high out of the water looking for his lost parent. When the mother surfaces, perhaps 20 m away, she calls; they join, rub noses

and make a new try. During these early synchronous dives, mother and young frequently have nose to nose contact under the water and often surface with noses together. Thus, during the daytime high tide periods on consecutive days, mother and young may be seen on swimming tours that gradually become longer. However, with the exception of five cases, these tours never took the couple more than 500 m away from the rookery. In these five cases, mothers with young varying in age from 36 to 41 days old were observed surfing and diving side by side as they disappeared out of view of the spotting scope on a course to the eastward.

LITERATURE CITED

Allen, J. A. 1880. History of the North American pinnipeds, a monograph of the walruses, sea lions, sea bears and seals of North America. U. S. Geological and Geographical Survey, Misc. Pub. No. 12, 785 pp.

Bartholomew, G. A. 1959. Mother-young relations and the maturation of pup behaviour in the Alaska fur seal. Anim. Behav., 7:163-171.

Bartholomew, G. A., and P. G. Hoel. 1953. Reproductive behavior of the Alaska fur seal, Callorhinus ursinus. J. Mammal., 34:417-436.

Bartholomew, G. A., and F. Wilke. 1956. Body temperature in the northern fur seal, Callorhinus ursinus. J. Mammal., 37:327-337.

Bonnot, P. 1928. Report on the seals and sea lions of California. Fish. Bull. 14, Calif. Div. Fish and Game, 62 pp.

Brooks, J. W. 1968. Personal communication.

Fiscus, C. H., and G. A. Baines. 1966. Food and feeding behavior of Steller and California sea lions. J. Mammal., 47(2):195-200.

Gentry, R. L. 1968. Personal communication.

Irving, L., L. J. Peyton, C. H. Bahn, and R. S. Peterson. 1962. Regulation of temperature in fur seals. Physiol. Zool., 35:275-284.

Kenyon, K. W., and D. W. Rice. 1961. Abundance and distribution of the Steller sea lion. J. Mammal., 43(1):68-75.

Luick, J. R. 1968. Personal communication.

Mathisen, O. A., R. T. Baade, and R. J. Lopp. 1962. Breeding habits, growth and stomach contents of the Steller sea lion in Alaska. J. Mammal., 43(4):469-477.

Mathisen, O. A., and R. J. Lopp. 1963. Photographic census of the Steller sea lion herds in Alaska, 1956-58. United States Fish and Wildlife Service, Special Scientific Report--Fisheries No. 424, 20 pp.

Naaktgeboren, C. 1963. Untersuchungen uber die Geburt der Saugetiere. Dr. Sci. Thesis. University of Amsterdam, 50 pp.

Newcombe, C. F., W. H. Greenwood, and C. M. Fraser. 1918. British Columbia sea-lion investigations; Part I; preliminary report of the commission on the sea-lion question, 1916. Contr. to Canad. Biol., 1917-1918, Sessional Paper No. 38a, Parts I and II:5-52.

Orr, R. T., and T. C. Poulter. 1967. Some observations on reproduction, growth, and social behavior in the Steller sea lion. Proc. Calif. Acad. Sciences, Fourth Series, 35(10):193-266.

Paulian, P. 1964. Contribution a l'etude de l'otarie de l'Ile Amsterdam. Mammalia, 28:1-146, 10 pls.

Peterson, R. S. 1965. Behavior of the northern fur seal. Dr. Sci. Thesis. Johns Hopkins University, Baltimore, Maryland, 214 pp.

Peterson, R. S., and G. A. Bartholomew. 1967. The natural history and behavior of the California sea lion. The American Society of Mammalogists, Special Publication No. 1, 79 pp.

Peterson, R. S., and R. L. Gentry. 1967. Biological investigations in Ano Nuevo State Reserve. Annual Report, 1966-1967, University of California, Santa Cruz, California. 20 pp., appendix.

Rand, R. W. 1955. Reproduction in the female Cape fur seal. Proc. Zool. Soc. Lond., 124(4):717-740.

_____. 1967. The Cape fur seal (Arctocephalus pussillus) general behaviour on land and at sea. Republic of South Africa, Department of Commerce and Industries, Division of Sea Fisheries Investigational Report No. 60, 39 pp.

Scammon, C. M. 1874. The marine mammals of the north-western coast of North America. John H. Carmany and Co., San Francisco, 319 pp.

Scheffer, V. B. 1945. Growth and behavior of young sea lions. J. Mammal., 26(4):390-392.

Slijper, E. J. 1956. Some remarks on gestation and birth in cetacea and other aquatic mammals. Hvalrad. Skr., 41:1-62.

_____. 1960. Die Geburt der Saugetiere, In Kukenthals Handbuch der Zoologie, 8. Band/25. Lief 9(9):1.

Smith, E. A. 1965. The effects of human interference in a grey seal breeding colony and the phenomenon of fosterage, In A seals symposium. E. A. Smith (Ed.). The Nature Conservancy, Edinburgh, pp. 63-75.

Starks, E. C. 1918. The sea lions of California. Amer. Mus. J., 18: 226-237.

Swainbank, R. 1968. Personal communication.

Thorsteinson, F. V., and C. J. Lensink. 1962. Biological observations of Steller sea lions taken during an experimental harvest. J. Wildl. Mgmt., 26:353-359.

Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behavior. Oliver and Boyd, Edinburgh, Scotland, 653 pp.