I. INTRODUCTION

In this paper we describe various aspects of the reproductive process in northern elephant seals, Mirounga angustirostris, particularly maternal behavior and the interaction of adult females and pups in the harem during the breeding season. We focused on the following subjects: (a) parturition — the time and place of occurrence and the events which follow it, (b) temporal aspects of reproductive behavior in females such as the interval between arrival on the rookery and parturition, parturition and copulation, and the length of the nursing period, (c) the proportion of females that foster alien pups and the circumstances in which it occurs, (d) suckling behavior of pups — the pattern and source of suckling, and (e) pup mortality — incidence, time course, and possible causes. Other subjects which bear on maternal and pup behavior such as moulting, seasonal movements, physical development, population dynamics and the role of vocalizations in maintaining the mother-pup bond are described in general terms in this paper and will be treated more fully elsewhere. Studies emphasizing male social behavior and copulatory behavior have appeared in previous papers (Bartholomew, 1952; Le Boeuf & Peterson, 1969a, 1969b; Le Boeuf, 1971, 1972).

Previous investigations most relevant to this paper are those of Bartholomew (1952), Klopf & Gilbert (1967), and Fogden (1968). Bartholomew first described parturition in this species and noted that elephant
seal cows generally accept their own pups and reject aliens, which they
distinguish readily. Klopfers and Gilbert asserted that nursing females
discriminate between their own young and alien pups on the basis of
vocalizations; they concluded that females are highly tolerant of alien pups
and will nurse them even if they have young of their own. Fogden found
that feeding between related animals was the most common state of affairs
but that feeding between unrelated animals was by no means infrequent.
The disagreement between these investigators seems to stem from lack of
data. One purpose of our study was to make more detailed observations
over a longer period of time and determine the proportion of females that
nursed alien pups and the proportion of pups that suckled alien females
and under what conditions these inconsistencies occurred.

Except for the studies mentioned above, little has been written concerning
maternal and pup behavior in the northern elephant seal. Several excellent
papers on the closely related southern elephant seal, M. leonina, have
appeared, especially those of Laws (1953, 1956a, 1956b), Carrick and his
coworkers (e.g., Carrick, Csordas & Ingham, 1962), and Bryden (1968),
which bear on the subjects of social organization of males, population
dynamics, and physiological processes. Areas which need further study are
pup mortality, and various aspects of behavior, particularly, the behavior of
females and pups.

II. METHODS

A. STUDY AREA AND TIME OBSERVED

This study was conducted at Año Nuevo Island, California, during the
breeding seasons of 1968, 1969, 1970, and 1971. The island is currently
the northernmost colony in the breeding range of northern elephant seals
and lies ½ mile offshore, 19 miles north of Santa Cruz, California. Elephant
seals breed on two beaches; the largest of the two is a sandy point called
area 17, and the other, a shallow beach bordered by ten foot high sand
banks, is called area 3 (Fig. 1; see also Figure 2 in Orr & Poulter, 1967).

Each year daily observations were made throughout the breeding season
at both study areas. The reproductive period in northern elephant seals starts
in early December and ends in mid-March. During this period, males arrive,
fight and set up social hierarchies. Females give birth, nurse their young,
copulate, and all adults depart by March leaving the young of the year behind
them on the rookery (Le Boeuf, 1972). Our observations began at sunrise
and terminated at sunset. A few observations were made at night when the
sky was clear and the moon full.

Observations were made from four blinds overlooking area 17 and one
blind above area 3, and were facilitated by binoculars, spotting scopes, timers, and an Esterline-angus event recorder. Each season approximately six to seven hours per day was spent observing the animals on area 17. On area 3, an average of one hour per day per season was spent observing in 1968 and 1969 and an average of four to five hours per day in 1970 and 1971. Altogether, over 3,000 hours were spent in observation.

B. MARKING

Cows and pups were marked with various colors of paint or bleached with peroxide on the dorsal surface of the body, especially around the head and nose. A cow and her pup were given the same type of mark shortly after parturition was witnessed. A few cows were marked as they hauled out and their pups were given identical marks when they were born. These marks permitted continuous recognition of the mother-pup pair during the nursing period.

During the 1970 breeding season, 18 of 39 mother-pup pairs on study area 3 were marked and observed. During the 1971 breeding season, 33 of 49 mother-pup pairs in the same area were marked and observed. Additional pups, not marked at parturition, were marked when they appeared injured or were separated from their mother.

As part of another study, plastic or monel tags bearing a serial number and the inscription "Notify U Calif, Santa Cruz, USA", have been attached to the webbing of the hindflippers of all pups born on Año Nuevo, as well as adult males and 10% of the female population, since 1968. Since these tags remain attached for years and the plastic type can be seen and read from a distance, we were able to follow individual animals from year to year. For example, this enabled us to document sexual maturity and the time of delivery in primiparous females and to compare the time of parturition in the same female from year to year.

C. BEHAVIORS RECORDED

The following behaviors and events were recorded: (a) the time, place, and behavior of females during parturition, (b) the response of females to their own pups and to alien pups, (c) the suckling pattern of pups, (d) the frequency of separation of a pup from its mother, and the response of pups to this separation, (e) a daily census of animals broken down into various age categories according to location on the island, and (f) the number of pups that died and the behavioral circumstance preceding death.

Our investigations at Año Nuevo Island were supplemented by observations made on other islands where elephant seals breed: San Miguel, San
Nicolas, Los Coronados, Isla de Guadalupe, Islas San Benito and Isla Cedros. We also made observations on Año Nuevo during the non-breeding season, particularly of weaned pups during April and May.

D. MORTALITY

During the 1969, 1970, and 1971 breeding seasons, dead pups were removed from the breeding beaches and measured, weighed and in some cases necropsied. Immediate removal of carcasses was necessary for obtaining an accurate estimate of the number that died since dead pups became buried in the sand soon after death or were washed out to sea at high tides.

Carcasses were examined for cuts, abrasions, and other external abnormalities, then weighed with a 100 lb capacity spring scale or a 250 lb capacity bathroom scale. Standard length (nose to tail), total length (nose to tip of hindflippers) and axillary girth were recorded.

In 1971, 43 pups were necropsied; 30 within a day after death. Carcasses were opened and the stomachs were examined for evidence of feeding. Abnormalities in the viscera, lungs, trachea and hearts were noted and blubber thickness between the scapulae was measured. Skulls were collected, prepared and examined for fractures.

III. RESULTS

A. THE FEMALE REPRODUCTIVE CYCLE

In a previous paper, one of us (Le Boeuf, 1972) presented data on the duration of various intervals in the reproductive cycle of females observed on Area 17 at Año Nuevo Island. Similar data was collected in this study from females on Area 3 to check on the reliability of the previous estimates. Table I indicates the length of time between some important reproductive events in the adult female. On the average, a female gave birth 6-7 days after she arrived on the rookery; 24 days later, she came into estrus, a period which usually lasted 3-5 days. She stayed on the rookery for a total of 34 days and throughout this time, she did not enter the water and therefore, did not feed. She nursed her pup from the day he was born until the day she left the island, a period of 27 to 29 days. Weaning was forced on the pup by the departure of his mother. Most females were still in estrus when they left the rookery.

The means in Table I are identical to those reported by Le Boeuf (1972), with one exception: the nursing period found in the present study is approximately 1½ days longer than the period reported in Le Boeuf's paper, a difference which is not statistically significant. The nursing period is the most variable of the periods shown in Table I. The close correspondence
TABLE I

Interval in days between female reproductive events from two breeding seasons on Año Nuevo Island (means ± one standard deviation; number of subjects in parentheses). Females that became separated from their pups are not included in this table.

<table>
<thead>
<tr>
<th>Event</th>
<th>1969-70</th>
<th>1970-71</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arrival to parturition</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>6.5 ± 1.4</td>
<td>6.5 ± 1.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(10)</td>
<td>(10)</td>
</tr>
<tr>
<td>Parturition to 1st copulation</td>
<td>24.6 ± 3.4</td>
<td>23.4 ± 4.2</td>
<td>24.0 ± 3.8</td>
</tr>
<tr>
<td></td>
<td>(9)</td>
<td>(12)</td>
<td>(21)</td>
</tr>
<tr>
<td>Parturition to departure</td>
<td>27.9 ± 4.0</td>
<td>29.0 ± 5.0</td>
<td>28.5 ± 4.5</td>
</tr>
<tr>
<td>(nursing period)</td>
<td>(12)</td>
<td>(29)</td>
<td>(41)</td>
</tr>
<tr>
<td>1st copulation to departure</td>
<td>3.3 ± 2.8</td>
<td>5.2 ± 2.2</td>
<td>4.2 ± 2.5</td>
</tr>
<tr>
<td></td>
<td>(9)</td>
<td>(11)</td>
<td>(20)</td>
</tr>
<tr>
<td>Arrival to departure</td>
<td>34.3 ± 3.6</td>
<td>34.6 ± 3.8</td>
<td>34.4 ± 3.7</td>
</tr>
<tr>
<td></td>
<td>(10)</td>
<td>(9)</td>
<td>(19)</td>
</tr>
</tbody>
</table>

of the means in these two studies is an indication of the high reliability of the figures.

After the breeding season ends, some females spend a brief period of time at sea, presumably feeding, and then return to the rookery to moult. This process involves a sloughing off of the outer layer of fur and epidermis and is usually complete in two to three weeks (see Ling, 1970). Adult females at Año Nuevo hauled out to moult over a six week period extending from late March to mid-May, the same time that juveniles, two to five years old, moult.

The time a female spends on land breeding and moulting is less than two months of the year; the rest of the year she spends at sea. Females are rarely observed on land during this period.

B. PARTURITION

Each year, births occurred over a six week period extending from 23 December to about 10 February. The peak period for births was the last two weeks in January during which approximately 50% of the pups were born. The majority of births occurred at night. During the four breeding seasons at Año Nuevo Island, in which approximately 1050 pups were born, we observed only 81 births during the day. Although we narrowly missed

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1) In May, 1971, at Isla de Guadalupe, we observed several sheepheads, *Pimelometopon pulchrum*, feeding on the sloughing skin and hair of elephant seals of both sexes which were swimming in the clear water near shore. An examination of the stomach contents of several sheepheads caught in the area, confirmed our behavioral observations.
observing several births during the day each season, the great difference makes it clear that most of the births occurred at night.

During daylight hours, two peak pupping periods were in evidence; one between 0900 and 1000 hours and the other between 1600 to 1700 hours. There was a marked low in parturition frequency between 1300 to 1500 hours, usually the warmest hours of the day and a period of low animal activity.

Virtually all females gave birth in a harem, i.e., within the compact aggregation of females on area 17 or area 3 (Fig. 2). The occasional female that gave birth on the island outside the perimeter of a harem usually joined the rest of the females within a day or two after parturition and her pup followed her.

The rest of this section describes a typical birth and the mother-pup interactions which follow (Figure 3). The preparturient female may be somewhat restive during the early phase of labor, shifting her weight from her ventrum to one side or the other. This is especially noticeable at times when the other females in the harem are asleep or inactive. During the final phase of parturition, the female lies on her belly and elevates her perineum one to two feet above the ground and swings it slowly from side to side. At the same time her foreflippers may be extended and her head and neck raised; her posture giving a “u”-shaped appearance. This posture is usually assumed during contractions from the time the foetus is visible to the moment of expulsion, and is a reliable signal that parturition is imminent. Females move very little during this period, although a few will circle slowly as the foetus is being expelled. The laboring female looks straight ahead and may close her eyes from time to time. Some females emit a low vocalization that resembles the utterance employed in low intensity aggressive encounters with other females. The extensive layer of blubber makes it difficult to monitor uterine contractions.

Defecation may occur just prior to the appearance of the foetus, which is first seen surrounded by the amnionic membranes (Fig. 3A). These usually rupture by the time the hindflippers or head of the foetus is visible (Fig. 3B) or, if not then, during the final expulsion of the foetus. The last phase of parturition, when approximately one half of the foetus is visible, lasts only a few seconds (Fig. 3C, D). The newborn explodes onto the sand, warm and wet; the difference between his temperature and the cold outside, causes him to “smoke” for several minutes.

The female turns immediately to face her pup (Fig. 3E, F); a maneuver which usually breaks the umbilical cord. As she turns she begins emitting a “warbling” vocalization in the pup’s direction as she approaches and
touches his body with her nose as if she were smelling it (Fig. 3G); she
does not clean or lick the newborn. Females do not emit the warble vocaliza-
tion before parturition, but the sound is given as soon as the pup is born and
she continues to employ it throughout the nursing period to attract her pup.
The sound is heard most frequently shortly after birth. The newborn usually
responds to his mother's warble with a vocalization of his own. All pups
make this sound within an hour after they are born; some vocalize almost
immediately. The form and significance of these vocalizations will be
treated more fully in a later section on the pup.

A birth attracts scores of Western gulls, Larus occidentalis, and Heer-
mann's gulls, Larus heermanni, who swarm to the area and devour the
placenta (Fig. 3H). The placenta is delivered with the pup or within an
hour after birth. Some gulls peck at the remnant of umbilical cord still
attached to the pup or, in a slow delivery, they may peck at the pup as it
is in the process of being delivered. The mother's threats to the birds have
little effect. The pup, with wobbly head, blinks at all the commotion.

The arrival of the newborn increases female aggression in the vicinity
Nearby females may approach the pup, sniff it (Fig. 3E, F), bite it, or
threaten and, in a few cases, move the mother away and take the newborn
as their own. Females with young pups of their own are particularly
curious about newborns. The mother, on the other hand, attempts to increase
the distance between her pup and other females; she threatens females
as they approach, or she initiates an aggressive encounter with nearby
females (Fig. 4). The outcome of these opposing interests often depends
on the size and related dominance of the females involved (see BARTHOLO-
MEW & COLLIAS, 1962). Within an hour or two after parturition, things
usually settle down and the pup suckles for the first time.

1. Presentation.

Presentation of the foetus at birth was observed in 29 females. Eighteen
or 62% of the births were cephalic presentations and 11 or 38% were caudal.
The duration of parturition (excluding stillbirths), from the time the
foetus was visible, was no different in cephalic and caudal presentations.
Cephalic presentations varied from 1½ to 30 minutes with a mean of
6.8 minutes; caudal presentations ranged from 1 to 28 minutes with a
mean of 8.8 minutes.

2. Delivery of the placenta.

In 10 of 37 births observed, delivery of the placenta occurred within a
few seconds after the pup was expelled. In another 10 females, the placenta
was delivered within two minutes after the pup and in the remaining 15 females, the interval varied from 6 to 47 minutes ($\bar{X} = 18.7$ min., $N = 15$, $s = 10.0$ min.). Two placentas were retrieved and weighed; one weighed 9½ lbs. and the other weighed 10 lbs. In a few cases the umbilicus did not break during delivery and the pup dragged the placenta behind him for as long as two days. Normally, the entire afterbirth was consumed by gulls during the day it was delivered, except for when it was covered by sand or an animal laid upon it.

3. **Stillbirths.**

Only four stillbirths were confirmed during four years of observation, although it is certain that more occurred but were not witnessed. In three cases, presentation was determined; two of them were caudal presentations. The first was by a 3 year old, primiparous female. The birth took 28 minutes and the pup emerged with the amnionic sac still encased around its head. The pup convulsed a few times then died. The mother paid little attention to the pup, only once giving the typical warble call. The pup was a male of normal weight. A field autopsy revealed foamy, white fluid in the trachea and partially collapsed lungs.

The second female bore a large full term male pup whose internal organs were necrotic. The mother ignored the dead pup and her sand-flipping behavior quickly covered it up.

The third female had great difficulty giving birth because of the position of the foetus in the birth canal. At 1041 in the morning, the female was observed with an edematous foreflipper protruding six inches from her anogenital opening. The female labored visibly until 1525 in the afternoon when observations were discontinued. Time after time, hard contractions pushed the foetus out two inches only to be followed by a recession of equal length when the female relaxed. The female shifted from her belly to her side several times and at 1330, she seemed to stop laboring. No progress in expelling the foetus was made during the entire period of observation. Before observations were discontinued, the female and the foreflipper of the foetus were marked with paint. On the following morning, the marked pup was found dead, in a very edematous state. The marked female was observed several meters distant from the pup sleeping with several other females and pups. She remained on the rookery several days before returning to sea.

4. **Premature pupping.**

Premature pups have never been observed in this species. This may
Figure 1. Aerial photograph of Año Nuevo Island in early December when adult males are just starting to arrive. The large sandy beach on the right is area 17 (arrow), the enclosed beach on the left is area 3 (arrow). The house is uninhabited except in September and October, when it is used by California sea lions.
Figure 2. The harem on area 17 in early February, 1971. The harem contains five adult males and over 200 females, most of whom have pups. Two blinds overlooking the area are visible in the foreground.
Figure 3. The typical sequence of events in an elephant seal birth. The foetus is first seen encased in the amnionic membranes (a). The latter usually rupture when the head or hindflippers begins to protrude (b). The following stages in parturition occur rapidly (c, d). A female with a young pup of her own approaches and sniffs the newborn (e). The mother turns and nuzzles her pup while at the same time emitting the "warble" vocalization (f, g). Gulls flock to the area and devour the afterbirth (h).
Figure 4. Females fighting. The female on the right has just given birth.

Figure 5. Four to six week old weaners in various stages of moult. The dark animals are just beginning to moult. The animal on the lower right is about 50% moulted and the lightcoated animals at left of center have nearly finished mouling.
Figure 6. An early morning aggregation of moulted weaners in shallow water at San Miguel Island (14 March 1969).
Figure 7. A frequent activity of weaners during the early morning and late afternoon is tail biting. One of the weaners in the foreground scratches himself, the other flips sand on his back. The animal in the upper right of the photograph is a yearling in moult.

Figure 8. Two weaners engaged in a “mock fight”, a common activity among young males and females.
Figure 9. The typical position assumed by female and pup during suckling. The pup is one week old.

Figure 10. Young pup pinioned by a bull in the process of threatening another bull.
Figure 12. Orphans and filial weaners of the same age differ in size. The small animal to the left of the picture is an orphan who was never adopted; the other weaners suckled their mothers.
indicate that abortions are rare or that, if they do occur, it is when the females are at sea and the foetuses sink or are eaten before washing ashore. Premature pupping is very common in Otariid species such as the California sea lion, *Zalophus californianus*, which usually aborts onshore. In this species, hundreds of abortions are observed each year beginning as early as four months prior to the start of the normal pupping period (Odell, 1970; Brownell & Le Boeuf, 1971).

5. **Primiparity.**

Females can give birth as early as their third year. During the 1971 breeding season, eight females that had been tagged as pups in 1968 gave birth on one of three rookeries. Three delivered on a different island than the one on which they were born, four gave birth on the island of their birth place and one female's birthplace could not be determined. The distance between birthplace and parturition site, when the two were different, was 112 kilometers in two cases (San Nicolas to San Miguel) and 480 kilometers in the other cases (San Miguel to Año Nuevo Island). The latter produced a stillborn; the rest of the females were observed with viable pups.

Eight recoveries is a small return considering that 538 female pups were tagged in 1968; 53 at Año Nuevo, 85 at San Nicolas Island, and 400 at San Miguel Island. Consequently, we feel that only a few females deliver in their third year and the majority give birth in their fourth or fifth year. Tag returns in the future will determine whether this speculation is correct.

Southern elephant seals at South Georgia normally give birth during their third year, although Laws (1953) reported the case of an individual who delivered a pup during her second year meaning she was impregnated the previous season when only one-year old! The onset of puberty at other Antarctic rookeries occurs between the fourth and seventh year (Carrick et al., 1962).

6. **Parturition from year to year.**

Observations of seven marked females for two to three consecutive years gives some indication of the consistency of individual deliveries with respect to time and place on a single rookery. These data are presented in Table 2. Three females, G73, G67, and G46, showed remarkable timing in giving birth on virtually the same calendar date from one year to the next. Except for female, G44, the timing of the other females may have been equally good but we did not witness parturition directly and this undoubtedly contributed variation. Six out of seven females returned to the same area to give birth in successive years.
TABLE 2

Date and location of parturition in consecutive years. The number in parentheses is the area on Año Nuevo where the female gave birth.

<table>
<thead>
<tr>
<th>Year</th>
<th>G73</th>
<th>G44</th>
<th>G63</th>
<th>G67</th>
<th>FANG</th>
<th>G46</th>
<th>F82</th>
</tr>
</thead>
<tbody>
<tr>
<td>1969</td>
<td>5 Jan</td>
<td>3 Jan</td>
<td>&lt;11 Jan</td>
<td>4 Jan</td>
<td>&lt;23 Jan</td>
<td>4 Jan</td>
<td>1 Feb</td>
</tr>
<tr>
<td></td>
<td>(17)</td>
<td>(3)</td>
<td>(17)</td>
<td>(17)</td>
<td>(17)</td>
<td>(17)</td>
<td>(17)</td>
</tr>
<tr>
<td>1970</td>
<td>3 Jan</td>
<td>11 Jan</td>
<td>4 Jan</td>
<td>4 Jan</td>
<td>&lt;22 Jan</td>
<td>5 Jan</td>
<td>25 Jan</td>
</tr>
<tr>
<td>1971</td>
<td>5 Jan</td>
<td>31 Dec</td>
<td>N.S.</td>
<td>N.S.</td>
<td>N.S.</td>
<td>*</td>
<td>N.S.</td>
</tr>
<tr>
<td></td>
<td>(17)</td>
<td>(17)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Lost tag on 22 February 1970 and therefore, could not be distinguished in 1971.

"<" Means the female was first observed with a pup on the date indicated and therefore parturition may have occurred earlier.

"N.S." Means the female was not seen, or could not be recognized (e.g., lost tag).

Several other females were observed for more than one season but in one of the years they were not seen with pups. We are not confident that these females were nulliparous in that year because they may have given birth then abandoned their pups or it is possible that we never saw mother and pup together. Females that gave birth around the peak of the breeding season when females were most numerous were difficult to locate.

C. PUPS — THE FIRST THREE MONTHS

Elephant seal pups are precocial at birth. Their eyes open immediately and they are able to hold up their heads, though somewhat unsteadily. They can move forward, scratch, vocalize and flip sand on their backs with their foreflippers within a few minutes after birth.

Pups suckle virtually every day until they are weaned at 27 to 29 days after birth. When the mother goes to sea, the “weaner” may try to suckle an alien female, but he is usually rejected and chased out of the harem. Weaners tend to congregate inland of the harems. The compactness of their pods varies with temperature. When it is cold, the pod is tight and all animals are in close contact. As it gets warmer the pod loosens up and the animals spread out.

Weaners moult between four and six weeks of age, their black natal pelage being replaced by a shiny silver coat (Fig. 5). It is also at this time that they begin to go into the shallow water offshore (Fig. 6). They go out in the late evening and return to the same pod location in the early...
morning to sleep throughout the day. As they get older, they leave earlier and return later. In late March and April, some weaners can be seen in the water throughout the day.

Weaner activity is crepuscular. In the early morning and late evening, they are frequently observed reaching backward trying to bite their own tails or "mock fighting" with each other in an approximation of the posture and pattern used by adults (Figures 7 and 8).

By the end of April, all but a few weaners have left Año Nuevo Island. The same time and pattern of departure seems to hold at other elephant seal rookeries. Evidence from tag returns indicates a northward migration. In April and May, pups born on Mexican islands are seen on southern California islands and pups born in southern California are observed on Año Nuevo Island. Pups born on Año Nuevo Island are seen on the Farallones Islands near San Francisco bay and other landfalls further north.

1. **Sex ratio at birth.**

The sex of more than 50% of the pups born each year at Año Nuevo Island was determined during tagging operations when the pups were about a month old. Ratios for each of the four breeding seasons are shown in Table 3. The sex ratio each year approximated 1:1 with the overall figure favoring the females slightly. Sex ratios obtained at other elephant seal rookeries were similar and are shown in Table 4. The overall ratio at Año Nuevo Island is exactly the same as the overall ratio of the other rookeries shown in Table 4.

2. **Size at birth.**

Viable pups were not weighed nor measured during the nursing period in order to avoid disturbance. However, these figures can be estimated for newborns from data obtained from pups that died within a few days after birth. From these data, it appears that newborns weigh about 65 lbs, although

<table>
<thead>
<tr>
<th>Year</th>
<th>Sexed</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>1968</td>
<td>112</td>
<td>51.8</td>
<td>48.2</td>
</tr>
<tr>
<td>1969</td>
<td>187</td>
<td>48.1</td>
<td>51.9</td>
</tr>
<tr>
<td>1970</td>
<td>114</td>
<td>47.4</td>
<td>52.6</td>
</tr>
<tr>
<td>1971</td>
<td>127</td>
<td>51.2</td>
<td>48.8</td>
</tr>
<tr>
<td>TOTALS</td>
<td>540</td>
<td>49.4</td>
<td>50.6</td>
</tr>
</tbody>
</table>
TABLE 4

The sex ratio of newborn pups tagged on several rookeries from January 1968 to January 1971

<table>
<thead>
<tr>
<th>Rookery</th>
<th>Number Sexed</th>
<th>Males</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>San Miguel Is.</td>
<td>2159</td>
<td>49.0</td>
<td>51.0</td>
</tr>
<tr>
<td>San Nicolas Is.</td>
<td>395</td>
<td>50.3</td>
<td>49.7</td>
</tr>
<tr>
<td>Is. de Guadalupe</td>
<td>1415</td>
<td>49.5</td>
<td>51.5</td>
</tr>
<tr>
<td>Is. San Benito &amp; Is. Cedros</td>
<td>106</td>
<td>51.9</td>
<td>48.1</td>
</tr>
<tr>
<td><strong>TOTALS</strong></td>
<td><strong>4075</strong></td>
<td><strong>49.4</strong></td>
<td><strong>50.6</strong></td>
</tr>
</tbody>
</table>

some may be as small as 48 lbs and others as large as 100 lbs. The mean standard lengths (nose to tail) is 50 inches (± 4 inches). The tip of the hind-flippers extends 10 inches beyond the tip of the tail.

The great length of the newborn compared to its relatively low weight gives the pup the appearance of being skinny. Indeed, the newborn has only a small layer of blubber, approximately 13 millimeters thick. During the nursing period, he gains weight very fast so that by weaning time, he weighs 300-400 lbs and has put on a thick layer of blubber. We did not measure growth rates in this study.

D. RESPONSE OF FEMALES TO PUPS

1. Acceptance and rejection.

A cow and her pup usually remain close together from the time the pup is born until it is weaned. The close proximity of pup and female is a sign of her acceptance of him, especially in the case where the pup is not her own. The female allows the pup to sleep next to her and she responds to its suckling attempts by assuming the nursing position, if she is not already in it (Fig. 9). She never solicits suckling directly. Mother and pup do not move around much in the harem, remaining in the same general location throughout the nursing period. If a situation arises which calls for relocation of the pair, such as high surf, the mother moves first and then the pup follows. However, there are times when a disturbance separates mother and pup, then the mother moves toward the pup and attempts to lure him back to the prior location or she simply relocates near him.

A close association between mother and pup is usually formed shortly after the pup is born and is maintained throughout the nursing period. The association serves two purposes: nurturance of the pup and by nature of the female's proximity, protection from injury by other females. The asso-
ciation is well formed by the end of the pup's first week of life since females separated from their offspring for several days during this period will reject attempts to suckle when the pair are reunited. Except for cases like the above, no marked cow was ever seen biting or behaving aggressively toward her own pup. When approached by human intruders, mothers do not carry or attempt to take their pups with them, as is common in some pinnipeds, for instance, the California sea lion. In this situation, the elephant seal cow attacks the intruder, holds her ground near the pup, or turns, flees and abandons it.

Vocalizations of females and pups carry information relating to identification, location and suckling intent of the pup and, proximity and emotional state of the female (see Bartholomew & Collias, 1962). Pups have only one type of vocalization, a shrill cry which is repeated several times at intervals of approximately one second. The cry is approximately 0.3 seconds in duration and rises and falls quickly. The fundamental frequency is between 1000 Hz and 1500 Hz. When a pup is ready to suckle and the female is lying on her side, he nuzzles the female's side, apparently searching for a nipple, and at the same time emits the stereotyped vocalization until the cow rolls on her side and exposes her teats. The shrill vocalization is also used when the pup has lost its mother or has been bitten or run over by an adult. In this situation, the cries may be more closely spaced and of greater intensity.

Females emit two distinct vocalizations: an attraction call and a threat. The first is a high frequency warbling sound which rises and falls in pitch five to six times per second. Each “wave” is accompanied by vertical head shakes made with the mouth held open. The fundamental frequency varies between 600 and 1000 Hz. Females emit this sound shortly after they give birth, but not before. As the cow turns to approach and nose her newborn, she begins to warble vigorously. For a few minutes after birth, the vocalization is issued toward the pup, a few inches from his face. When the newborn cries, the female responds immediately by warbling. A duet between mother and newborn pup may continue for several minutes. This vocal response of the female to her pup's cries can be heard throughout the nursing period. The female employs the warbling sound to attract her pup. For example, if a cow and pup become separated and the pup begins to vocalize, the cow raises her head, looks in the pup's direction and warbles. Sometimes, she moves toward the pup while warbling, although usually she waits for the pup to come to her. For example, we observed a female give birth in the wash zone of a small inlet adjacent to area 3. Fearing that the pup would drown, we moved him to a safer location 30 feet higher up the
beach. From a distance, we watched as the female warbled in response to her pup's distress calls. The newborn crawled slowly all the way back to its mother who remained fixed near the water's edge where she had just given birth.

When females find their pups absent, they do not move about searching for them nor do they issue the attraction call. Only when the pup is vocalizing does the female seem to notice the pup's absence and respond.

In most situations where a pup is in danger, such as being bitten by an alien female or pinioned by the weight of a bull, the mother does not threaten the source of danger but rather, she warbles at her pup. This strategy has no effect when the pup is buried in the sand by a two-ton bull (Fig. 10). The bull typically remains impervious to pup and female sounds alike.

The threat vocalization of females is a loud, prolonged, low frequency, rasping noise made with the mouth held wide open. Most of the energy in this vocalization is below 700 Hz. It is used in numerous situations such as: (a) rejecting the sexual approaches of a male, (b) rejecting the suckling attempts of an unwanted alien pup or weaner, (c) in aggressive encounters with other females, and (d) in threatening an approaching human. The open-mouthed threat usually precedes a bite.

Most females reject the suckling attempts of alien pups. A female does this in various ways: by moving away, by turning on her belly or by not assuming the nursing position, and more frequently, by threatening the pup vocally or by moving toward it and biting it. Pups may be bitten anywhere on the body but most often it is on the nose or head. Some females will bite pups on the rump or hindflipper as they turn to flee, or as they pass fleeing from another aggressive female.

Some females will nurse alien pups briefly; other will do so for long periods of time, as the next section shows. However, we never saw a cow attempt to prevent her pup from suckling an alien female.

2. Nursing behavior of females and sexual receptivity.

In general, females can be grouped into three categories according to their maternal response to pups; these categories, the variations which occurred in each one of them, as well as the ensuing receptivity of the females are shown in Table 5 for marked pairs observed on area 3.

a. Females that nursed their own pups.

Seventy-two percent of the 50 females in the sample nursed their own pups until they were weaned at approximately 27 days of age. Two females that
TABLE 5

*Nursing relationships and sexual receptivity of females on area 3 during 1970 and 1971*

<table>
<thead>
<tr>
<th>Females (N = 50)</th>
<th>Females Copulating (1971 only; N = 33)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>frequency</td>
</tr>
<tr>
<td>Nursed own pup to weaning age</td>
<td></td>
</tr>
<tr>
<td>a. Exclusively</td>
<td>25</td>
</tr>
<tr>
<td>b. And an alien occasionally</td>
<td>9</td>
</tr>
<tr>
<td>c. And an alien as well</td>
<td>2</td>
</tr>
<tr>
<td>Nursed alien after losing own pup</td>
<td></td>
</tr>
<tr>
<td>a. Exclusively (adoption)</td>
<td>5</td>
</tr>
<tr>
<td>b. Occasionally</td>
<td>3</td>
</tr>
<tr>
<td>Did not nurse</td>
<td></td>
</tr>
<tr>
<td>a. But remained in harem</td>
<td>5</td>
</tr>
<tr>
<td>b. Did not give birth but “accepts” alien</td>
<td>1</td>
</tr>
</tbody>
</table>

departed after nursing their pups for only five and 15 days, respectively, were not included in this category. The first pup died of starvation and the second pup was adopted shortly after his mother went to sea by an alien female who had lost her own pup. The alien female fostered this pup for 25 days. Although 48 days old at weaning, the pup was still smaller than other weaners.

The majority of females that nursed their own pups rejected suckling attempts of alien pups. Nine females were seen nursing an alien between bouts of nursing their own pup on one to five occasions. One cow allowed five different pups to suckle on separate occasions. In most of these suckling bouts, the female was asleep and did not appear to distinguish between the alien and her own pup.

Two females nursed an alien pup in addition to their own. In the case of one female, both pups were weaned at approximately 30 days and were indistinguishable from each other. Both of them were considerably smaller than normal weaners. A similar situation was observed on area 17 in 1970. The two pups that suckled the other female on area 3 both died. One pup was separated from its “mother” for brief periods and during this time, it was bitten twice by females and rolled on once by a male. Severely injured when weaned at 29 days, the pup disappeared at 35 days and later was found dead, apparently from drowning. The other pup, although separated, was bitten twice and disappeared at 15 days of age. We could not determine which was the alien and which was the female’s own pup. It is possible that
### TABLE 6

*Vital statistics for foster females and their adopted pups (in days)*

<table>
<thead>
<tr>
<th>Adopted Pup</th>
<th>Foster Female</th>
<th>Interval between parturition &amp; adoption</th>
<th>Interval between parturition &amp; depart.</th>
<th>No. days nursed own pup before adoption</th>
<th>Interval between end of nursing own pup &amp; adopting alien</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foster Pairs</td>
<td>Duration Suckled by Mother</td>
<td>Age at Adoption</td>
<td>Interval between sep. from Mother &amp; Adoption</td>
<td>Duration nursed by foster Mother</td>
<td>Age at Weaning</td>
</tr>
<tr>
<td>1</td>
<td>22</td>
<td>22</td>
<td>0</td>
<td>25</td>
<td>47</td>
</tr>
<tr>
<td>2</td>
<td>0</td>
<td>&lt;1</td>
<td>0</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td>3</td>
<td>7</td>
<td>12</td>
<td>5</td>
<td>16</td>
<td>28</td>
</tr>
<tr>
<td>4</td>
<td>6</td>
<td>7</td>
<td>1</td>
<td>16</td>
<td>23</td>
</tr>
</tbody>
</table>
they were twins. Laws (1953; 1956a) and Bryden (1966) have observed a few cases of twins in the southern elephant seal.

Most of the females that nursed their own pups to weaning age were seen copulating before departure.

b. Females that nursed alien pups only.

Eight females that lost or became separated from their pups either adopted alien pups and nurtured them to weaning or nursed alien pups only occasionally. More detailed information about adopted pups and the five females that fostered them is given in Table 6. It is evident that the age of a pup when adopted varied greatly, from the day he was born to 22 days of age. Most of these pups were orphaned only a brief time before being adopted. Only pup No. 2 was not nursed by its genetic mother. All adopted pups were uninjured at the time of adoption. Those that were a week old or more when adopted, were small for their age, particularly No. 1. Each pup suckled for the remainder of its foster mother's time ashore. This period was always shorter than the four-week period that a female normally nursed her own offspring. All fostered pups survived to weaning and their health was good, but most of them were smaller than most other weaners. Age at weaning varied greatly.

Foster females adopted alien pups after their own pups died or they were separated from them. The interval between parturition and adoption of an alien pup varied from one to a little more than three weeks. During this time, these females nursed their own pup or various aliens from four to 12 days before adopting a single pup. Apparently, they went for one to ten days without nursing. Four of the five foster females spent more time ashore than normal (cf. Table 1). Females No. 1, 3, and 4 were observed copulating before departure.

Three females remained in the harem after losing their pups and nursed alien pups to varying degrees (Table 5). Two of them were observed nursing an alien on one occasion only; milk was not observed. The other female nursed seven different alien pups on at least seven occasions. Milk was observed once. None of the females were seen copulating and none of them were mounted by males within the week prior to departure.

Two females on area 17 in 1971 allowed as many as 13 pups to "suckle" them or, at least, to attempt to do so. They were situated next to each other in the same location for approximately two weeks. However, detailed information, such as the status of the pups and whether or not the females had given birth was not obtained. Moreover, we could not determine whether the pups actually obtained milk from these females.
c. Females that did not nurse.

Five females, separated from their pups shortly after parturition, remained in the harem for a mean of 26.5 days after parturition and were never observed nursing pups. None of them were observed copulating nor were any of them mounted during the week prior to departure.

One female, who did not give birth, accepted a newborn that had been abandoned, but since she had no milk, the pup died of starvation in six days. This two to three year old female departed 28 days after she arrived. Other females were generally aggressive toward her, treating her like a large weaner. This female was not seen copulating.


We can summarize the main points of this section as follows: (a) The majority of females (72%) nursed their own young until weaning age, (b) Twenty-six percent of the females abandoned or became separated from their own pups, (c) Thirty-eight percent of the females that lost their pups adopted an alien pup and nursed it to weaning age, (d) Females did not nurture two pups to weaning age as efficiently as females that nursed a single pup, (e) Females that refrained from nursing for as much as ten days did not lose their milk, (f) Females that gave birth but did not nurse still remained in the harem the usual length of time, and (g) Females that gave birth but did not nurse, or nursed only occasionally, were not observed to copulate.

E. BEHAVIOR OF PUPS

1. The suckling pattern.

As previously noted, elephant seal pups begin suckling within an hour after birth, in some cases as early as 15 minutes post-partum. The pup usually lies at approximately a right angle to the cow and elevates its head to reach the nipple by using its foreflippers as props (Fig. 9). The pup suckles until satiated before the bout is terminated. The cow rolls onto her stomach within a minute or so after the pup stops suckling.

Pups do not suckle continuously during a suckling bout. A pup will often stop suckling, yet remain with his mouth in contact with the nipple, or he may alternate sucking one nipple then the other. In 22 undisturbed suckling bouts of pups of various ages, a mean of 68% of the time in each bout was spent "on" the nipple (s = 12.5%). Nipple changes increased with the duration of the suckling bout. Even when pups were on the nipple, we could not determine if they were getting any milk, except in those few cases
where the thick fluid could be seen trickling from the pup’s mouth and down the female’s belly.

Laws (1956a) noted that young southern elephant seal pups took milk from the lower nipples only. We found no evidence for nipple preferences in the pups we observed, regardless of their age. However, it was obvious that pups became more adept at locating the female’s nipples as they became older.

In 1971, we examined the suckling pattern of six pups by recording each of their suckling bouts between 0700 and 1700 hours every Wednesday of the four week suckling period. The pattern for these four days is shown in Figure 11. It is evident that the suckling pattern is quite variable in the same individual as well as across individuals. Some pups suckled as much as several times in one day, while others did not suckle at all. Pup PW did not suckle the first day he was observed when a week old, but suckled seven times on the last day observed, when he was four weeks old. Figure 11 also suggests that suckling bouts are more frequent late in the afternoon and that more time is spent suckling during the last week.

We documented the change in frequency and duration of suckling with age
by observing 13 mother-pup pairs 27 hours per week (successive Tuesdays, Wednesdays, and Thursdays) until the pups were weaned. Table 7 shows that suckling frequency and duration doubled from the first week of suckling to the last. Bryden (1968) found a similar increase in suckling frequency and duration with age in southern elephant seals; in this species, 21 day old pups (they are weaned at 23 days, Laws, 1953) suckled more frequently ($\bar{X} = 7.0$ times per day) and for a longer period (58.8 minutes per day) than four-week old northern elephant seal pups.

**TABLE 7**

*Frequency and duration of suckling bouts of 13 elephant seals pups at Año Nuevo*

<table>
<thead>
<tr>
<th>Age of pup (days)</th>
<th>Mean Suckling Frequency per day</th>
<th>Mean Suckling Time (minutes)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-7</td>
<td>2.1</td>
<td>17.7</td>
</tr>
<tr>
<td>8-14</td>
<td>2.5</td>
<td>23.2</td>
</tr>
<tr>
<td>15-21</td>
<td>3.5</td>
<td>30.1</td>
</tr>
<tr>
<td>22-28</td>
<td>4.2</td>
<td>40.0</td>
</tr>
</tbody>
</table>

2. *Source of nurturance.*

We showed earlier that most pups suckled their mothers throughout the nursing period, but various exceptions occurred. Often an alien female was interposed between a pup and its mother or the nipples of the alien female were more accessible than its mother's. Under these conditions pups suckled from adjacent alien females.

During the 1970 and 1971 breeding seasons, 30 out of 50 pups followed on area 3 suckled their mothers throughout the nursing period to weaning. We will call these “normal” or “filial” pups. Of the 30, eight or 27% were never observed suckling an alien female. Three pups attempted to suckle an alien female, but were unsuccessful. The remaining 19 were observed suckling an alien female from one to three times. There was no difference in attempts to suckle alien females by pups of 1-2 weeks of age and pups 3-4 weeks of age.

When a breakdown in the relationship between mother and pup occurred, such as physical separation or abandonment by the female, mothers did not search for their pups, but pups moved about the harem attempting to suckle from any available female. Under these circumstances, the consequences for pups were as follows: (1) it was unsuccessful in finding an
alien female to suckle, (2) it was injured by a male or female while moving about attempting to suckle, (3) it suckled successfully from various females, or (4) it was adopted and suckled permanently by one alien female. We will call pups in the first three categories “orphans” and pups in the fourth category, “fostered” or “adopted” pups, to distinguish them from filial pups.

During the 1970 and 1971 breeding seasons, 14 of 20 marked pups that were separated from their mothers died because of injuries or starvation because they could not find alien females that would nurse them (four separations in 1970 and 16 in 1971). Of the remaining six pups, one successfully suckled several females until it was weaned and the other five were adopted permanently by alien females. In other words, only 30% of the pups separated from their mothers survived to weaning age.

The behavior of adopted pups and their foster mothers was indistinguishable from that of cows with pups of their own. No difference in the suckling frequency or duration of filial and adopted pups was noted. However, both of the above suckled eight times as frequently as orphaned pups. Normal and fostered pups did differ with respect to age and size at weaning. Weaned-fostered pups ranged in age from 17 to 48 days (Table 6). All adopted pups were smaller at weaning age than filial weaners. Orphaned pups that succeeded in suckling several females until they were “weaned” were even smaller and without exception, heavily scarred (Fig. 12). BARTHOLOMEW (1952) observed runty pups of weaning age on several northern elephant seal rookeries, and so have we. LAWS (1953) reports the occurrence of “dwarfs” in the southern elephant seal.


We can summarize suckling from the pup’s point of view as follows: (1) 60% of the 50 marked pups suckled their mothers until they were weaned but only 22% did so exclusively, (2) 80% of the pups attempted to suckle an alien female or succeeded in doing so occasionally, (3) 40% of the pups were separated from their mothers and of these, 70% died before weaning age, and (4) a separated pup was most apt to survive if fostered exclusively by one alien lactating female.

F. PUP MORTALITY

1. Injuries

The most immediate and serious danger to pups was being bitten or crushed by adult males and females. Virtually all biting injuries were caused by females. In 1971, we documented 40 cases of a female biting a pup; most
of these occurred when pups tried to suckle alien females. In no instance did a female bite her own pup. Only once did we see a male bite a pup and this was a neck bite inflicted during an attempted mount.

In nine out of ten cases where an adult animal trampled a pup, the animal was a male. The danger posed was most acute during the pup's first week of life and diminished as the pups developed.

Orphans were bitten three times as often and crushed more than twice as often as adopted and normal pups.

2. Mortality at Año Nuevo Island in three breeding seasons.

Table 8 indicates the number of pups born on Año Nuevo Island in 1968, 1969, 1970 and 1971, and of these, the proportion which died before weaning age. It is evident that the number of pups produced on Area 3 fluctuated from year to year, while the number born on Area 17 increased steadily, the net effect being a continuous increase in pups for the entire island over the four years. Mortality for the entire island was very consistent over the four year period, ranging from 13.0% to 14.5%. However, the yearly mortality rate, was much more variable on Area 3 than on Area 17. What could have caused this great fluctuation? Winter storms, which created more of a problem on area 3 than area 17 were most severe in 1968, when mortality was not unusually high. The weather was unusually good in 1971. Our presence and operations were similar during each of the four years on area 17 and during the last two years of study of area 3. Mortality was largely independent of yearly population fluctuations since the highest mortality on area 3 occurred in 1971 when relatively few pups were born.

<table>
<thead>
<tr>
<th>TABLE 8</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mortality of pups on the two breeding beaches at Año Nuevo Island during four breeding seasons</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>13.8</td>
<td>9.1</td>
<td>8.1</td>
<td>41.7</td>
<td>7.0</td>
</tr>
<tr>
<td></td>
<td>(82)</td>
<td>(44)</td>
<td>(62)</td>
<td>(48)</td>
<td>(43)</td>
</tr>
<tr>
<td>17</td>
<td>13.8</td>
<td>13.8</td>
<td>15.9</td>
<td>9.5</td>
<td>15.1</td>
</tr>
<tr>
<td></td>
<td>(106)</td>
<td>(203)</td>
<td>(239)</td>
<td>(262)</td>
<td>(324)</td>
</tr>
<tr>
<td>Total: entire island</td>
<td>13.8</td>
<td>13.0</td>
<td>14.3</td>
<td>14.5</td>
<td>14.2</td>
</tr>
<tr>
<td></td>
<td>(188)</td>
<td>(247)</td>
<td>(301)</td>
<td>(310)</td>
<td>(367)</td>
</tr>
</tbody>
</table>

The top figure gives the percent of total pups born which died prior to weaning; the figure in parentheses is the total number of pups that were born. In 1968, a record of where the pups died was not obtained; we have assigned an equal percentage of dead to each area. The mortality estimate for area 3 in 1968 is probably low. * The 1972 data was added in proof.
and, the lowest mortality on area 17 was in 1971 when the greatest number of pups were born.

The excessive mortality on area 3 in 1971 seems to have been due to an increased amount of disturbance created by an unusually non-aggressive alpha bull. This bull tolerated subordinates entering the harem which caused great disturbance to the nursing cows. As many as 10 bulls were in the harem at the same time attempting to copulate with females even before they came into estrus. This caused females to avoid these males and in doing so, they were often separated from their pups. Pups were bitten by alien females or crushed by bulls fighting in the harem. In contrast, the alpha bull in 1970 was extremely aggressive and chased all subordinates from the harem and did not allow them to approach within three meters of any female. The relative effectiveness of these bulls in keeping subordinates from females is indicated by the fact that the 1970 beachmaster was responsible for all copulations on area 3 in the season of his reign. In the following season, his counterpart accounted for only 56% of the copulations, sharing the copulatory chores with eight other bulls.

The case for a more permissive social organization among males in the 1971 breeding season creating greater disturbance, and thus accounting for the increased mortality, is further substantiated by the data in Table 9 which uses interruptions of suckling bouts as an index of disturbance. The greatest increase in the interruption of suckling bouts from 1970 to 1971 was caused by peripheral males attempting copulation and by aggressive interactions between cows. The first phenomenon, due to the presence of more males, facilitated the second and vice versa. Cows moved away from males attempting to mount them and in doing so, aroused nursing cows. An aggressive

TABLE 9

<table>
<thead>
<tr>
<th>Cause of Interruption</th>
<th>Frequency in 1970</th>
<th>Frequency in 1971</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alpha bull attempting to copulate with a female</td>
<td>3</td>
<td>8</td>
</tr>
<tr>
<td>Peripheral sub-adult or adult male attempting to copulate with a female</td>
<td>2</td>
<td>24</td>
</tr>
<tr>
<td>Fights between sub-adult males and/or adults</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Aggressive interactions between cows</td>
<td>3</td>
<td>23</td>
</tr>
</tbody>
</table>
interchange between two cows usually caused one of them to retreat. Often, the retreat carried the female within range of a peripheral bull who mounted her and caused a repetition of the cycle.


The period of time in which mortalities occurred varied from year to year. In 1969, deaths occurred during the 24 days between 15 January and 8 February. In 1970, the interval was 39 days, between 4 January and 12 February. The longest period of mortality was in 1971, with pup deaths occurring between 12 January and 5 March, an interval of 52 days.

Most of the deaths on area 17 occurred between 16 January and 10 February, an interval which coincided generally with the time of maximum number of females and suckling pups. Each year, virtually all the deaths occurred during this time when the harem contained over 150 females (97% in 1969, 95% in 1970, and 93% in 1971) and over 75 suckling pups (97% in 1969, 95% in 1970, and 86% in 1971). Most deaths occurred before the peak period of copulation, 10 February to 15 February.

4. Age, size and sex of pups at death.

The age at death was determined for 14 pups. Mean age at death was 11.3 ± 7.5 days. Five pups died in their first week of life, five in the second, one in the third, and three in the fourth week. The three pups which died in their fourth week were notably smaller than pups of the same age which were subsequently weaned. These three pups were injured by females, 11, 14 and 16 days prior to death.

Table 10 gives the weights and measurements of dead pups collected during three breeding seasons. The lightest pup weighed 44 lbs; the heaviest weighed 145 lbs. The range of standard lengths was 39 to 60 inches. The mean standard length of 24 weaners measured in 1971 was 56.8 ± 5.9 inches.

<table>
<thead>
<tr>
<th></th>
<th>1969</th>
<th>1970</th>
<th>1971</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weights (pounds)</td>
<td>75.8 ± 21.4</td>
<td>64.1 ± 11.8</td>
<td>75.4 ± 15.4</td>
</tr>
<tr>
<td></td>
<td>(15)</td>
<td>(27)</td>
<td>(39)</td>
</tr>
<tr>
<td>Standard Lengths (inches)</td>
<td>49.8 ± 3.8</td>
<td>50.5 ± 5.6</td>
<td>49.3 ± 2.9</td>
</tr>
<tr>
<td></td>
<td>(28)</td>
<td>(35)</td>
<td>(39)</td>
</tr>
</tbody>
</table>

Figures are means ± one standard deviation. Figures in parentheses are the number of pups measured.
The male to female ratios of dead pups on the entire island was 4 to 5 in 1969, 1 to 1 in 1970, and 9 to 11 in 1971.

5. Necropsies and possible causes of death.

The results of 43 field necropsies performed in 1971 are shown in Table I. Seventy nine percent of the dead pups examined showed evidence of some type of injury. Cuts and abrasions were found on 67% of the pups and an equal percentage showed evidence of internal trauma (e.g., skull fractures, internal hemorrhage or ruptured organs).

![Figure 13. Depressed (a, b) and penetrating (c, d) skull fractures found in elephant seal pups.](image)

Thirteen out of 38 skulls examined were fractured and appeared for the most part to have been caused by bites. Figures 13 and 14 show examples of how the bone was depressed or punctured in small, well-defined areas rather than the entire skull being disarticulated, as one would expect if the pup had been crushed. Figures 13a and 13b depict typical depressed fractures (pups 8 and 28 in Table I). Figures 13c and 13d illustrate the more severe penetrating skull injuries (pups 12 and 13). The distance between the punctures on the skull shown in Figure 13d corresponds to the distance between the upper canine teeth of adult females. Figure 14 shows a puncture of the right posterior part of the skull (pup 5).

Ten pups showed signs of internal hemorrhage in the visceral cavity and six pups had ruptured livers or spleens associated with internal hemor-
### TABLE II

**Results of 43 necropsies performed in 1971. Pups are numbered in the order that they died**

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*Note: X indicates presence of lesion.*
rhage. Varying amounts of blood were found in the bronchi of nine animals. These injuries were probably caused by crushing. Fluid was found in the bronchi of 21 of the 38 pairs of lungs examined. The lungs of 15 pups contained white foamy mucus which normally appears in the bronchi of dying animals. One pup found in a tide pool had a large amount of water in its lungs and had apparently drowned. 1)

![Figure 14. A large, penetrating fracture of the occiput (a = right side, b = rear view).](image)

Seven animals had necrotic viscera which made an accurate examination impossible. One of the two stillborn pups had necrotic viscera the day it was born, indicating that it was dead "in utero".

Only five of 38 stomachs examined contained milk, a sign that feeding immediately before death was rare. Twenty stomachs contained yellow bile, evidence that feeding had taken place several hours previous but that digestion had not been completed at the time of death. Twelve stomachs were empty.

6. Case histories.

A chronicle of important events leading up to the time of death in selected individuals aids in interpreting the data in Table II.

Pup No. 3: Separated from mother on day 7 when mother and another female began fighting. Bitten on the head by alien female on day 8. Did not respond to mother's attraction call after this time and was not reunited with mother, although she was not very far away. Died on day 10. Necropsy: extensive surface head wounds and large fractures in both frontals and the left parietal of the skull (Fig. 13d).

1) Note added in proof. Fifty two pups were necropsied in 1972. The frequency of injuries was similar to that found in 1971. Forty one percent of the pups had skull or jaw fractures in both years; 43 percent of the necropsies in 1972 showed evidence of internal hemorrhage or ruptured organs as compared with 39 percent in 1971.
Pup No. 19: Severe wounds on the head were noted on day 10. Pup remained with mother after injury but did not suckle. Died on day 12. Necropsy: fracture on the right fronto-parietal suture.

Pup No. 28: Bitten on the head when mounted by a subadult male on day 1. Suckled twice on day of injury but was not observed feeding thereafter. Remained near mother until death on day 12. Necropsy: punctured left eye, four major scalp wounds, and a depressed fracture of the left fronto-parietal part of the skull (Fig. 13).

Pup No. 33: Separated from mother on day 12. Suckled and later bitten by alien female on day of separation. Bitten by another female and trampled by alpha bull on day 13. Suckled various females until death on day 25. Necropsy: cuts and abrasions on head and body and blood in the bronchi of one lung.

Pup No. 34: Crushed by a female on day 1 and bitten several times by two other females on day 2. Suckled mother, as well as several other females, until death on day 14. Necropsy: large suppurring wound over right eye and ruptured liver with internal hemorrhage.

Pup No. 39: Marked when separated from mother at approximately one week of age (exact age unknown). Bitten twice on day of separation, once three days later, and once again, 16 days later. All bites were by females. Observed suckling 9 days after separation. Died 23 days after separation. Necropsy: cuts and abrasions on head and body, light weight (58 lbs) and thin layer of blubber (5 mm).

7. Summary.

The most frequent necropsy findings were external skin wounds, internal hemorrhage, ruptured organs and skull fractures. The nature of these injuries, as well as behavioral observations made prior to death, points to female bites and trampling by males as the major causes of death.

IV. DISCUSSION

Our data show that mortality prior to weaning in elephant seal pups is primarily socially induced. Rather than a single principal cause being responsible for most of the deaths, various social contingencies involving adult animals initiate and facilitate a pup's decline and eventual demise. These include: mother-pup separation, failure of females to nurse alien pups, female aggression to alien pups and the tendency of bulls to move directly over pups in their paths.

Temporal aspects of the syndrome are important. Separation of mother and pup is the first step. Pups born during the peak population of females are more likely to become separated from their mothers than those born earlier or later in the season. Crowding during the peak season increases interfemale aggression and since one female usually retreats during an encounter, mothers and pups become separated easily. Because of the high number of animals involved, a reunion is less likely at this time than early or late in the season. Separation is also instigated by social disorganization among males and tolerance on the part of the alpha bull which results in many bulls
entering the harem. These activities disturb nursing females and increases the probability of mother-pup separation.

Regardless of when separation occurs, the pup loses a source of nurturance, and to some degree, protection from injury by adult males and females. He will starve within a few days unless he moves about and reunites with his mother, is adopted permanently by a surrogate mother, or manages to scavenge milk on a daily basis from one or more nursing females without their noticing it.

But in moving about the harem in search of food, the pup exposes himself to numerous dangers. When crying for his mother he may elicit the attention of alien females who approach, sniff him and often bite him after he is recognized as an alien. Removed from the safety of his mother's side, he is more likely to be trampled by breeding bulls charging in and out of the harem. Lastly, should the starving pup succeed momentarily in suckling a nursing female, he is apt to be discovered, bitten savagely and chased away.

As the time from his last meal increases, the pup becomes weaker and slower at avoiding danger. He is less likely to reunite with his mother, get adopted, or get a single meal. His chances for survival are near zero if he gets injured. The injury may prevent him from vocalizing, suckling or even moving. Females do not adopt injured pups.

We saw evidence of this syndrome on other islands where elephant seals breed: pups being injured, skinny orphans, and dead pups with multiple wounds on their heads. Bartholomew (1952) reported seeing females biting pups and males crushing them on several rookeries in Mexico and southern California. Others (Rice, Kenyon & Lluch, 1965) have remarked on the high number of dead pups on some rookeries in Mexico.

Our data indicate that 70% of pups separated from their mothers die before they reach weaning age. Some of those that survive to this age, the orphans, have a smaller fat store than normal weaners and are probably less likely to survive once they go to sea. Thus, separation of mother and pup is a most important event affecting the survival of elephant seal pups, for it exposes them to several situations which set up the final and principal causes of death.

Estimates of the mortality in southern elephant seal pups are lower than those we found at Año Nuevo Island. Laws (1953) estimated the percentage of deaths prior to weaning on several rookeries at South Georgia in 1951 at 0.8 to 6.8%. He admits that these estimates are low because many dead pups were washed out to sea, buried, or could not be seen in the crowded rookeries. Pup deaths at Macquarie Island in the late 1950's were estimated at 2 to 16% (Carrick et al., 1962). Under adverse weather conditions, pup
mortality may increase significantly. At Signy Island in 1948 and 1949, pup mortality reached 80% when fast-ice broke up and crushed or caused the drowning of pups born on the sea-ice (Laws, 1953).

The lower mortality figures in the Antarctic seals can be explained for the most part, by the manner in which the figures were obtained. We observed a small population every day and removed pups as soon as they died. This was not attempted with the southern seals. Indeed, it may not have been possible considering the large size of the populations investigated.

Pup deaths in the southern elephant seal, although not studied in detail, have been attributed to similar causes as those we found operative in the northern elephant seal, i.e., starvation after cow and pup were separated, injuries due to female bites and crushings by males, and drowning caused by extreme weather conditions (Laws, 1953; Carrick et al., 1962). A few cases are reported of southern pups being injured or killed by "bachelor" bulls attempting copulation with them (Matthews, 1929; Laws, 1953). Less than 1% of the dead pups at South Georgia and Macquarie Island were stillborn (Laws, 1953; Carrick et al., 1962). Bryden (1968) took a closer look at pup mortality. He dissected 54 pups at Macquarie Island in 1965 and found a "remarkably high incidence of injuries among them." These included extensive bruising of superficial tissues, breaks in the skin, and bone fractures. It is not clear whether he looked for head injuries.

Laws (1953) mentions one factor that does not operate in the northern hemisphere. Pups born early in the season at South Georgia cause the underlying snow to melt and they become entrapped in icy holes 4 to 6 feet deep and starve to death.

Disturbance is emphasized as an important, indirect contributor to mortality in the southern elephant seal. Carrick et al. (1962) noted that disturbances in the harem, such as fights between bulls, intrusions of "bachelor" males or squabbles between cows cause separation of mothers and their pups. Bryden (1968) believes exploitation at Macquarie Island has resulted in bulls breeding at an earlier age giving rise to more bulls of a smaller size in the harems. This created greater disturbance to cows and pups, which interfered with pup's feeding and growth and caused injuries. He concludes that the principal cause of a lesser growth rate of pups at Macquarie Island, in comparison with the Falkland Islands Dependencies, is disturbance within the harems.

Our data underscores the important influence of disturbance on pup mortality in elephant seals and, in addition, illustrates that small changes in male social order can produce great fluctuations in disturbance. On area 3 at Año Nuevo Island, the simple substitution of one alpha bull for another
was primarily responsible for more than a four-fold increase in mortality. One could well see that selectively cropping out the largest bulls for commercial exploitation (the current practice in some Antarctic rookeries) would result in increasingly smaller bulls ascending to alpha positions. These males would not be as effective at keeping their peers out of the harems as larger and older bulls, and disturbance would increase.

Pup mortality in other phocids which have been studied in sufficient detail, resembles the situation in elephant seals. In their excellent investigation of grey seals, _Halichoerus grypus_, on the Farne Islands, Coulson & Hickling (1964) found that pup mortality ranged from 2.3% to 23.0% on several rookeries during the years 1956 to 1962. The mean percentage mortality was 14.9%, a figure that is remarkably similar to the one we obtained (see Table 8). They listed five general causes of mortality in order of importance: (a) starvation, (b) stillbirths and mortality associated with birth, (c) injuries inflicted by adult seals, (d) infections, and (e) misadventure. Starvation resulted from early separation of mother and pup. Injuries were caused by adult males biting and trampling pups, and cows biting pups which approached them or their own pups. Specific injuries resembled those which we observed in elephant seals, *e.g.*, "In some cases, the skull had been badly damaged and the brain case forced through the dislocated jaws, and it is clear that the calf had been killed by considerable force... in other instances, severe wounds have been found on the head, body and particularly on the hind limbs...". Coulson & Hickling do not state the proportion of pups that died from starvation and injuries.

Wirtz (1968) recorded pup mortality rates of 21.9% in 1964 and 16.7% in 1965 in the monk seal, _Monachus schauinslandi_, at Kure Atoll in the Leeward Hawaiians. Apparently, most deaths were caused by predation and injuries inflicted by adult seals.

Pup mortality in seals that breed on ice is difficult to determine. Mansfield (1958) points out that mortality among Weddell seal pups, _Leptonychotes weddelli_, varies considerably depending upon when the ice breaks up. Man exploits Harp seal pups, _Pagophilus groenlandicus_, so no figures of natural mortality are available.

Pup mortality in Otariid seals has not been investigated specifically except in the Alaska fur seal, _Callorhinus ursinus_. Mortality on several rookeries on the Pribilof Islands in 1964 and 1966 ranged from 7 to 13% during the two month period following birth (Anonymous, 1969a, 1969b). In this species, socially induced mortality in the form of trauma and malnutrition, accounts for around 50% of the pup mortality, a smaller proportion of the total pup mortality than we found in the population of elephant seals at
Año Nuevo Island. The primary causes of death in slightly more than 100 pups collected on Reef Rookery in 1964 and 1966 were: malnutrition (38 and 50%), hookworm disease (12 and 24%), trauma from bite wounds (17 and 6%), and infection, primarily navel (16 and 11%). Bite wounds from females was the leading cause of death during the first two weeks of the pupping period, malnutrition during the next five weeks and hookworm during the eighth week. Obviously, trauma is not as important a cause of pup mortality in this species as in elephant seals.

Our observations on the nutritional relationships between elephant seal females and pups substantiate and refine earlier conclusions reached by Bartholomew (1952) and Fogden (1968). The majority of females nurse their own young and reject pups belonging to other females. Some females, with or without a pup of their own, adopt motherless pups and nurse them until weaning. A small number of females permit several pups to suckle and remain close to them. Pups are less discriminating than females and will suckle any females that are accessible and permissive. Most pups separated from their mothers die; survivors are adopted by an alien female or manage to "steal" milk from several females on a day to day basis.

We found no evidence for Bartholomew's speculation (1952, pp. 393, 419) that mothers desert their pups for several days when they go to sea to feed. The normal state of affairs is for females to remain onshore continuously until they have given birth, nursed their young and copulated. Only then do they depart the rookery, not to return until several weeks later to moult, a time when they have no maternal affiliation with pups. The few nursing females we observed going to sea abandoned their pups, and in the few cases in which they returned, they did not reunite with their young.

Our findings contradict the major conclusions of Klopfner & Gilbert (1967) who summarized their brief observations on Año Nuevo Island and San Nicolas Island as follows: "Undisturbed elephant seals (Mirounga angustirostris) are highly tolerant of alien young, even to the extent of allowing them to nurse, and irrespective of whether their own young are near them or not. Only upon being approached by a human observer do the cows begin threatening and biting pups, aliens as well as their own." Tolerance and nursing of alien young is clearly exceptional female behavior in the Año Nuevo population and, according to our own observations and Bartholomew's (1952), in other rookeries as well. Although human observers can create disturbances which cause females to bite alien pups, this is not the only stimulus which brings this about. We have described the circumstances in which females bite alien pups and the effect of this behavior on pup mortality. This behavior occurs normally and in the absence of
human interference; human intrusion merely increases the frequency of occurrence in much the same way as the intrusion of one or more subadult males. Furthermore, we never saw females bite their own pups.

A source of error and misinterpretation in some early studies may have arisen from the failure of the investigator to verify the true female parents of pups. In the field, parentage can be ascertained in only one way, by marking mother and pup after witnessing parturition. Proximity of female and pup, or even nursing, is not proof of a filial relationship, as our study shows. Brief studies, where these precautions are not undertaken, can lead to more confusion than enlightenment.

The nursing behavior of Grey seals, *Halichoerus grypus*, is similar to that of elephant seals. Females may nurse only their own pup, another pup in addition to their own, or adopt one or more pups when their own pup dies (Smith, 1968; Hewer & Backhouse, 1960). Fogden (1968) found that most pups on Ruskholm, Orkney suckled the same female partner. Some of Smith's provisional conclusions for the grey seal hold equally well for the northern elephant seal: "(1) A pup seen feeding from a cow is usually, but not necessarily, the offspring of that cow. (2) A pup abandoned by its cow will not necessarily starve to death. (3) A cow deprived of her pup will still feed other pups; she thus remains in the breeding colony and does not necessarily have a reduced chance of mating."

Rejection of alien pups by females has been reported in several phocid species, e.g., Grey seals (Coulson & Hickling, 1964), Harbor seals, *Phoca vitulina* (Bishop, 1967), and Weddell seals (Mansfield, 1958). This appears to be the rule in Otariid seals where mothers nurse only their own young, e.g., Alaska fur seal (Bartolomew & Hol, 1953) and California sea lion, *Zalophus californianus*, (Peterson & Bartolomew, 1967).

Our observations of non-nursing females suggest a link between lactation and estrous behavior. All of the eight females that did not nurse or nursed only occasionally after having given birth, were not observed copulating. On the other hand, 67% of the 24 females that nursed pups to weaning age were seen copulating. Obviously, this type of mechanism would exert great negative selection pressure on non-nursing females since, by not copulating, they would fail to produce a pup in two consecutive years. Females that adopted an alien pup would copulate and produce a pup the following year. It is also tempting to speculate on the neuro-endocrine basis of such a relationship. But eight females is a small sample. The phenomenon deserves further study.
SUMMARY

Northern elephant seal females and pups were observed during four breeding seasons at Año Nuevo Island, California.

Six to seven days after a female arrived on the rookery she gave birth to a single pup which she nursed for four weeks. Estrus began 24 days after parturition and lasted an average of four days. Females spent a total of 34 days on the rookery before returning to sea. The only other time females came ashore was to moult, a period which lasted a few weeks.

Most births occurred in the harem at night during the last two weeks of January. Cephalic presentations were more frequent than caudals (62% vs. 38%) and both were equally rapid. The placenta was delivered immediately after the pup or within an hour after birth. Stillbirths were infrequent and premature pups were never observed. The sex ratio was 49.4 males to 50.5 females.

Eight females gave birth for the first time during their third year but most females are believed to give birth later. Three females gave birth on a different rookery than their own birthplace. The time of parturition from year to year was very consistent in individual females.

Newborn pups weighed 65 lbs at birth and were 60 inches long. They are precocial and suckled for about four weeks before being weaned. Weaners moulted their natal pelage at four to six weeks of age, a time when they began entering the water. Most weaners left the rookery headed north during the month of April.

Females accepted a pup by allowing it to nurse and rejected alien pups by biting them. Females emitted two vocalizations: a pup attraction call and a threat vocalization. Pups emitted a single vocalization which functioned in several situations.

Seventy-two percent of the females observed nursed their own pups to weaning and rejected most of the sucking attempts of alien pups. A few females nursed an alien pup in addition to their own. Twenty-six percent of the females became separated from their pups or their pups died. One third of these females adopted an alien pup. Females that gave birth, but did not nurse for several days, did not copulate.

The frequency and duration of suckling increased as pups developed. Pups attempted to suckle any available female but were rejected by most alien females. Sixty percent of marked pups suckled their mothers. The remaining forty percent were separated from their mothers and most of them died. Those that survived were adopted by an alien female or were suckled by several different females each day.

Pup mortality at Año Nuevo Island was very consistent over the four year period, ranging from 13.0% to 14.5%. Most mortalities were socially induced; pups separated from their mothers starved or were injured by adult males and females. The probability of separation was increased by high numbers of females and disturbances created by intrusions of breeding bulls into the harem.

REFERENCES


PERINATAL BEHAVIOR OF NORTHERN ELEPHANT SEAL


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Nous avons observé des éléphants de mer, femelles et jeunes, dans l'île Año Nuevo, en Californie, pendant quatre périodes de reproduction.

Six ou sept jours après son arrivée dans la zone de vêlage ("rookery"), la femelle donne naissance à un seul petit qu'elle allaite pendant quatre semaines. La période de rut commence 24 jours après l'accouchement et dure en moyenne quatre. Les femelles passent 34 jours dans la zone de vêlage avant de retourner dans la mer. Elles ne reviennent sur le rivage que pour muer, ce qui demande quelques semaines.

La plupart des naissances ont lieu dans le harem, pendant la nuit, durant les deux dernières semaines de janvier. Les accouchements où les petits sortent la tête la première sont plus fréquents que ceux où les petits sortent la queue la première (62% contre 38%) mais dans les deux cas l'accouchement est de courte durée. Le placenta est expulsé immédiatement après le petit ou dans l'intervalle d'une heure suivant l'accouchement. Les petits morts-nés sont rares et les naissances prématurées n'ont jamais été observées. Les proportions des sexes sont les suivantes : 49,4 de mâles et 50,5 de femelles.

Huit femelles ont porté pour la première fois pendant leur troisième année mais la plupart des femelles donnent naissance à un âge plus avancé. Trois femelles ont mis bas dans une zone de vêlage qui n'était pas celle où elles étaient nées. Chaque année, la femelle accouche à la même époque.

Les nouveau-nés pèsent 65 livres à la naissance et ils ont 60 pouces de long. Ils donnent de nombreux signes d'activité et têtent leurs mères pendant quatre semaines environ avant d'être sevrés. Pendant le sevrage, ils perdent leur pelage initial à l'âge de 4 à 6 semaines, âge pendant lequel ils commencent à entrer dans l'eau. Les petits sevrés quittent la zone de vêlage et se dirigent vers le Nord pendant le mois d'avril.

Les femelles acceptent un petit quand elles lui permettent de têter et elles rejettent les étrangers en les mordant. Les femelles émettent deux sons : un appel destiné à attirer les petits et un son de menace. Les petits émettent un seul son qui sert dans plusieurs situations.

72% des femelles observées ont allaité leurs propres petits jusqu'à la période du sevrage et ont rejeté la plupart des tentatives de petits étrangers qui voulaient les têter. Un petit nombre de femelles ont allaité un petit étranger avec les leurs. 26% des femelles furent séparées de leur petit ou vinrent leur petit mourir. Un tiers de ces femelles adoptèrent un petit étranger. Les femelles qui accouchèrent mais qui n'allaitèrent pas pendant plusieurs jours ne copulèrent pas.

La fréquence et la durée de l'allaitement augmentent pendant le développement du petit. Les petits essaient de têter auprès de toutes les femelles disponibles mais la plupart des femelles les rejetten. 60% des petits catalogués têtèrent leurs mères. Le reste (40%) furent séparés de leurs mères et la plupart d'entre eux moururent. Les survivants furent adoptés par une femelle étrangère ou bien ils têtèrent auprès de différentes femelles chaque jour.

La mortalité infantile dans l'île Año Nuevo fut très régulière pendant quatre ans, ne variant que de 13,6% à 14,5%. La majorité des morts eurent des causes sociales : les petits séparés de leurs mères moururent de faim ou furent blessés par des adultes mâles ou femelles. La probabilité de séparation augmentait quand le nombre de femelles était très élevé et par les troubles occasionnés par les intrusions de mâles en rut ("breeding bulls") dans le harem.