Behav. Ecol. Sociobiol. 3, 337–367 (1978)

Behavioral Ecology and Sociobiology

Northern Elephant Seal Development: The Transition from Weaning to Nutritional Independence

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Received September 5, 1977

Summary. 1. The $2^1/_2$-month period from weaning to departure from the rookery was studied in northern elephant seal pups at Año Nuevo Island, California. After being weaned at 4 weeks of age, pups fast completely while learning to swim and dive before going to sea in search of food.

2. Pups increase their birthweight by a factor of 3–7 times on mother's milk alone. Males weigh more than females at birth and at weaning, and are nursed an average of one day longer.

3. Some newly weaned pups prolong the suckling period by stealing milk from nursing females or by being adopted by foster mothers. Males are more persistent and more successful at milk stealing than females and, consequently, exceptionally large weaners are always males. These sex differences are predicted from the manner in which adults maximize their reproductive success. An advantage in size and condition benefits a male much more than a female. Molting and canine eruption occur later in males than in females and these differences may be an adaptation in the former which facilitates milk stealing.

4. Sexual differentiation is evident in the earliest social interactions. Males interact more frequently than females and their bouts last longer. Behavioral components in the interactions of males and females resemble those of fighting adults of each respective sex.

5. Weaners begin entering the water when $6–7^1/_2$ weeks old. They learn to swim and dive gradually. As swimming proficiency increases, they venture further away from their birthplace. They are excellent swimmers and can stay underwater for 15 min by the time they leave the rookery at $3–3^1/_2$ months of age.

6. Although pups are born over an 8-week period, the majority of them depart the rookery over a 3-week period. Pups weaned late in the breeding season are stimulated to enter the water by those weaned earlier. Departure from the rookery is correlated with the onset of coastal upwelling and the latter is correlated with food abundance in the ocean.

0340-5443/78/0003/0337/$06.20

7. Few weaned pups die before leaving the rookery. Mortalities result from injuries inflicted by adult males and females, trauma or drowning due to storms and high surf, overheating, accidents, and shark predation.

8. Survival after the first period at sea to 7 months of age is at least 50%. Thereafter, the survival rate declines gradually to a minimum of 12% at 3 years of age. There are no sex differences in survival to age 2. Pups born early in the breeding season exhibit a higher survival rate during the first year than those born later in the season; females born early in the season exhibit the highest parity rate in their cohort at age 3.

9. Early sex differences are interpreted as subserving the different adult reproductive strategies of each sex.

Introduction

The termination of parental investment in offspring, as defined by Trivers (1972), varies widely in mammals. In most species, the transition from dependence on the parents for nourishment and protection to independence is very gradual. Long after weaning from mother's milk, parental investment in the young may continue in the form of feeding solid foods, guarding, aiding, carrying, or training. This is the typical pattern in some rodents and ruminants, many carnivores, and several primates. At the opposite end of this continuum are a few species in which no further parental investment is provided after nursing ceases. Well-documented examples are grey seals (Davies, 1949; Anderson et al., 1975) and elephant seals (Laws, 1956; Carrick et al., 1962; Le Boeuf et al., 1972). In these species, the transition is abrupt. The weaner gets no help from either parent in securing food or learning to fend for itself.

The period immediately following the cessation of parental investment is a critical time in the development of mammals, especially for those that are independent after weaning from mother's milk. The individual is vulnerable to predators and must secure its own food at a time when it is relatively defenseless, inexperienced at survival, and not fully developed. In many species, the mortality rate is high at this stage of development. Moreover, since the fitness of the developing individual as well as the fitness of both parents is at stake, strategies for survival, growth, and development during the postweaning transition period must be subject to strong selection pressure. It is helpful to view early behavioral development from this dual perspective.

The purpose of this paper is to describe important events in postweaning development of northern elephant seals, *Mirounga angustirostris*, an animal in which all parental investment in the single pup born annually ceases with weaning from mother's milk. This species is particularly interesting to study for several reasons. All parental investment in the young is done by the female. The mother nurses her pup daily for four weeks during which time she fasts completely (Le Boeuf et al., 1972). The cost of reproduction to the mother can be estimated readily since all nourishment for her and her young comes from her body stores (Ortiz et al., 1978). At the end of nursing the female is visibly emaciated. In this brief period, the pup increases its birthweight three- to sevenfold on a diet of mother's milk alone. By the time it is weaned, a

pup is 'ludicrously obese' and 'nearly globular' (Bartholomew, 1952, p. 391). Its huge fat store allows a weaner to fast for a minimum of $2–2^1/_2$ months while on its own, learning to swim, dive, and live in a new medium, the sea, before going off in search of food.

Specifically, we describe the manner in which elephant seal pups make the transition from birth on land and dependency on the mother for nourishment and protection to aquatic self-sufficiency, the time course of this development, and adaptations that appear to enhance survival and future reproductive success. We observed various aspects of development in pups from the time of weaning until departure from the rookery, a period when pups are $1–3^1/_2$ months old. We focused on the following topics: (1) weaning and the behavior of newly weaned pups, especially attempts to steal milk from other mothers, (2) physical development after weaning: molting, dentition, and weight, (3) activity and social behavior on land, (4) transition from land to water, the development of swimming and diving, and departure from the rookery, (5) injuries and weaner mortality before leaving the rookery, and (6) survival after prolonged feeding periods at sea. Lastly, we were especially watchful for sex differences in all behaviors observed.

Pertinent background information on elephant seal behavior and biology are provided in several papers (e.g., Bartholomew, 1952; Le Boeuf, 1972, 1974; Le Boeuf and Briggs, 1977; and Le Boeuf et al., 1972).

Methods

The major part of this study was carried out on Año Nuevo Island, California, during five breeding seasons extending from December 1972 to April 1977. This small island, consisting of only 12 acres, is located 32 km north of Santa Cruz, California (Le Boeuf, 1972). During the study period, females bred in three harems containing 6–740 females at peak season. Additional observations made on other rookeries during this period will be included where appropriate. Each year we focused on a different aspect of study; the time that each of these specific observations were made will be specified in the results. Approx. 4800 h were devoted to the entire study on Año Nuevo Island, alone.

Marking, Tagging, and Tag Recovery. During the 1973, 1974, and 1975 breeding seasons, approx. 90% of all pups produced in the colony were marked and tagged on the day of weaning or shortly thereafter, i.e., when they emerged from the female harems. Approx. 294 pups were weaned in 1973, 404 in 1974, and 505 in 1975 (Le Boeuf and Briggs, 1977). Green, numbered, plastic tags were placed in the interdigital webbing of the hindflippers of each weaned pup and the corresponding tag number or a name was bleached onto both sides of each individual's back (Le Boeuf and Peterson, 1969; Le Boeuf et al., 1974). At this time, or when the opportunity arose, the sex of each weaned pup was determined by observation of the genitalia (males have a penile opening posterior to the umbilical scar) and recorded along with other pertinent tagging information, such as the date, location, and mother's tag number. When marking with a bleaching agent was not possible, pups were marked with paint using a long pole or with the aid of a Nel-spot paint pellet pistol.

Bleach- or paint-marked individuals in or near harems were identified from observation posts on the island with the naked eye or with the assistance of binoculars. With patience and persistence, individuals could also be identified in the shallow water offshore. Thus, marking made it possible to follow individuals on a daily basis from the time they were weaned until they departed from the rookery.

Data on movements, dispersion, philopatry, and survival were obtained by resighting tagged individuals. The plastic tags we used remain intact and legible for three years or more. The paint and bleach marks disappear in less than a year. Efforts to read tags were made daily during each breeding season on Año Nuevo Island and approximately bimonthly during the rest of the year. A similar procedure was employed by researchers from the Point Reyes Bird Observatory on Southeast Farallon Island, an elephant seal rookery located 89 km north of Año Nuevo Island (see Le Boeuf et al., 1974). As part of related investigations, Le Boeuf and collaborators made annual or biannual expeditions to rookeries in southern California and Baja California, Mexico, for the purpose of reading tags. All elephant seal rookeries were monitored at least once every two years. In addition, information on tagged animals sighted by others visiting these rookeries was sent to us. This 10-year-old tagging program has yielded an understanding of the general direction of pup movements throughout the breeding range (Le Boeuf et al., 1974, 1975, 1976).

Censuses. On Año Nuevo Island, weaned pups were censused at midday during each of the five breeding seasons in the study period. The time interval extended from the first week in January when the first pup is weaned, to 15 March, a few days after all pups have been weaned. Weekly censuses were made from 15 March to the end of April, the time when the majority of weaners have departed the island. During the 1974 season, daily censuses were made at sunrise, 1200 h, 1600 h, and at sunset during the period from 7 January to 15 April. At the time of each census, weather conditions, temperature, and tidal conditions were recorded.

Censuses yielded a single figure representing the number of weaners present on land and in the water, as well as the specific location of each marked individual. Censuses yielded information on: (1) the number of pups weaned annually, (2) the pattern of daily movements of the entire weaner population, and of specific individuals on land and from land to water, (3) the rate and time of departure of weaners from the rookery, and (4) the relationship between time of weaning and time of water entry and departure from the rookery.

Weights and Measurements. Thirty weaned pups, 15 males and 15 females, were weighed and measured during the 1975, 1976, and 1977 breeding seasons on Año Nuevo Island. Selection of subjects was made on the basis of convenience, accessibility, and available manpower. Four or five researchers wrestled the weaner into a canvas sock designed for the purpose, straps were tightened to further restrain the animal, and the weaner was carried to a scale nearby. The scale, a Chatillon WT-10, with a capcity of 1000 lbs plus or minus 5 lbs, was hung from a tripod constructed of aluminum pipes. A hook suspended from the scale was attached to eyelets on the canvas sock and the weaner was lifted by a winch connected to the tripod. Weight was recorded, the subject was lowered to the ground and the following were recorded: the tag number of the animal, percent molt, and the degree of canine tooth eruption. In a few cases, length and girth were measured. The entire operation lasted less than 5 min.

Behavioral Observations. The behavior of weaners was observed from blinds situated on ledges overlooking the principal breeding beaches (see Le Boeuf, 1972; Le Boeuf et al., 1972). Binoculars and spotting scopes were used when needed and a serial log of important events was recorded. A closed-circuit television camera (Coho photomultipler) and recorder with the capacity to operate under conditions of very dim illumination were used on occasion to observe the animals in the early morning hours before the sun had risen, in the evening when the sun had gone down, and at night when sufficient light was provided by the moon and stars.

During virtually every day of every breeding season in the study period, someone was in the major blind during daylight hours recording pertinent aspects of weaner behavior. The particular behavior observed varied from year to year. For example, in 1974 we focused on social interactions between weaned pups, the manner in which interactions were initiated, their duration, and the extent to which they varied with the sex of the actor. We monitored the daily movement pattern of weaners from land to water and back and we recorded time of initial water entry, development of water skills, and time of departure from the rookery in known-age individuals. In 1975, we focused on observations of weaner reentry into the female harem. All attempts to suckle alien females were recorded as well as the circumstances and consequences, i.e., whether the weaner was successful in stealing milk or whether it was discovered and chased away or bitten. In all observations, we attempted to focus on individuals whose age, date of weaning, and sex were

known. In 1975, 1976, and 1977, we weighed weaners and collected tag return data to obtain an estimate of survival. We collected information on weaner adoption, molting, and dentition during the 1976 and 1977 breeding seasons.

Observations of weaners were carried out on other rookeries in southern California and Mexico on annual or biannual censusing and tagging expeditions. For example, we observed weaners reentering harems to suckle on Isla de Guadalupe in February 1974 and 1977. At the same time, we made observations on weaner mortality and the circumstances surrounding it. Detailed procedures employed on other rookeries will be presented in the results section.

Results

1. Overview

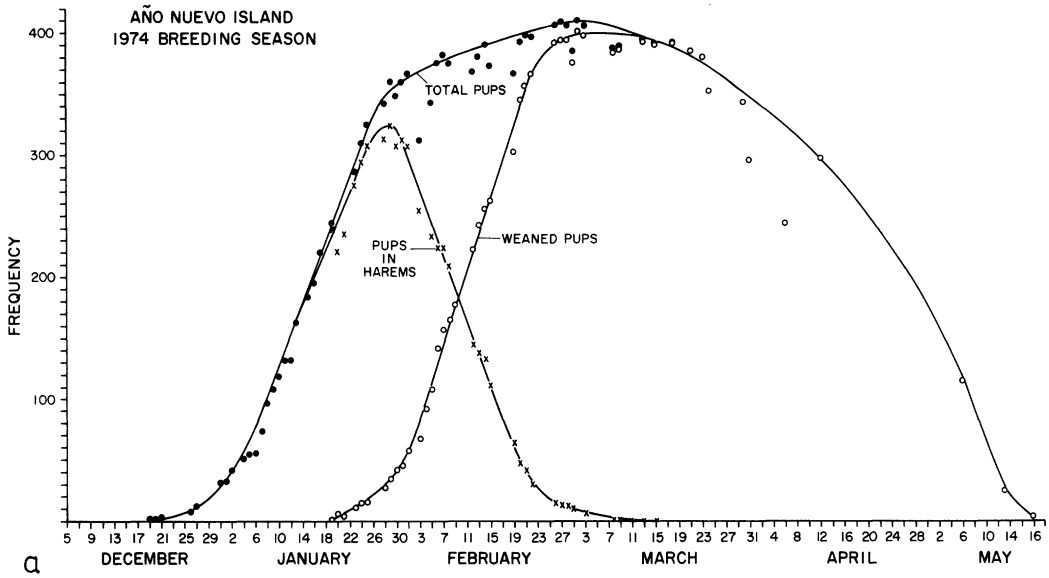
A brief overview of important events in weaner development will aid the reader in understanding the detailed results which follow.

Pups are weaned between mid-January and mid-February when they are approx. 1 month old. The majority of them exit from the female harem and congregate in weaner 'pods.' For the remainder of their stay on land, they spend most of the daylight hours sleeping. Social interactions ('play') are most obvious early in the morning and late in the afternoon. Two to three weeks after weaning, from late February to mid-March, weaners begin entering the water in the early evening, at night, or early in the morning. Development of water skills progresses gradually. As swimming and diving become more proficient, exploratory behavior increases. Departure from the rookery occurs between early April and mid-May when the animals are $3–3^1/_2$ months old. Figure 1 presents frequency distributions of pups in the harems and weaned pups present on Año Nuevo Island in 1974, 1975, and 1976. Elephant seals return to the rookery of their birth, or a nearby rookery, in the following fall or spring.

2. Weaning and the Behavior of Newly Weaned Pups

Cues to the imminence of weaning are the following: (1) the relative size of the mother and her pup; the female has lost a great deal of weight and this is reflected by her slender appearance while her pup has ballooned in size and shape, (2) the female begins to copulate, usually 1–5 days before severing the relationship with her pup, and finally, (3) the female starts moving slowly through the harem to a point where she makes her exit to the sea. More subtle cues can be discerned. For example, pups may attempt to suckle more frequently toward the end of the nursing period (Le Boeuf et al., 1972). This may be in response to the dwindling supply of milk that the mother provides or to the greater capacity of the pup to suckle.

On the day of weaning, the female moves toward the periphery of the harem. If she is located in the center, or if she must move past females dominant to her, this may take several hours. Her pup may or may not follow her. She may start her move while her pup is sleeping. The female doesn't appear


AÑO NUEVO ISLAND
1974 BREEDING SEASON
TOTAL PUPS
PUPS IN HAREMS
WEANED PUPS
FREQUENCY
400
300
200
100
5 9 13 17 21 25 29 2 6 10 14 18 22 26 30 3 7 11 15 19 23 27 3 7 11 15 19 23 27 31 4 8 12 16 20 24 28 2 6 10 14 16
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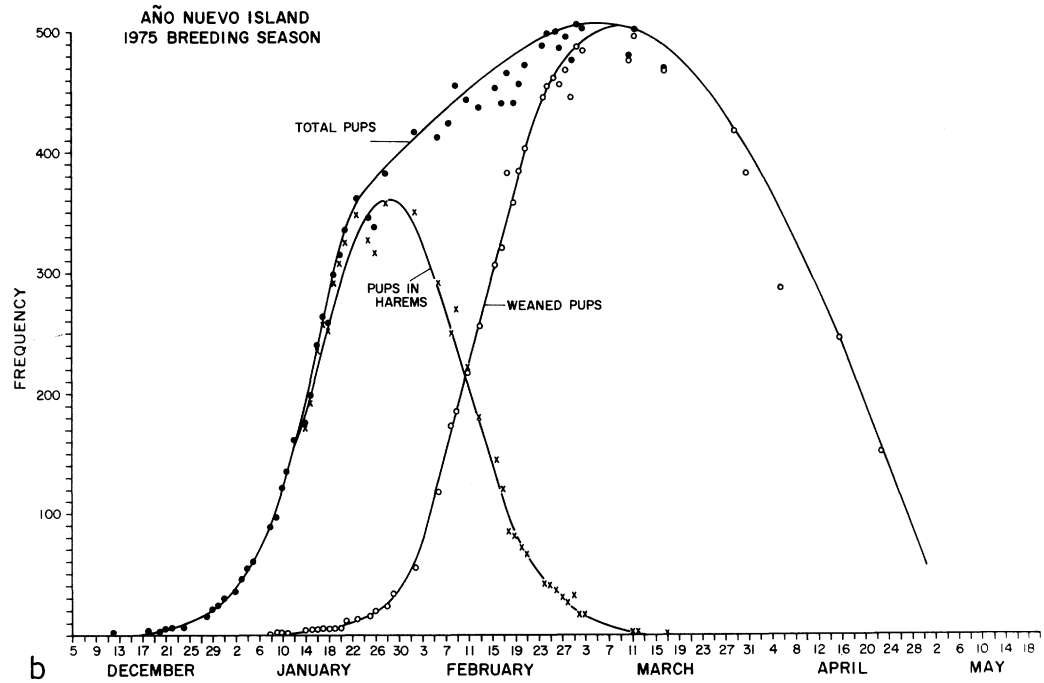
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1975 BREEDING SEASON
TOTAL PUPS
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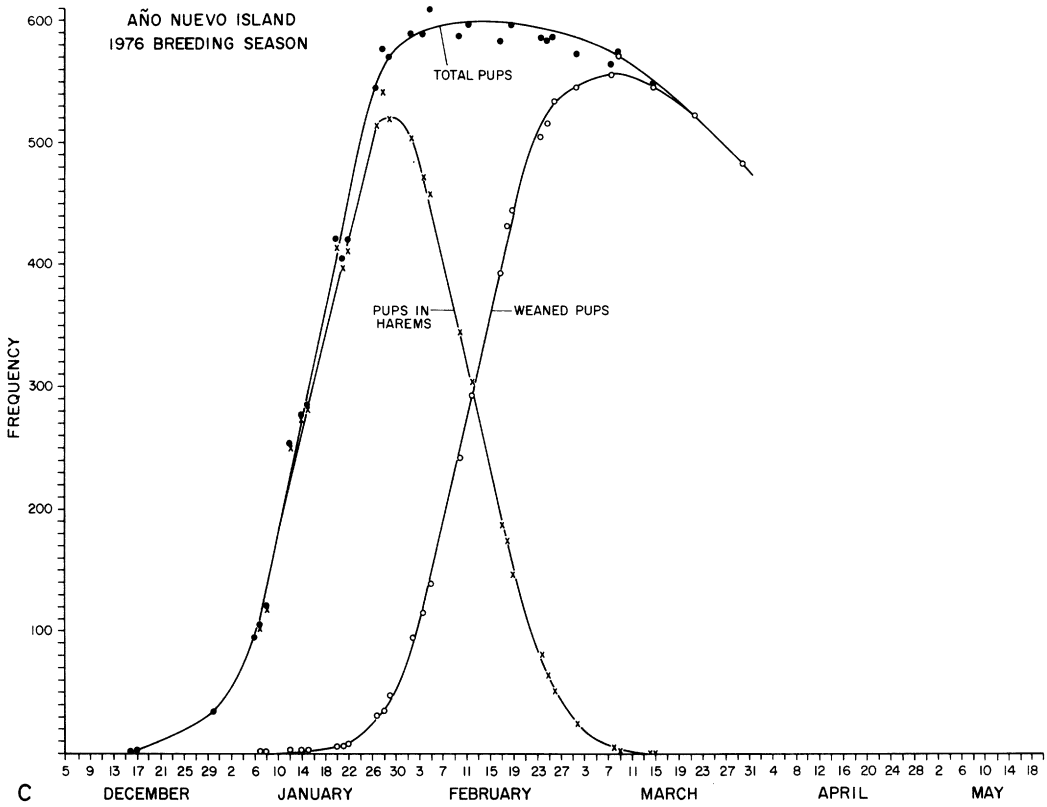


Fig. 1a–c. Frequency distribution of suckling pups and weaned pups on Año Nuevo Island during the 1974, 1975, and 1976 breeding seasons

to mind very much whether the pup follows, a noticeable change from her response in the previous weeks. Finally, the female moves out of the harem toward the water, leaving her pup behind in the harem. She usually copulates again at the water's edge or in the water as she makes her departure (Cox and Le Boeuf, 1977). This is the end of the filial relationship in this species. When the female returns to the rookery to molt, in late March or April, many weaned pups will already have left the rookery or females and pups will be indifferent to each other and even occupy different places on the beach. Thus, there is little likelihood that a mother encounters her pup again on the rookery or that she recognizes it. Reunion at sea is unlikely because of the temporal hiatus in the relationship and the different hauling-out patterns of pups and adult females subsequent to weaning.

Males are weaned one full day later than females ($\bar{X}=27.8\pm1.54$ days vs. 26.6 ± 1.42 days, $n=44$, Le Boeuf et al., unpublished data). This difference is statistically significant ($t=2.70$, $df=42$, $P<0.05$).

The weaned pup finds itself in a hostile environment after the departure of its mother. It is surrounded by alien mothers, protective of their milk and their own pups, and generally hostile to all other pups and weaners. If a newly

weaned pup attempts to suckle an alien female, it is usually repulsed and bitten. Aggressive females soon drive it out of the harem. As a result, most pups leave the harem within a day or two after their mother departs. They join up with other weaners in one or more weaner pods that form inland from the female harem. Here, weaners spend most of their daylight hours sleeping. Interindividual space within pods varies with ambient temperature. In cold weather, the individuals are in close contact; in warm weather, the weaners spread out. Isolated weaners that do not join pods risk being mounted by males that roam the periphery of the harem. Being mounted by males, which involves a neck or head bite, can cause serious injury and pups make vigorous attempts to escape (see later section on injuries and mortality).

Each breeding season, approx. 10% of the weaned pups obtained additional sustenance by surreptitiously suckling alien females in the harem. Sex differences and two different strategies were apparent.

Milk Thieves. The most frequently observed strategy of weaned pups was to attempt to steal milk from unwary females when the opportunity arose. These milk thieves remained in the harem after their mothers departed or they left after weaning only to reenter the harem subsequently in order to steal milk. Successful milk thieves returned to weaner pods to rest only after being chased out of the harem by aggressive females. Some individuals were only successful on occasion, while other became proficient thieves and enjoyed repeated success.

Several behaviors were useful in stealing milk: approaching the female quietly from the rear, nudging a female or biting her gently to prompt her to assume the nursing position (nursing females often did not check to see whether the stimulus came from their own pups), displacing younger, smaller pups from the nipple without attracting attention, and inhibiting vocalizations even when caught in the act. Since a mother recognizes the vocalizations of her own pup, calls of alien pups or weaners reveal their presence to the female. In short, weaners employed the signals an unweaned pup transmits to its mother to get her to assume the nursing position, with the exception of vocalizing. Figure 2 shows a weaner displacing a much younger pup from its mother's nipple.

Stealing milk or simply exploring the possibilities by entering the harem was a dangerous enterprise. When a weaner was caught, the female attempted to bite it just as she attempted to bite orphaned pups that attempted to suckle (Le Boeuf et al., 1972; Le Boeuf and Briggs, 1977). Females often pursued a parasitic weaner for 2–3 m or more. Bites were directed to the head, but if the weaner was moving away, it was bitten on the rump or hindflippers. These bites sometimes resulted in serious injuries. If a weaner cried out as it fled, it attracted the attention of neighboring females who often joined in attempting to bite the fleeing animal. The result was that weaners caught trying to steal milk were usually chased out of the harem. An unsuccessful attempt to suckle is shown in the sequence of line drawings from photographs in Figure 3.

Males were clearly more successful at stealing milk than females, they attempted to steal milk more frequently, they were more persistent, and they pursued this strategy for a much longer period of time. We saw 87 instances

Fig. 2. A weaned pup steals milk from an unwary female by usurping the nipple from her much younger and smaller pup

of successful milk stealing by weaners. Of these, 52 cases involved males and only six involved females. We identified 30 different individuals that stole milk; 26 were males and four were females. These suckling bouts nearly always ended when the weaner was discovered and bitten or chased away by the female. In 81 instances, we observed weaners being repulsed while attempting to suckle. The sex of the weaner was known in 54 of the episodes; 49 attempts were by males and five were by females. In 75% of the cases where a weaner was discovered before it could steal milk, it was bitten. In addition, we saw 67 cases where weaners were in the process of being chased out of the harem by one or more females. We do not known whether these weaners were being ejected for trying to steal milk or simply because of their presence in the harem. In 62% of these expulsions the weaner was bitten. Males were more persistent than females. We saw several episodes in which a male attempted to steal milk from as many as 5–10 females in succession, and although thwarted and bitten each time, it did not give up until it was either ejected from the harem or, more typically, succeeded in suckling an unwary female. In contrast, we saw only one female persevere in attempting to steal milk shortly after being bitten in an unsuccessful attempt. Some male weaners pursued the milk-stealing strategy daily for as long as $3^1/_2$ weeks. On the other hand, it was rare for

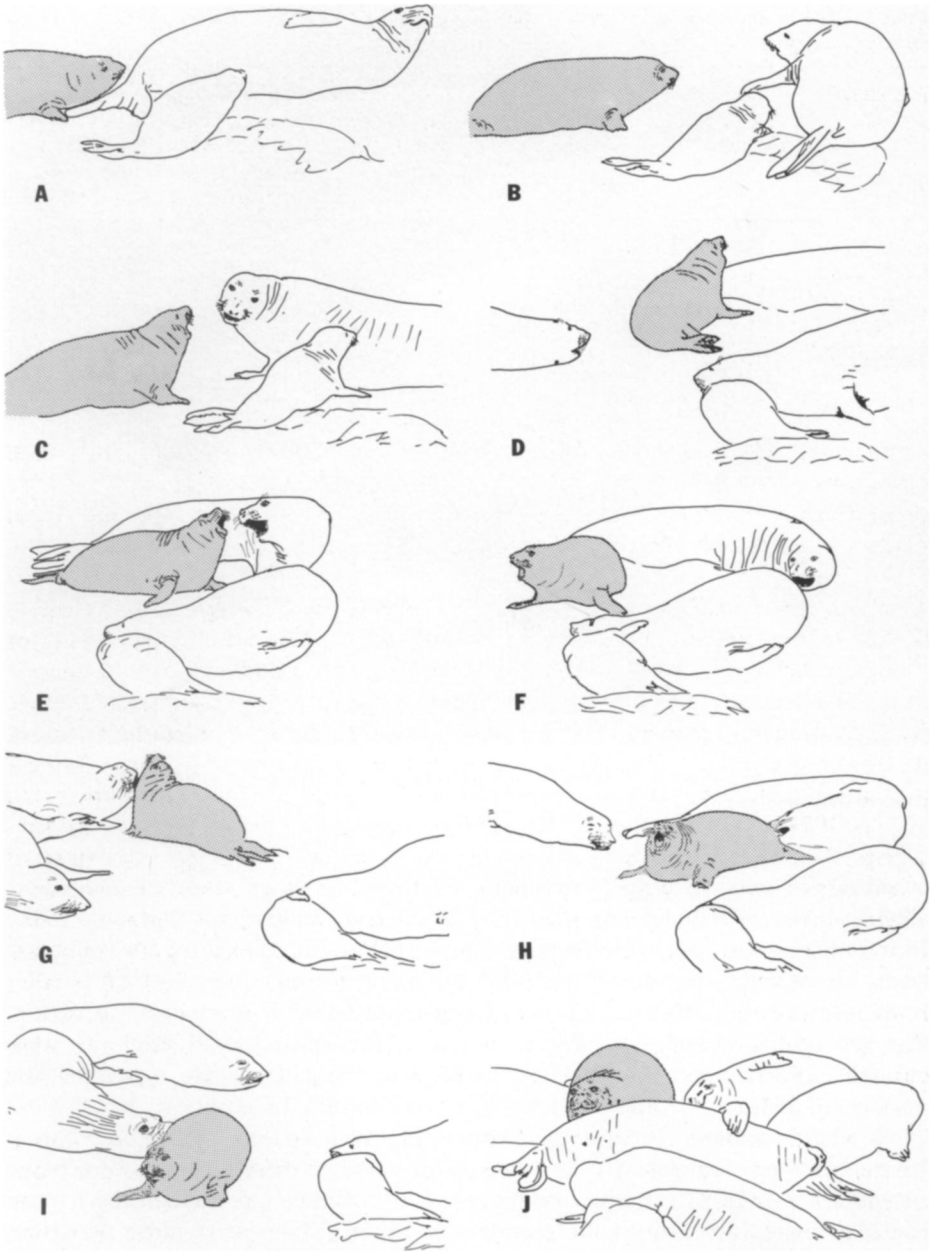


Fig. 3. A sequence of line drawings from photographs indicating a weaner's unsuccessful attempt to steal milk resulting in it being chased out of the harem. In the last illustration the weaner is seen resting outside the harem with a group of other weaned pups

Table 1. Double-mother sucklers: Data on pups that suckled a female in addition to their mothers on a regular basis

Pup identity and sex	No. days pup suckled filial mother	Age of pups when fostering began	Foster mother: days between parturition and adoption	No. days pup suckled filial and foster female simultaneously	No. days pup suckled foster mother after filial mother departed
a – Male	29	5	5	24	11
b – Female	32	2	2	30	3
c – Female	23	16	?	7	7
d – Male	26	22	21	4	16
e – Male	26	26	18	0	20
f – Male	~27	~35–40	28	0	12

a female weaner to steal milk for more than a single day. In summary, although numerous weaners stole milk successfully, it was clearly a dangerous venture that almost always involved a bite from one or more females, a risk that males evidently undertook more readily than females.

Double-Mother Sucklers. A safer and more effective strategy than returning to the harem and attempting to steal milk from an unwary female was for a pup to suckle two females on a regular basis either simultaneously or successively. That is, some pups were adopted and nursed by another female either while still suckling their mothers or after being weaned by their mothers. Foster mothers were almost always females who had lost their own pups. Table 1 presents illustrative data on six double-mother sucklers observed during the 1976 or 1977 breedings seasons. All six foster mothers had been observed nursing a pup for only two days or less prior to adopting. Fostering was initiated when pups a and b were very young, only 5 and 2 days old, respectively. This was precisely the same age as the lost or dead pups of the foster mothers. In cases like these, it appeared to us that foster mothers mistook the adopted pups for their own offspring. Initially, the foster female and the filial mother fought frequently over the disputed pup. After about a week of bickering, the two females compromised and shared the pup. When the filial mother left the rookery, the foster mother continued to nurse the pup until she too was ready to leave.

A slightly different relationship is exemplified by pups c and d in Table 1. These two pups were already 2–3 weeks old when fostering began. Each one of them was nursed by two females until the filial mother departed. When this happened the foster female continued the relationship. In this situation there was little aggression between the two 'mothers.' Indeed, it is quite likely that the pups, being 2–3 weeks old and mobile, solicited the foster relationship by wandering away from the filial mother to steal additional milk.

In the third type of situation, exemplified by pups e and f, pups are adopted after they are already weaned. Indeed, pup f was adopted as a completely molted pup (age estimated at 35–40 days), one who had been identified previously as a proficient milk thief. Unlike the other cases in Table 1, these foster mothers

had no relationship with the filial mothers or the pups before the latter were weaned. Note that the females that fostered pups e and f had given birth 18 and 28 days before adopting. Having lost their pups on the day of birth, they had been pupless since the day of parturition. Interestingly, females that lose their pups tend to remain on the rookery several days longer than females that give birth and nurse their own pups exclusively. A previous study indicated that many females that do not nurse fail to copulate (Le Boeuf et al., 1972). It may be necessary for a female to nurse a pup in order for her to come into estrus.

All of the pups in Table 1 must have received a considerable amount of milk in addition to what their filial mothers provided, since they all appeared considerably larger than the average weaned pup. The largest weaners in Table 1 were the two males e and f. We estimate that they weighed approx. 227 kg, almost twice the size of the average weaned pup. Our estimate was based on the resemblance of these pups to pups of known weight (see later section on weights). Since both of these pups were fostered long after being weaned, this suggests that pups may receive more nourishment when suckling two females successively rather than simultaneously.

It was our strong impression that many more males than females were double-mother sucklers. The fact that males were the largest weaners seen on the rookery each year lends support to this idea (see later section on super-weaners).

3. Physical Development after Weaning: Molting, Dentition, and Weight

Elephant seals have a black pelage at birth. At weaning or shortly thereafter, pups begin to molt. The coarse natal pelage is shed in patches and replaced by a smooth, shiny silver coat of short hairs. The process is gradual and takes 1–3 weeks to complete but there is great interindividual variability. Figure 4 shows that there are sex differences in molting. Females differ from males in that they molt earlier, the process seems to be of shorter duration, and there is less within sex variability in the initiation of the process. Although not evident in Figure 4, we observed a few females begin molting when only 2 weeks old. On the other end of the dimension, all weaned pups complete the molt by the time they are 7 weeks old.

The sexes also differ greatly in the time of canine tooth eruption during development. All pups shed their deciduous teeth after birth but before weaning (Briggs, 1974). However, permanent canines erupt before weaning in females but not until approximately four weeks after weaning in males; there is virtually no overlap between the sexes in this character (Anne Hoover, personal communication). Thus, canine tooth eruption is useful in sexing animals shortly after weaning and the character can also be used to estimate age in pups less than 2 months old.

There is also a sex difference in weight of weaners. Males outweigh females shortly after weaning. In a random sample of 15 male and 15 female pups, 4–7 weeks old, weighed during the 1975, 1976, and 1977 breeding seasons,

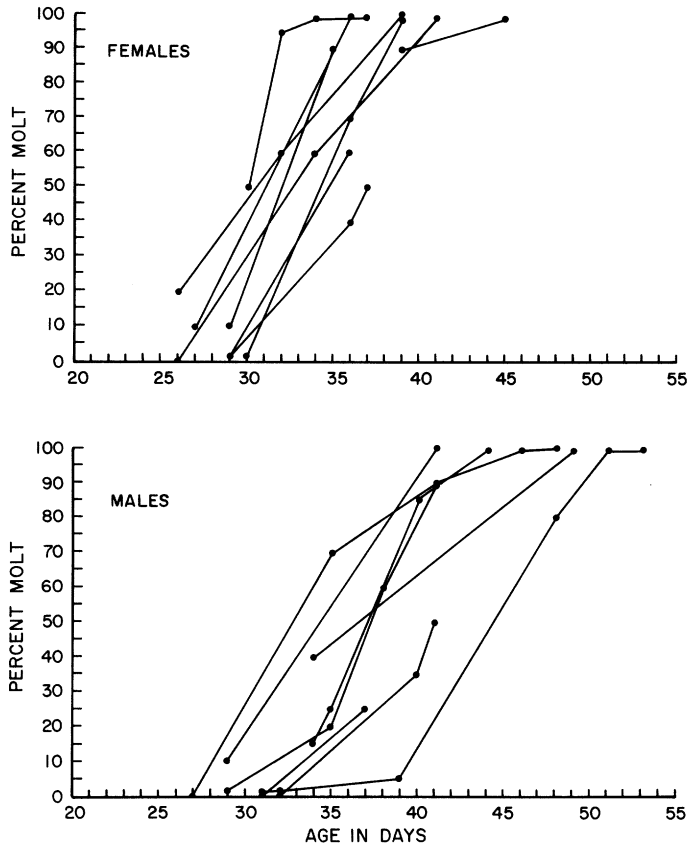


Fig. 4. Percent molt as a function of age. Each line represents an individual; each black circle represents an estimate of percent molt

the mean weight of males was 144.09 kg ($\pm$34.79) and that of females was 128.19 kg ($\pm$18.84). However, this difference is not statistically significant ($t=$ 1.56, $df=28$, $P>0.05$). Nine pups were weighed within four days of being weaned. The mean weight was 134.07$\pm$15.65 kg. The mean weight of five males was 137.53$\pm$19.30 kg; the mean weight of four females was 129.73$\pm$10.55 kg. Orphaned pups weighed separately rarely exceeded 68 kg. Some moribund orphans weighed as little as 26 kg at 4 weeks of age.

The mean weights of weaned pups on Año Nuevo Island are higher than those obtained on 4- to 7-week-old pups sampled on San Miguel Island in 1977 (Le Boeuf et al., 1976). On San Miguel Island the mean weight of 30 males exceeded that of 30 females, 133.21$\pm$26.62 kg to 115.29$\pm$29.27 kg. This difference is statistically significant ($t=2.48$, $df=58$, $P<0.05$).

It is important to emphasize that many variables cause fluctuations in weaner weights. A very large number must be sampled to derive reliable and valid estimates. Our sample on Año Nuevo Island was too small to yield confident estimates of the population parameters. These data should be considered preliminary estimates.

Superweaners. In nearly every year, we observed a few exceptionally large weaners on Año Nuevo Island as well as on other large rookeries. These animals were so large that their corpulence impeded their movements. All of these supernormal weaners were males. The only superweaner we succeeded in weighing was fully molted, i.e., he was at least 35–40 days old and weighed 238 kg. Others we observed through the years appeared to be in the same weight category. Observations of two of these animals, one in 1974 and one in 1977, revealed that their size was due in large part to being successful at acquiring additional milk after being weaned by their mothers.

Weight Loss in Fasting Weaners. While a few pups increased or maintained their weight after weaning due to receiving additional milk, the majority of weaners lost weight during the 8- to 12-week stay on land after weaning. When pups stop suckling, they apparently stop feeding altogether. We never saw feeding during the $2–2^1/_2$ months that weaners remain on the rookery before going to sea. In a concomitant study by Ortiz et al. (1978), repeated weights were obtained on five pups for several weeks after weaning. The average weight loss per pup ranged from 0.58 to 0.87 kg per day and was accompanied by a decrease in girth. This same study yielded physiological data consistent with the hypothesis that weaners do not feed while in the water during the postweaning period before they leave the rookery; they obtain all necessary fluids from catabolization of fat stores. Ortiz et al. (1978) estimated that weaners lose approximately one-half of one percent of their body weight per day. Thus, approximately one-quarter of their body weight at weaning is lost by the time they depart from the rookery.

4. Activity and Social Behavior on Land

Prior to weaning, pups rarely interact with anyone but their mothers. This is probably because interactions with other pups might lead to separation from the mother or to being bitten by another pup's mother. Social interactions with other weaned pups are first seen in the few days following weaning when the pup leaves the harem and joins a weaner pod. Rasa (1971) described social behavior and object manipulation in weaned pups on Año Nuevo Island during the 1970 breeding season. We made daily observations of weaned pups from 15 January to 1 April, 1974. For each social interaction observed between two weaners, we recorded the sex of the actors, the manner in which the bout began and ended, and time of day and the duration of the episode. We summarize briefly our findings and those of Rasa (1971).

One can readily distinguish two types of social interactions on land which we will call space arguments and mock fights. The first type lasts only a few seconds and involves altercations over personal space. As one animal moves, the disturbed neighbor typically reacts with an open-mouth raspy growl or a sharp high-pitched cry. The other weaner may respond in kind and the pair erect their vibrissae and make quick, jerky head feints as if to strike a blow or defend against one. These 'head banters' may be interspersed with nipping

Table 2. The relative frequency of behavioral components in social interactions displayed by male and female weaners. There was an equal number of males and females when the observations were made

Sex	Head banters	Bites	Neck grabs	Neck presses	Rear and slams	Totals
Male	98	32	151	25	39	345
Female	60	13	9	2	1	85
Totals	158	45	160	27	40	430

and biting. These short encounters end when the moving weaner stops, passes by, retreats, or lowers its head. This type of argument is observed in the youngest and oldest weaners. The context in which these interactions occur and the behavior of the participants is similar to the behavior seen in a dense aggregation of breeding females.

Mock-fight interactions are the other type of weaner social behavior observed. These last from a few seconds to several minutes with the longest bouts lasting 10–15 min. Mock fights increase in frequency, in the complexity of the repertoire exhibited, and in the coordination of movements as the weaned pups mature over the 4-week period following weaning. The repertoire is complete and the movements well-coordinated by the time pups are 6–7 weeks old. Three different elements are readily distinguished and a bout may include one or more of these as well as head banters and bites. A 'neck grab' is a prolonged bite to the neck, head, or foreflippers of another weaner. 'Neck presses' usually occur after an interaction is in progress and involve both weaners lifting their heads and pushing against each other's necks. If one weaner is momentarily down, the other may bounce its head and neck on the neck of the supine individual. The 'rear and slam' tactic requires the greatest coordination. One weaner lifts its head and tail so that its body assumes a U shape. It rocks back and forth, then slams the weight of its head and forequarters down against its opponent. These elements in mock-fight interactions resemble the components of fighting behavior in adult males except that the movements of pups are slower and more exaggerated.

Rasa (1971) noted that females were most frequently involved in brief space encounters either with other females or other males. In contrast, prolonged mock fights lasting one minute or longer occurred between two males, or less frequently, between a male and a female, never between two females. In heterosexual bouts, it was always the male that initiated the interaction and he did this by biting the female's neck. Females only performed male behaviors like neck grabs when interacting with a male. Rasa concluded that the motor patterns exhibited by weaners in these two types of interactions are similar to those found in adults of the respective sexes and that these sex differences are apparent from the time that social behavior is first displayed.

Our observations corroborated those of Rasa. In addition, we determined the relative frequency of behavioral components of social interactions employed by males and females. Table 2 shows that: (1) Males exhibited more of each

behavioral component in the weaner repertoire than females. (2) Males displayed 95% of the behaviors that resemble components of adult male fighting, i.e., neck grabs, neck presses, and rear and slams. Females rarely exhibited these behaviors. (3) The behavioral component most frequently exhibited by males to opponents was the neck grab (43.7% of the time). (4) Females most frequently exhibited head banters (70.5% of the time). (5) The majority of female behaviors observed, head banters and bites, resemble the aggressive behavior of adult females.

Since males were most frequently involved in social interactions, they initiated more bouts than did females. Moreover, females differed from males in that they more often declined to interact.

When not interacting with other pups, weaners on land frequently explored and mouthed objects around them, such as clumps of seaweed, stones, or flotsam of similar size lying on the beach. Sometimes, in the absence of anything else, the animal may inspect the substrate or one of its own foreflippers. Weaners were especially attracted to moving objects such as gulls flying overhead, people walking by them, dangling objects, or their own bodies. They often bent the head over the back at a sharp angle and, upside down, stared at objects directly behind them. For example, they showed intense interest in a piece of cord or string swaying overhead in the wind. The typical response was to lift the head high, rocking back on the hindquarters (as in mock fighting) while reaching up for the object with the mouth. A typical weaner also spent several minutes a day bending its head back over its body in a U shape, trying to bite its own tail. These behaviors, like social interactions, occurred most frequently in the early morning or late afternoon before the animals started to spend a substantial part of their time in the water.

Sand flipping was the most ubiquitous activity of weaners. This behavior is characteristic of elephant seals of all ages. Sand is scooped up with the foreflippers and flung backward onto the back. This activity is seen throughout the day and night. It occurs most frequently when the animals are stressed, whether by heat (White and Odell, 1971) or by man or other seals (Heath and Schusterman, 1975).

5. Transition from Land to Water and the Development of Swimming and Diving

Weaned pups begin to move down to the water when they are 6–$7^1/_2$ weeks old. Because of their great bulk, they move slowly and rest often; moving only about 2–3 m at a time. Most weaners experience their first contact with the water by following older weaners with whom they are interacting. The presence of weaners in or near the water stimulates others to follow. Sometimes, we saw as many as eight weaners in a line moving toward the water. Thus, the time of initial water entry by an individual is subject to social faciliation. The later in the season a pup is weaned, the shorter the latency to enter the water because other weaners already in the water serve as a stimulus.

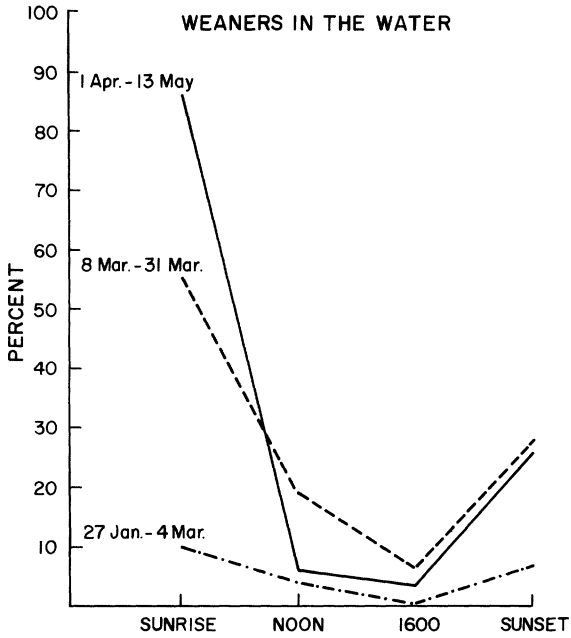


Fig. 5. Weaners are observed in the water at sunrise and sunset. This pattern becomes more pronounced as the animals get older

The first individuals to approach the water do so with great curiosity and interest. At first, a weaner goes no further than the splash zone. When a wave washes up and its ventrum gets wet, the weaner typically noses or perhaps smells the water. On the first day or two out, it does little more than get its belly wet while lying on the wet sand or wallowing in tidepools. Usually, a weaner spends a short time near the water inspecting objects, trying to bite its tail, or mock fighting with another weaner before moving into the shallow water or back up the beach to rejoin a weaner pod to sleep for the remainder of the day.

Censuses taken four times daily throughout the 1974 breeding season reveal a crepuscular movement pattern to and from the water (Fig. 5). This figure also shows that this daily pattern persisted until April and May, the time when most weaners depart the rookery. It shows that an increasing percentage of weaners on the beach move to the water daily as the season progresses.

Once a weaner begins to visit the water, it usually does so twice a day. With each successive day, the weaner becomes more accustomed to the new medium. It puts its head underwater, begins to thrash about in the shallows, and spends increasingly more time near the water's edge. About 1–2 weeks after first approaching the water, the weaner becomes sufficiently familiar with the new environment so that it ventures out beyond where it is touching bottom and it begins to make short dives lasting several seconds.

Its initial swimming attempts are clumsy and uncoordinated. Adult elephant seals propel themselves in the water by a side to side skulling movement of

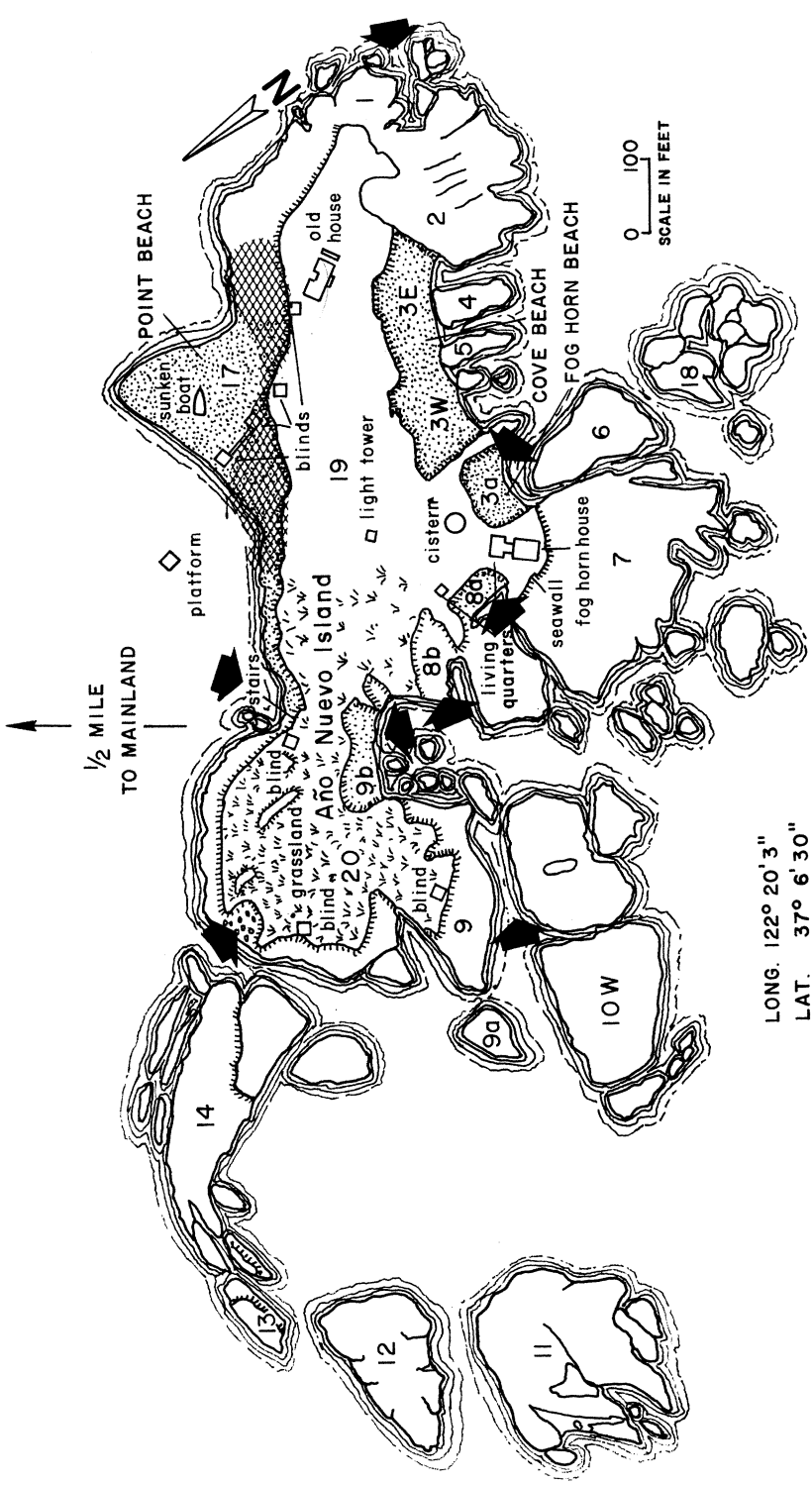


Fig. 6. A schematic map of Año Nuevo Island showing the principal harem on the Point Beach. Flanking areas are cross-hatched and remote areas that weaned pups frequented are indicated by arrows

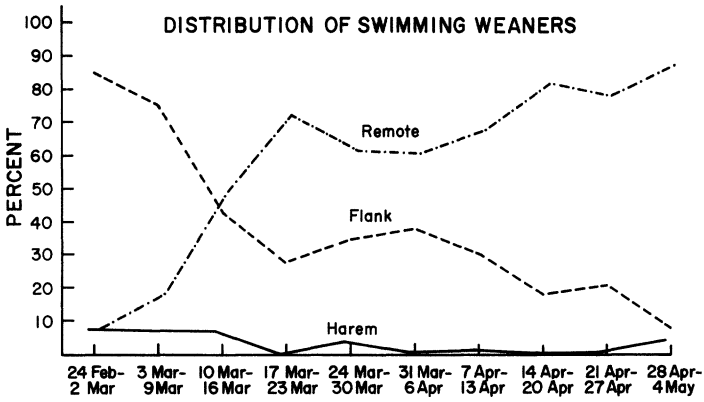


Fig. 7. As weaners mature they swim into increasingly remote areas from the harem site where they were born

the hindflippers. When weaners are learning to swim, their entire torso as well as the hindflippers moves from side to side vigorously, and this occurs near the surface of the water. The result is a great deal of thrashing about, splashing, wasted effort, and only a short distance is covered. However, improvement in swimming is rapid. After only a week's practice, movements in the water become coordinated and effortless. They become adept at swimming upside down, floating in the water with the head up or belly up, and diving in a circle. As novice swimmers, weaners usually remain underwater for only a few seconds or a minute or two, at most. When they have been swimming for 2–3 weeks, they begin to dive for several minutes and sleep underwater for up to 7 min. When they have been swimming for five weeks, they typically sleep for 10–15 min underwater.

As swimming proficiency increases, weaners begin to venture to other beaches and coves on the island which are relatively free of adults. Two changes in the population of weaners on Año Nuevo Island were apparent as the season progressed: (1) the weaners moved further from the female harems when resting on land, and (2) as they became more proficient in the water, they swam further from the point of initial water entry near the harem. We quantified their movements by following marked weaners born on Area 17, the principal breeding beach, and by taking daily censuses of all areas on the island. We classified areas of the island into three zones defined by differences in geography, and density of adult animals and suckling pups (Fig. 6). We defined the harem area, Area 17, as the principal breeding beach containing adult males and females, the birthplace of pups, and the initial location of weaner pods. We did not monitor pups born on the other breeding beach, Area 3, as fewer than 10% of the pups produced on the rookery were born there. Peripheral areas providing access to the water on both sides of the harem on Area 17 were called flanking areas. Flanking areas contained subadult and adult males but few females and pups. Remote areas were defined as all areas that weaners could reach only by swimming. Figure 7 shows that as weaners matured they spent increasingly more time near areas remote from the harem site of their

birth. Once they were able to swim to remote areas, they tended to haul out and rest there. Adults were rarely observed in these areas and therefore they served as a sanctuary where weaners were rarely accosted by males or threatened by females.

Shortly before they left the rookery, weaners spent as much or more time in the water as on land. They were excellent swimmers when they left the rookery at $3–3^1/_2$ months of age.

6. *Water Entry and Departure as a Function of Date Weaned*

The pattern of development in an individual weaner varies with the time it is born and weaned. To facilitate understanding this aspect of weaner development, we identified three groups of pups according to when they were weaned during the 1974 breeding season. Pups weaned early in the season between 17 January and 4 February ($n=65$) were classified as the Early Group. Those weaned in midseason between 5 February and 20 February ($n=187$) were called the Middle Group. The Late Group consisted of pups weaned between 21 February and 8 March ($n=97$). Animals in each group were marked individually and their movements and location noted daily until they left the rookery.

The context in which weaners from each of the above categories were born, nursed, and weaned differed considerably. Early Group pups were born in a harem containing few females and pups but they were weaned when the harem was most crowded (Fig. 1; see also Fig. 3 in Le Boeuf and Briggs, 1977). Being the first pups weaned, they had only themselves to consort with at this time. Weaners in the Middle Group were born when the harem was approaching peak size and weaned during the time of greatest breeding activity. There were many others weaners grouped in weaner pods at the time they were weaned and weaners in the Early Group were beginning to go to the water. Pups in the Late Group were born in a crowded harem that was decreasing in size daily and were weaned when there were only a few females left on the beach. However, at this time there were several hundred weaners in weaner pods and in the water, many of them already proficient swimmers.

The relationship between time of weaning, initial water entry, and departure from the rookery is shown in Table 3. The data are based on individuals within each group on which the most complete data were available. This table shows that weaners born early in the season were slower to enter the water than

Table 3. Mean interval in days ($\pm$one standard deviation) between events in the development of pups born and weaned at different times in the breeding season. The number of animals on which each statistic is derived is in parentheses

	Early group	Middle group	Late group
Weaning and water entry	24.8 ± 8.3 (20)	15.6 ± 8.8 (15)	13.8 ± 8.3 (16)
Water entry and departure from rookery	49.3 ± 10.9 (19)	54.4 ± 10.7 (14)	42.0 ± 14.2 (14)
Weaning and departure from rookery	73.5 ± 7.6 (26)	70.0 ± 8.1 (20)	55.6 ± 13.2 (20)

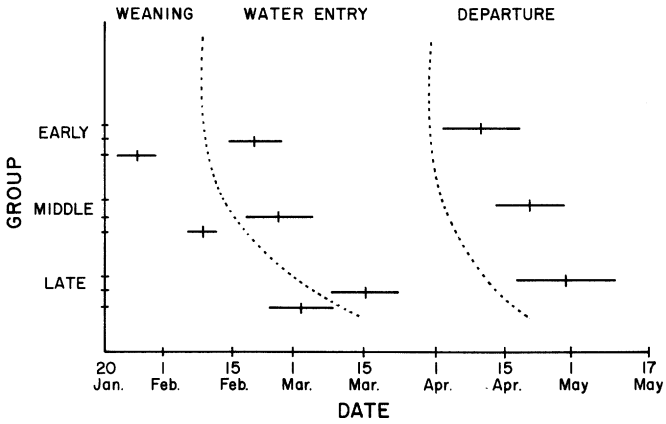
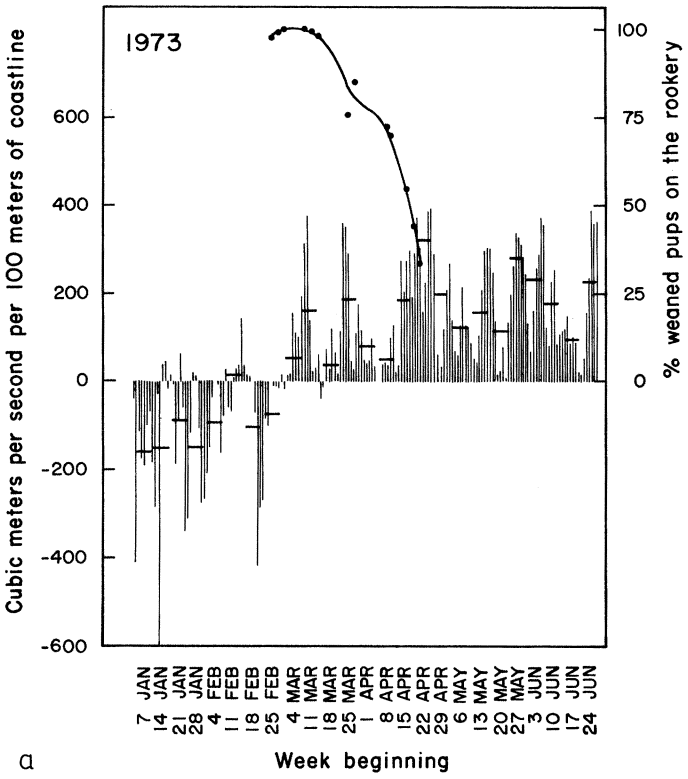


Fig. 8. Means (vertical mark) and standard deviation (horizontal line) of the time that Early, Middle, and Late groups of weaned pups were weaned, entered the water, and departed the rookery

those born later in the season ($F=8.86$, $df=2, 48$, $P<0.05$). After entering the water, weaners in the Early Group swam an average of seven weeks, those in the Middle Group, eight weeks, and those in the Late Group only six weeks before leaving the rookery. That is, members of the Late Group spent less time in the water before leaving the rookery than members of the other two groups ($F=3.86$, $df=2, 44$, $P<0.05$). Finally, the mean number of days spent on the island after weaning varied significantly from approximately eight weeks in members of the Late Group to $10^1/_2$ weeks in members of the Early Group ($F=20.19$, $df=2, 63$, $P<0.05$). By plotting the means and standard deviations for each group against time (Fig. 8), it is evident that the early discrepancy in time of weaning became greatly attenuated by the time the animals departed the rookery. That is, although the majority of pups were weaned during an 8-week interval, departure from the rookery occurred during a 3-week interval.

The departure of the majority of weaners from the rookery in a short period of time coupled with the fact that they had been fasting for $8–10^1/_2$ weeks suggested to us that departure might be triggered by some environmental stimulus such as abundance of prey. Since it is well known that coastal upwellings along the west coast of North America result in enrichment at the very base of the food chain, and through complicated interacting biological processes and a time lag, this phenomenon has important effects on fishery resources, we looked for a correspondence between upwelling indices and the time weaners departed the Año Nuevo Island rookery.

The procedure for calculating upwelling indices relies on measurements of synoptic surface atmospheric pressure fields and is presented in detail by Bakun (1973). The area closest to Año Nuevo Island measured by Bakun (1975) is located at 39°N Lat, 125° W Long, an area off Cape Mendocino, California. The correspondence between upwelling and a frequency distribution of weaner departures from the rookery is shown in Figure 9 for the years 1973, 1974, and 1975. It is evident that weaners begin to leave the rookery at approximately the same time as the initiation of coastal upwelling. Moreover, they remain


1973
Cubic meters per second per 100 meters of coastline
% weaned pups on the rookery
600
400
200
0
-200
-400
-600
100
75
50
25
0
7 JAN
14 JAN
21 JAN
28 JAN
4 FEB
11 FEB
18 FEB
25 FEB
4 MAR
11 MAR
18 MAR
25 MAR
1 APR
8 APR
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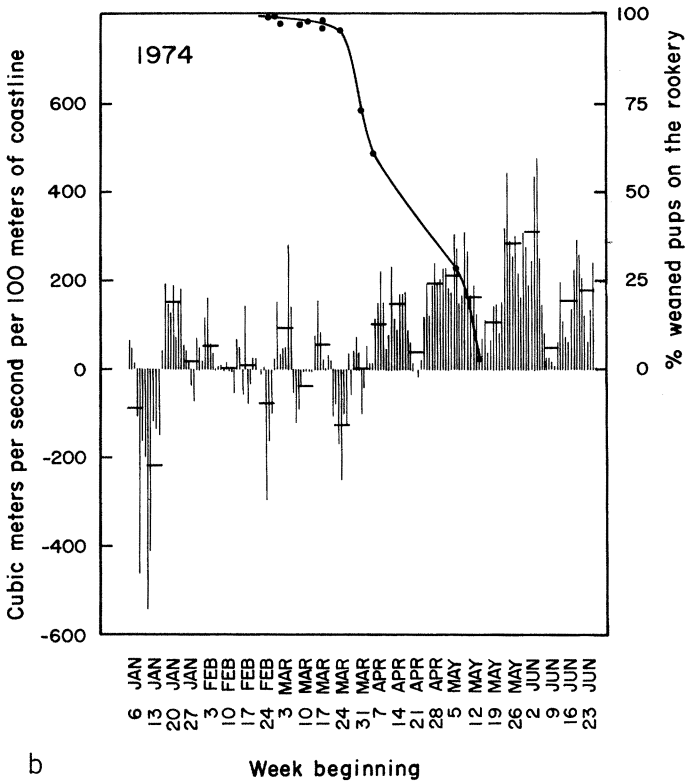
22 APR
29 APR
6 MAY
13 MAY
20 MAY
27 MAY
3 JUN
10 JUN
17 JUN
24 JUN
Week beginning

a


1974
Cubic meters per second per 100 meters of coastline
% weaned pups on the rookery
600
400
200
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-200
-400
-600
100
75
50
25
0
6 JAN
13 JAN
20 JAN
27 JAN
3 FEB
10 FEB
17 FEB
24 FEB
3 MAR
10 MAR
17 MAR
24 MAR
31 MAR
7 APR
14 APR
21 APR
28 APR
5 MAY
12 MAY
19 MAY
26 MAY
2 JUN
9 JUN
16 JUN
23 JUN
Week beginning

b

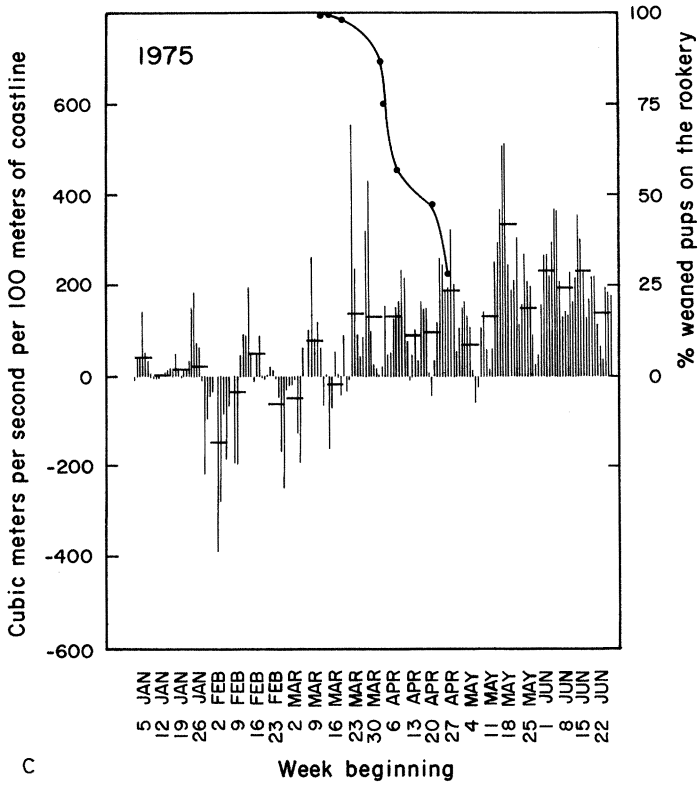

Fig. 9a–c. Daily (vertical lines) and weakly means (horizontal bars) of upwelling index computations in relation to percentage of weaned pups (back circles) remaining on the Año Nuevo Island rookery relative to the total produced in 1973, 1974, and 1975. The curves of weaner departure are fitted by inspection. The units for measuring upwelling are metric tons per second per 100 m of coastline. Values above zero indicate upwelling. Measurements were made at 39° N Lat, 125° W Long

at sea throughout the period of upwelling and do not return to Año Nuevo Island or to nearby Southeast Farallon Island until the fall (Le Boeuf et al., 1974), the time when the upwelling period ceases (Bakun, 1973, 1975).

7. Injuries and Weaner Mortality before Leaving the Rookery

Nearly all pup deaths occur within two weeks after birth (Le Boeuf and Briggs, 1977). Less than 1% of pups weaned in good condition die during the $2^1/_2$-month period before they leave the rookery. The mortality rate among weaned pups on Año Nuevo Island has been approximately one in every 250 pups weaned in recent years. Mortalities in this age category appear to be somewhat higher in the extreme southern part of the range and may be related to high temperatures. On periodic expeditions to Isla de Guadalupe we saw several fat, dead, weaned pups without any external wounds. The location of these corpses, inland from the harem, leads us to suspect that they may have died from overheating.

Fig. 10. A subadult male, approx. 6 years of age, bites a weaned pup on the head as a preliminary to mounting it. This can cause severe injury to weaners and they struggle hard to escape

On very hot days, females and their pups move slowly to the water's edge where they lie on wet sand and are exposed to sea spray. Weaned pups may have difficulty moving through the aggressive females to the water and, thus, they are forced to remained exposed to the hot sun throughout the day. Given their thick layer of blubber (approx. 7.5 cm), it is likely that they experience great difficulty keeping cool.

Several sources of injury leading to weaner mortality were observed directly at several rookeries during the study period. These included: (1) head wounds incurred while being sexually accosted by subadult and adult males (Fig. 10), (2) bites on the head inflicted by adult females, (3) death due to accidents such as falling down cliffs or getting stuck between holes in rocks, (4) storms with attendant high surf caused injuries and death by drowning or by dashing weaners on the rocks, and (5) predators, such as great white sharks and killer whales, killed some weaned pups before they departed the rookery.

8. Survival after Going to Sea

Weaned pups go to sea during the spring (Fig. 1). They disperse northward and many of them feed off the coast of northern Washington (Le Boeuf, unpublished data). The majority of them do not reappear on land until the following September. They rest on land during the fall until the beginning of the breeding season in early December, at which time they return to sea and remain there

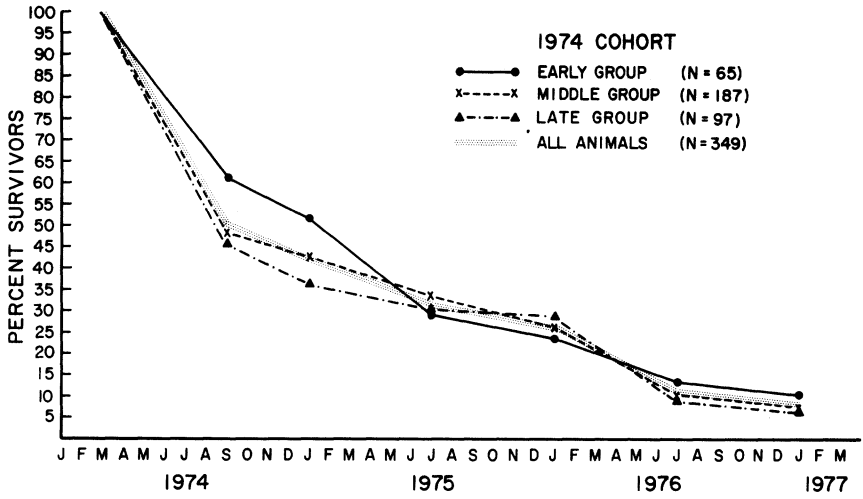

Fig. 11. Minimal return rates for pups weaned in 1974

until the end of the breeding season. Evidence from tagged animals reveals that pups born on Año Nuevo Island return to this island or to nearby Southeast Farallon Island during the fall after their first stay at sea (Le Boeuf et al., 1974). Observations during the study period corroborated this finding. Periodic observations of rookeries to the south revealed few tagged seals, less than 3 years of age, that were born on Año Nuevo Island. However, animals tagged on southern rookeries were often seen on rookeries to the north.

By monitoring returning tagged animals on Año Nuevo Island and Southeast Farallon Island, we obtained a minimal estimate of survival or its reciprocal, a maximum estimate of mortality. The survival estimate must be considered minimal because: (1) some tagged animals may have been present but were not observed, (2) some animals may have deviated from the pattern of the majority and stayed at sea, (3) some animals hauled out on the mainland, and (4) some animals may have lost their tags.

Clearly, the validity of the survival estimate based on a tag-recapture study is a function of the intensity and thoroughness of the search for tagged animals. We recorded all tag recoveries on Año Nuevo Island and the adjacent mainland daily during each breeding season in the study period and approximately once a week during the rest of the year. The ease of reading tags varied with the time of year due to fluctuations in group composition and density. Harriet Huber and colleagues from the Point Reyes Bird Observatory recorded tagged animals daily throughout the year on Southeast Farallon Island. Although our search for tagged animals was intensive, we missed reading the tags of some animals that could not be approached. We estimate that the number of animals whose tags could not be read or the number of animals that did not appear on land was low but we cannot quantify this estimate. Tag loss was estimated to be less than 5% (see Le Boeuf, 1974).

Minimal return rates for pups born in 1974 are presented in Figure 11. Pups born during the early, middle, or late parts of the breeding season are

plotted separately. At least 50% of the marked pups in the cohort survived to 1 September 1974 after going to sea, i.e., to 7 months of age. Thereafter, the percent of seals sighted declined with time. With additional observations, more marked animals will be seen that were not previously observed and this will permit revision and improvement of the 'survival' curves up to the third year of life.

Relative to the number of pups *born* in 1974, the minimal survival rate to 7 months of age is 42.1%. This is based on the observation that 15.8% of the 480 pups born in 1974 died on the rookery before weaning (Le Boeuf and Briggs, 1977).

There were no sex differences in resighting tagged seals up to 2 years of age. During the third year, more females than males were observed because some females reach reproductive maturity at this time and, as a result, they appear on the rookeries and can be identified while most males of comparable age remain at sea. For example, 26 females in the 1974 cohort (15.4% of the females weaned) were present on Año Nuevo Island, the Año Nuevo mainland, or Southeast Farallon Island during the 1977 breeding season, whereas only three males were observed (1.8% of the males weaned).

Figure 11 also shows that pups weaned early in the season were observed in greater numbers at 7 months of age and at 1 year of age than pups weaned subsequently. The difference at 7 months of age is statistically significant ($\chi^2=4.15$, $df=1$, $P<0.05$); the difference at 1 year of age is not ($\chi^2=2.66$, $df=1$, $P>0.05$). Beyond 1 year of age even the small differences between the groups disappear.

It is interesting to note that 17 females (10.1% of those weaned in 1974) gave birth in 1977. The Early-weaned group had the highest parity rate (15.6%) followed by the Middle Group (8.9%) and the Late Group (8.5%). These differences are not statistically significant ($\chi^2=1.36$, $df=2$, $P>0.05$) but the higher figures for the Early Group are worth noting. Fourteen females gave birth on Año Nuevo Island or the adjacent mainland and three gave birth on Southeast Farallon Island. An additional nine females appeared on Año Nuevo Island during the 1977 breeding season in a nonparous condition (5.3% of the females in the 1974 cohort). One of these females was in the Early-weaned group, six in the Middle Group, and two in the Late Group.

Minimal return rates for the 1975 cohort ($n=448$) are more incomplete than the 1974 data, since less time transpired and, hence, less effort was expended in searching for tagged animals. Nevertheless, a few points deserve mention: (1) the return rate to 7 months of age was 29.2%, much lower than in 1974, (2) as in the 1974 cohort, there were no sex differences in returning animals during the first two years of life, and (3) the Early-weaned group, as in 1974, showed a higher return rate at 7 months of age (Early Group=40.7%, Middle Group=25.0%, and Late Group=29.2%, $\chi^2=6.32$, $df=1$, $P<0.05$) as well as at 1 year of age (Early Group=25.9%, Middle Group=18.1%, and Late Group=16.7%, $\chi^2=9.86$, $df=1$, $P<0.05$). As in the 1974 cohort, these differences tend to disappear with time but more data are needed to verify this trend.

Discussion

The most significant findings that emerged from this study are differences between the sexes during early development. These differences can be viewed as evolved elements in the long-term reproductive strategies of each sex. Consideration of this perspective will be aided by a brief review of the reproductive strategies of adults.

Adult males and females maximize their reproductive success in quite different ways. The optimal strategy of males is to inseminate as many females as possible. A male does this by dominating his rivals and preventing them from gaining access to females. The most successful males are always full-grown adults, usually 10–12 years of age, who are large and aggressive. One or a few males monopolize breeding around a harem of females; a successful male may sire over 250 pups in a lifetime while most males breed little or not at all. Thus, males concentrate their reproductive effort into one or a few breeding seasons when they are in prime condition to compete effectively, there is great variation in reproductive success among them, and each individual has great reproductive potential (Le Boeuf, 1974). In contrast, females distribute their reproductive effort throughout most of their lives. Since it takes an entire year for a female to gestate a single pup and nurse it to weaning, a female leaves maximal offspring by maturing rapidly (primiparity normally at age 3 and occasionally at age 2), consistent reproduction (being pregnant 11 months of the year throughout most of her life) and living long (approx. 14 years). Virtually all females are impregnated annually during a postpartum estrus, but the most pups one individual can bear in a lifetime is about 11. Compared with males, there is little variation in reproductive success among females and the reproductive potential of an individual is low (Le Boeuf et al., 1972; Le Boeuf and Briggs, 1977). If one considers offspring sex in this species as a parental wager for leaving maximum genes in future generations, a male offers the possibility of a high risk with a high gain while a female provides a low risk with a correspondingly low return.

Our findings reveal that pups of both sexes embark early on their respective reproductive strategies. Sexual differentiation with respect to size and social behavior is most obvious. Male pups are larger at birth and at weaning than females and this relationship is still evident when they leave the rookery to go to sea for the first time. Males are weaned one full day later than females, more males than females attempt to obtain additional sustenance after being weaned, they work harder at it, and they are more successful than females. Extremely large weaned pups are always males. These differences are consistent with adult reproductive strategies. Because of the wide discrepancy between the sexes in reproductive potential, slight advantages in size or condition might be expected to result in disproportionate effects on male reproductive success compared with the effects on female reproductive success (Trivers and Willard, 1973). If a male outweighs his cohorts early in life and this size advantage is maintained to adulthood, he will have an edge in the aggressive competition for inseminating females. Indeed, the nursing period is an optimal time to

obtain an advantage in size and condition over competitors because this is when the rate of growth is most rapid. During this relatively brief period, elephant seals can increase their birthweight by a factor of 3–7 times by feeding on mother's milk that averages 55% fat (Le Boeuf and Ortiz, 1977).

Moreover, securing additional milk after weaning provides an excellent opportunity for an individual to obtain an advantage over others because it prolongs the growth period at a time when the majority of weaned pups in the cohort are fasting and losing weight daily. Milk thieves do not simply derive a weight advantage by putting on more fat, they obtain proteins, calcium, vitamins, and other elements from milk which are essential for muscle, tissue and bone growth.[1] Our results show that females do not risk injury to steal milk as readily as do males. This suggests that selection for great size is less intense in females than in males. This is not to say that size is not important in female-female competition. Indeed, the fattest female pups may become the biggest mothers and bigger mothers are better than smaller mothers at insuring the survival of their pups (Ralls, 1976; Christenson and Le Boeuf, 1978). However, this reproductive benefit is small compared with the gain in fitness achieved by a male that dominates breeding for an entire breeding season or more. The extreme sexual dimorphism characteristic of this species lends further support to this argument.

The finding that molting and canine eruption occur later in the development of males than females may be, in part, adaptations that facilitate milk stealing in weaned pups and prolong growth. Since unmolted weaners have the same color pelage as suckling pups, the resemblance may facilitate the former's efforts to remain in the harem after weaning or to reenter it after weaning. This might give them an edge in avoiding detection while attempting to suckle females. Female pups begin molting prior to the milk-stealing period (the week after weaning) while males molt during it or after it is over. If pelage mimicry confers an edge in stealing milk, the males would have it. Although we have no quantitative data confirming that black-coated weaners are more successful milk thieves than molted silver-coated weaners, we strongly suspect that this is the case. Males may have been subjected to more intense selection to delay canine eruption than females for the same reason. If we assume that a toothsome suckling stimulus is aversive and more readily commands the attention of a nursing female than does a toothless stimulus, the latter would be more likely to detect a parasitic weaner with teeth than one without. Blaxter (1961) notes that the canines of piglets and the incisors of calves and ewes often cause lacerations of the teats during nursing; in farm practice, the canines of piglets are often removed. Moreover, elephant seal pups often nip their mother's side to urge them to adopt the nursing position, particularly during the last week of suckling. Milk thieves will also do this to nursing females sleeping on their bellies. The female often rolls over into the nursing position without bothering to check that it is her own pup prompting her to nurse. If a mother has

[1] Despite the close match between our findings and our logical expectancies, we do not yet know the relationship between size and condition at weaning and reproductive success among males. It will take several years to determine empirically whether the fattest are the fittest

been nursing a toothless pup for several days and suddenly she is nipped by a set of incipient canines, the difference should stand out in sharp relief and cause her to investigate. Thus, the sex differences in the time of molting and canine eruption suggest that males, more so than females, have been selected to pursue a growth strategy, even at great risk, and particularly during the nursing period and shortly thereafter. We have purposely restricted our analysis to ultimate factors; we are aware that numerous proximate factors may influence these morphological sex differences.

Sexual differentiation in social behavior is also apparent soon after weaning. Young males become involved in more social interactions than do females, they initiate more mock fights, and interactions between males last longer than those involving two females. To a remarkable degree, males exhibit the most prominent components of fighting in adult bulls while females exhibit the basic elements commonly observed in quarreling adult females. Evidently, the fitness of individuals of both sexes is enhanced by being aggressive, but as is the case in competing for an edge in size and condition, the ultimate reproductive gain would appear to be greater for males than females.

Sex differences are notably absent in behaviors that do not influence sexual selection directly, e.g., latency to enter the water, acquisition of aquatic skills, initial exploration of the water and shoreline, time of departure from the rookery, and survival to 2 years of age.

While a growth and aggressive strategy appear to enhance the fitness of developing males, and less so, developing females, it must also enhance the fitness of their parents, If a parent, especially the mother in this highly polygynous species, can do something to get her pup started on a beneficial strategy in life, she will enhance her offspring's fitness as well as her own. Therefore, to fully understand long-term reproductive strategies, we must investigate how selection acts on the mother as well as on the developing individual. For example, it seems that there is an optimal time for a female to give birth to maximize her pup's size and condition when it leaves the rookery. Mothers should be selected to give birth early in the season when their offspring have the opportunity to steal milk after their departure. Pups weaned late in the season cannot steal milk because there are no nursing females left on the rookery. It should be to a female's advantage to give birth early in the season no matter what the sex of her offspring, but it is obviously most important if she is bearing a male pup. Females should compete to give birth at this optimal time and we would expect large females in their prime to win out in this competition. Preliminary results support this prediction and show that the youngest females tend to give birth late in the season and in inferior locations (Le Boeuf and Panken, 1977).

In conclusion, differences in size, condition, and social behavior in early development appear to have an important influence on reproductive competition in adulthood. Conversely, it is the consequences of reproductive competition in adulthood that select for the appearance of certain behavioral and morphological traits and sex differences in early development. The pattern of development subserves and is shaped by reproductive competition.

Acknowledgements. We thank numerous colleages for assistance in the field, especially: M. Bonnell, S. Cantrell, D. Costa, R. Gisener, A. Hoover, C.L. Ortiz, K. Panken, J. Perlsweig, M. Pierson, M. Reidman, K. Skaug, and B. Tyler; D. Ainley and H. Huber and colleages from the Point Reyes Bird Observatory for providing information on tagged animals sighted on Southeast Farallon Island; K.T. Briggs for helpful suggestions; M. Sylvan for statistical advice. We thank K. Panken for allowing us to report data she helped to collect on sex differences in weaning age and weaner adoption. Supported in part by National Science Foundation grant BNS 74-01363 AO2 to B.J. Le Boeuf.

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