

FEMALE COMPETITION AND REPRODUCTIVE SUCCESS IN NORTHERN ELEPHANT SEALS

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Abstract. The probability of weaning a healthy pup increases with age in female northern elephant seals, *Mirounga angustirostris*. On Año Nuevo Island, California, weaning success among 'prime' females, those 6 years of age or older, was more than double that of 'young' females, those 3 to 5 years old. Prime females were better mothers than young females because of superior size, higher social dominance, and greater maternal experience; they were more likely to mate with high-ranking males and gave birth at an optimal time and place, circumstances that maximized the probability that their pups would survive, develop, and reproduce. The competitive advantage of prime-age mothers over younger ones was greatest when female and pup density was high. Young females improved their chances of reproducing successfully by emigrating from crowded harems and establishing new colonies.

Introduction

The key to understanding sexual selection, the evolution of mating systems, and much of the individual behaviour of organisms is to determine how individuals of each sex maximize their reproductive success. It is especially important to determine how females maximize their reproductive success because in most animals they are the limiting sex (Trivers 1972); the net reproductive output of a species, a population, or a colony is limited by the number of females that reproduce.

Data on reproduction in long-lived mammals are especially difficult to collect because of their long generation time. Evidence is meagre or incomplete about the developmental patterning of reproductive effort and reproductive success, obtained through long-term monitoring of the reproductive success of offspring.

The aim of this study was to determine the factors that influence variance in reproductive success of female northern elephant seals, *Mirounga angustirostris*. We focused on variables that affect a female's ability to obtain the best genotype for her pup and those that affect her ability to feed, protect, and provide the optimal milieu for her pup's birth, growth, survival, and eventual reproductive success. Some of these variables are (1) the influence of age and its correlates: size, experience, and aggressive dominance; (2) the role of social and populational factors such as female density and overt intrasexual competition; and (3) the effect of physical factors such as weather and the topography of the parturition site. Once we have presented data bearing on these points, we will consider the consequences of reproductive competition between females for

dispersal and the establishment of new breeding colonies.

Northern elephant seals are polygynous, extremely sexually dimorphic marine mammals that breed on land in dense aggregations. Previous studies have shown that there is considerable variance in male reproductive success and only negligible variance in female reproductive success when one considers reproductive success over a lifetime (Le Boeuf et al. 1972; Le Boeuf 1974). Most males do not exhibit maximal reproductive effort until about 4 years after puberty when they are 8 years old, an age at which they have attained sufficient size to compete aggressively with other males. Only a few males survive to peak breeding age and only a few of the most pugnacious of these monopolize mating. The most successful males may sire over 100 pups in one breeding season alone and over 250 pups in a lifetime. Thus, male reproductive effort is concentrated over a short period late in life, reproductive potential is great, and selection puts a premium on quantity of pups sired. In contrast, the reproductive effort of a female is spread throughout her lifetime. A female first gives birth early in life in the interval between ages 2 and 5, a time when she is still growing. Once she gives birth for the first time, a single pup is produced annually until death, which usually occurs before 14 years of age. Thus, a female's reproductive potential is low, a maximum of 10 to 12 progeny in a lifetime, but virtually all adult females reproduce annually. Moreover, a female may improve the quality of her offspring by mate selection, which affects its genotype and by parental investment during gestation and during the interval between birth and weaning. Clearly, females and males of this

species are selected to increase their reproductive success in quite different ways.

Relevant background material on the reproductive behaviour and biology of northern elephant seals can be found in a number of papers (e.g. Bartholomew 1952; Le Boeuf 1972, 1974; Le Boeuf et al. 1972; Le Boeuf & Briggs 1977; Cox & Le Boeuf 1977; Reiter et al. 1978).

Pregnant females begin arriving on the rookeries in mid-December. They congregate in groups called harems. A harem may be composed of 2 to over 1000 females, their pups, and one or several males, one of which is dominant to all others (Laws 1956; Le Boeuf 1972, 1974). In the early years of research only one male controlled the mating in a harem. Although some of the female groups are now larger than can be reproductively monopolized by a single male, we here retain the use of the term 'harem' for all of these groups. The number of females in a harem reaches a peak in late January and then declines steadily until all females have left the rookery by mid-March. Each female gives birth to a single pup approximately 6 days after arrival. Normally, a female nurses her own pup for about 4 weeks before weaning it by returning to sea. Copulation takes place during the last few days of nursing. Thus, a female's average stay on land is 34 days. Females do not feed or drink or enter the water during this period. This is an astounding feat for a mammal, especially when one considers that pups weigh approximately 40 kg at birth and about 136 kg at weaning. All of this mass gain is derived from mother's milk. We estimate that a female loses over 270 kg during the 4-week period from parturition to weaning.

Materials and Methods

This study was conducted on Año Nuevo Island, California, during the period 1968 to 1980 and on Año Nuevo mainland from 1975 to 1980 (Le Boeuf 1972; Le Boeuf & Briggs 1977; Le Boeuf & Panken 1977). Additional data bearing on this study were collected on an adjacent colony, Southeast Farallon Island, by D. Ainley, H. Huber, and collaborators from 1972 to 1979 (Le Boeuf et al. 1974).

Colony Status and Characteristics of Harems Observed

The principal part of this study was conducted during five breeding seasons, 1976 through 1980. We monitored the reproductive success of known-age females in several harems that varied greatly in number of females, density, age composition

of females, and exposure to flooding at high tide. Our sample of harems is representative of the range of breeding situations seen on other colonies (islands, island groups, or peninsulas) where northern elephant seals breed.

On Año Nuevo Island, we monitored females and their pups on two breeding beaches that have been used annually by elephant seals for the last 19 years (Le Boeuf & Briggs 1977). Each year, one harem formed on each beach. The already large and crowded Point harem increased from 650 females at peak season in 1976 to approximately 1100 females at peak season in 1979. During the last 3 years, crowding on this beach was as great as we have observed on any other island in the northern-elephant-seal range. In contrast, harem density was low on the Cove beach, where the number of females at peak season did not exceed 35 between 1976 and 1979. Thus, the Point harem was large and crowded while the Cove harem was small and uncrowded. Both harems contained females of all ages. Portions of both harems were exposed to high surf at peak season.

The breeding area on the mainland, less than 1 km across the channel from the island, was established in 1975 (Le Boeuf & Panken 1977). In 1976, seven females gave birth in three different locations. By 1980, six harems were in evidence and they contained a total of 150 parturient females. All harems on the mainland were small (containing 62 females or fewer at peak season), uncrowded, and composed almost exclusively of young females. Two of the new harems established in 1979 were exposed to high water at peak season.

In 1973, females began breeding inland of the Point and Cove beaches on the island in the 'Saddle' area. This harem was formed in response to crowding on the other beaches during stormy weather. It contained from 1 to 31 females.

Female Density and Reproductive Success

Harem density, the number of females per unit area of breeding beach, varies as a function of the interaction of three variables: (1) harem number, the number of females in the harem; (2) harem area, the space occupied by females and their pups; and (3) beach utilization, the amount of available beach space occupied by the harem (see Le Boeuf & Briggs 1977). Spacing between females usually ranges from 1 to 2 m to light contact by part of the body. Mutual aggression maintains this spacing until all of the beach area is occupied or the females are forced to get closer

to each other. High density results when harem number increases without a corresponding increase in harem area, or when harem area decreases without a corresponding drop in harem number. As a result, the highest density and, by definition, greatest crowding of females and pups occurs in a large harem on a fully utilized beach at peak harem number when high tide and high surf conditions reduce the effective harem area. This condition may last several hours until the tide ebbs and females spread out once again. Interfemale aggression increases with density (Le Boeuf & Briggs 1977).

We evaluated the effect of female density on reproductive success by (1) plotting the annual percentage of females in the Point harem that weaned their pups successfully as female density increased, and (2) comparing the reproductive success of females in a high-density harem to that of females in low-density harems.

The Point beach was the site of a high-density harem (Fig. 1, Plate I). At peak season (greatest number of females) during 1976 to 1979, the harem contained 650 to 1100 females and 10 to 25 adult males. Females were in prolonged, close physical contact with each other and occupied the entire sandy beach area to the water's edge. Female movement was restricted and many pups were born in the midst of hostile females. Births occurred where crowding was so great that the mother had difficulty turning to face her newborn pup to establish a bond with it.

Low-density harems usually contained fewer than 65 females at peak season and sufficient beach area for the females to avoid physical contact with each other (Fig. 2, Plate II). That is, only a portion of the beach was utilized and the distance between females was usually 1 m or more. All other harems we observed fell into this category. These harems were small enough to be dominated by one bull, who kept all other males out of the harem and usually mated with all of the females.

In order to compare the reproductive success of females on the periphery of a large harem with those in the centre, we defined the periphery as a band, three females wide, around the perimeter of the Point harem. This is approximately equivalent to one-half of the females counted in aerial photographs taken 1 week before and 1 week after the highest female census in 1976 and in 1977.

Ageing and the Identification of Females and Their Pups

We were able to determine the age of 85 to 115 females each year because they bore num-

bered plastic or metal tags permanently attached to their hindflippers 4 to 7 weeks after they were born (see Le Boeuf & Peterson 1969). This sample size represents approximately 10% of the entire population of females that bred in the Año Nuevo region each study year. Since 50 to 90% of the pups born on Año Nuevo Island were tagged annually since 1963, as well as a variable number of pups born on other rookeries (Poulter & Jennings 1966; Le Boeuf et al. 1974; Bonnell et al. 1978), known-age females up to 13 years old could be identified and studied. Each year we bleach-marked (Le Boeuf & Peterson 1969) all accessible known-age females within a few days of their arrival, or as soon as we were able to read their tags. We marked their pups with paint within hours or days after birth. Subsequently, pups were remarked with bleach and tagged at weaning.

Tag reading and identification of marked females and pups was aided by the use of binoculars, spotting scopes, and a Questar telescope.

Estimating Female Size

We measured female size (standard length from nose to tip of tail) in order to correlate this variable with age and reproductive success. One of three methods was used: (1) direct measure of dead animals ($N = 10$), (2) direct measure of live animals ($N = 18$), and (3) indirect measure from photographs ($N = 33$). The last method was used to measure females that could not be approached closely. Photographs were taken with a Polaroid camera at a known distance from the subject, determined with a range finder having 99% reliability at 7.62 m. Simple geometry was used to calculate female length. This method did not deviate by more than 2.5 cm for measuring known length objects at distances of 6, 12, and 18 m.

Censuses and observations. Censuses were conducted daily on Año Nuevo Island and the adjacent mainland during each breeding season. We monitored the total number of animals present for each location by both sex and age. Each day, we searched for marked females and their pups. We recorded a female's date of arrival, location and daily movements, time and place of parturition, time and frequency of copulation and identity of her partners, and the date that the female departed the rookery and weaned her pup. Marked pups were followed daily in the same way. We recorded observations throughout daylight hours from blinds or hidden perches overlooking harems. Aerial photographs were

PLATE I

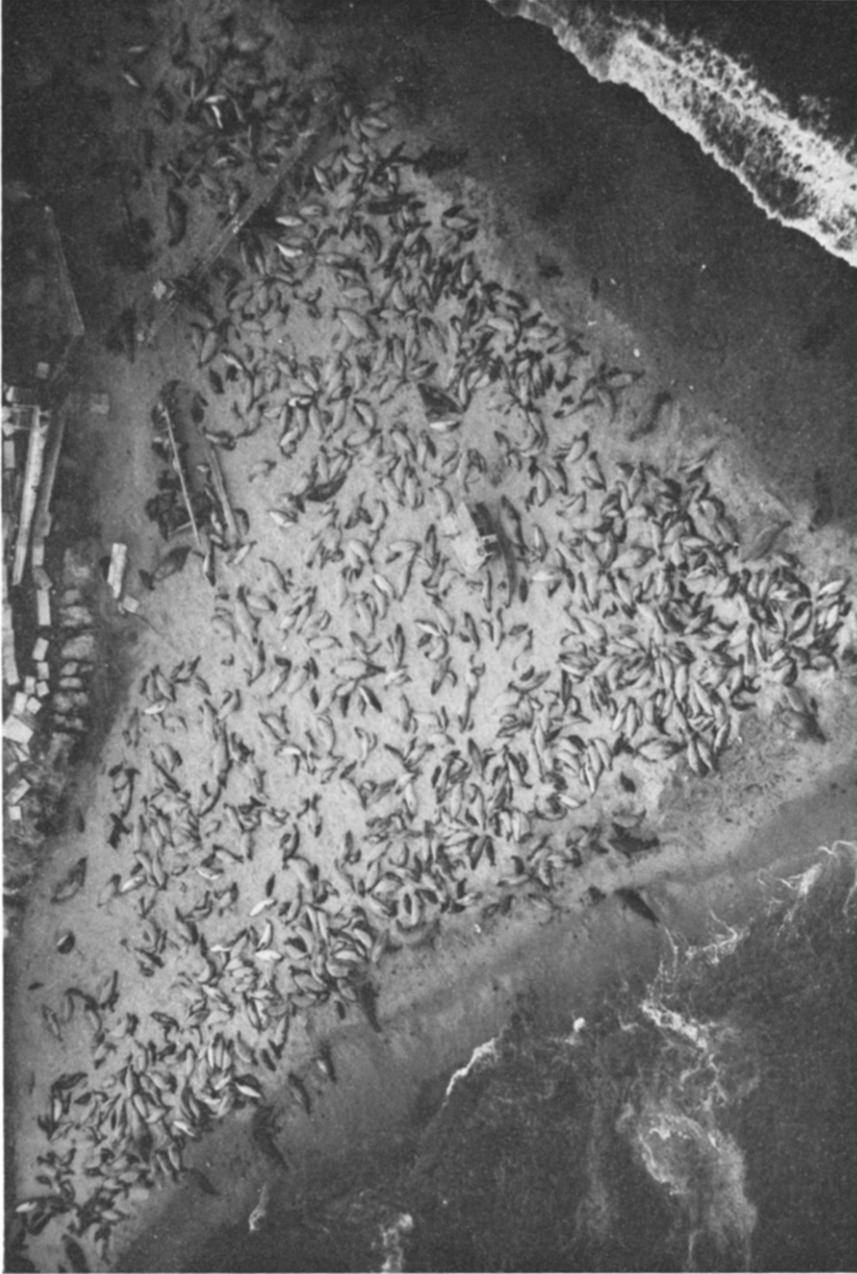


Fig. 1. High female density characterized the Point harem on Año Nuevo Island at the peak of each breeding season from 1976 to 1980. This photograph was taken at high tide on 4 February 1976 when the harem contained approximately 600 females, their pups, and several males. The alpha male is in the centre of the beach. Note the high female density on the periphery near the water's edge. On this same date in 1980, over 1200 females were crowded together on this beach.

PLATE II

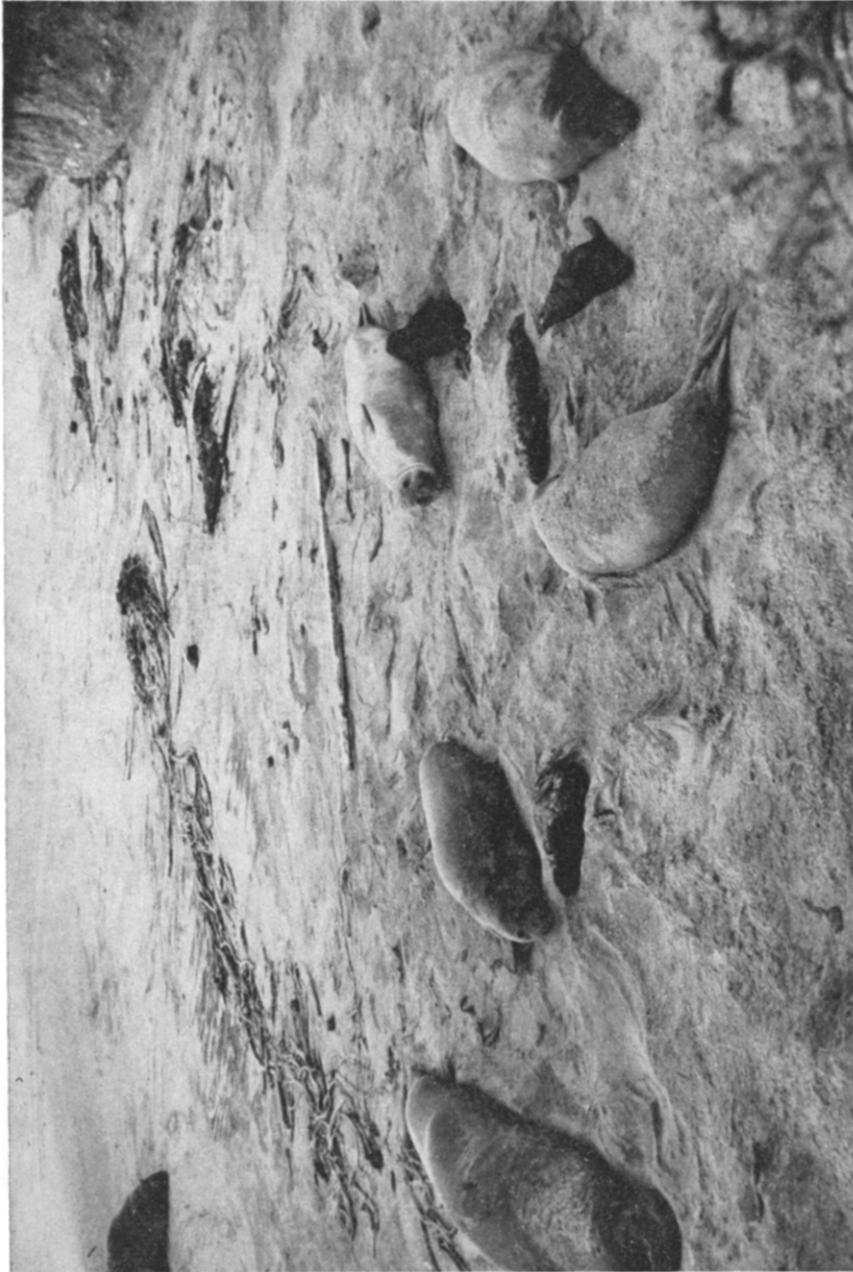


Fig. 2. Low female density characterized the small harems on the Año Nuevo mainland. This harem, photographed at peak season in 1979, contained four females, their pups, and one male.

taken at peak season to provide a check on the ground census method.

Principal measure of reproductive success. We measured reproductive success by direct observation of known-age females and their known-age pups. A female was considered to be successful if she protected and nursed her pup until it was weaned in a healthy condition. A female was considered unsuccessful if: (a) her pup died before weaning age, (b) she became permanently separated from her pup, (c) she and her pup became temporarily separated three or more times for one or more days, or (d) she did not nurse her pup exclusively but rather nursed several pups in addition to or instead of her own. Most pups in categories b, c, and d die from injury or starvation (Le Boeuf et al. 1972; Le Boeuf & Briggs 1977).

We assessed quality of maternal care by noting the size and condition of all weaned pups. We weighed weaned pups directly (for method, see Reiter et al. 1978) or ranked them as being small, average, or large, based on similarity to known-weight animals. External wounds and scars incurred in attempts to suckle from alien females, a sign of maternal neglect, were noted. When possible, we monitored survival of pups through the first few years of life and noted age at first reproduction.

Results

I. Variation in Female Reproductive Success

Density and weather dependence of colony reproductive success. The pup mortality rate on Año Nuevo Island over a 13-year period ranged from 13 to 40% of pups born (Le Boeuf & Briggs 1977). The reciprocal indicates that 60 to 87% of the pups born during this period survived to weaning. This gives us an estimate of the range of female reproductive success in the entire colony.

Figure 3 also shows that colony reproductive success was limited by the interaction of physical and social factors. The weather was unusually mild during the 1976 and 1977 breeding seasons, when harem density began to increase. In contrast, the weather was exceptionally bad in 1978. Storms with high surf and high tides hit Año Nuevo Island on 18 days between 1 January and 20 February, the period when peak numbers of females and pups were present. Surf and tides inundated a large portion of the Point harem on 7 days, causing many pups to be orphaned, injured, or drowned. The subsequent year, 1979, was a typical California winter. On 9 days at peak

season, weather and tidal conditions combined to increase pup mortality. However, conditions were considerably better than in 1978. The last year, 1980, was characterized by typical winter weather, much like 1979.

Pup mortality was highest when bad weather, storms, and high surf occurred in conjunction with high density. The increasing number of pups as well as breeding males and females filled the beaches to near capacity during the late 1970s. Clearly, colony reproductive success, the reciprocal of the pup mortality rate, is density-dependent. The relationship is not smoothly graded, but rather fluctuates greatly at high densities as a function of the weather.

Reproductive success and age. Table I shows that there was considerable variation in reproductive success as a function of female age. Reproductive success rose with advancing age. This is evident for the 4-year totals as well as for each individual year.

It will be helpful here and throughout the rest of this paper to make a distinction between females that are at least 6 years of age and females that are 3 to 5 years of age. We shall call the former 'prime' females and the latter 'young' females. Comparison of young and prime females each year reveals that prime females were about twice as successful as young females in rearing pups to weaning (Fig. 4). The discrepancy between the two categories of females was greatest during 1978 and 1979, when the weather was bad

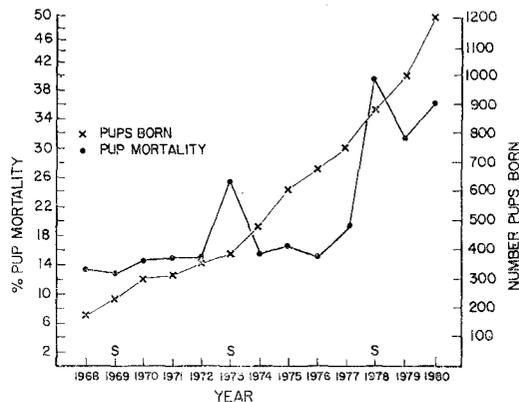


Fig. 3. Pup mortality relative to annual births on Año Nuevo Island during the period 1968 through 1980. The mortality rate is calculated from pups that died prior to weaning. 'S' denotes storms that struck the rookery at peak season, when the maximum number of females and pups were present. Data from 1968 to 1976 are from Le Boeuf & Briggs (1977).

Table I. The Percentage of Females in Various Age Categories which Produced Pups that Survived to Weaning Age on Año Nuevo Island (*N* is in parentheses)

Breeding season	Age in years										
	3	4	5	6	7	8	9	10	11	12	13
1976	25 (4)	65 (17)	47 (17)	100 (4)	86 (14)	100 (2)	—	—	—	—	—
1977	36 (11)	50 (10)	73 (11)	88 (8)	100 (3)	100 (15)	—	100 (1)	100 (1)	—	—
1978	0 (4)	13 (16)	0 (1)	20 (5)	30 (10)	50 (2)	30 (10)	0 (1)	100 (1)	100 (1)	100 (1)
1979	13 (16)	25 (8)	40 (10)	33 (3)	100 (1)	67 (3)	100 (3)	100 (5)	—	100 (1)	—
Totals	20 (35)	39 (51)	51 (39)	65 (20)	68 (28)	91 (22)	46 (13)	86 (7)	100 (2)	100 (2)	100 (1)

or when harem density was high. If one sums the values in Table I from all 4 years, only 38% of the young females were successful in weaning their pups compared to a success rate of 73% for prime females.

Both Table I and Fig. 3 illustrate the negative effect of bad weather on female reproductive success, especially when it was coupled with high female and pup density. As a result of the storms that flooded the harems at peak season in 1978, the reproductive success of both prime and young females plummeted from the success rate of the previous year. The fact that most of the sample of 9-year-old females was collected in this storm year accounts in large part for their poor overall performance relative to other prime females.

Reproductive success and harem density. Table I and Fig. 3 treat Año Nuevo as a whole and include data from three harems. In Table II we analyse the high-density Point harem on Año Nuevo Island separately from low-density harems on

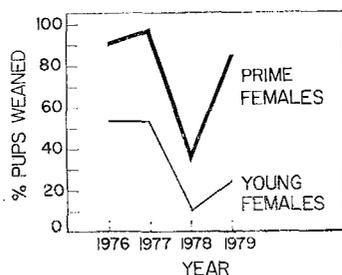


Fig. 4. Percentage of pups weaned by young and prime females during a 4-year period on Año Nuevo Island.

both the island (the Cove and Saddle harems) and the mainland. Note these points: (1) Young females were less reproductively successful in the high-density harem than they were in low-density harems. This generalization held true every year. Young females that bred in low-density harems were on the average more than twice as successful as their counterparts in the high-density harem. (2) Young females were less successful than prime females in both the high- and the low-density harems; the discrepancy was much greater in the high-density harem. (3) Prime females were only slightly more successful in low-density harems than in the high-density harem, except in years when the weather was unusually severe.

As we compare years within the cells, bear in mind that the high-density Point harem continued to increase in density from 1976 to 1979, i.e. harem number increased without comparable increase in available space. Note that: (1) In the high-density harem, the reproductive success of young females decreased annually with increasing density and was lowest during the storm year. (2) In the high-density harem, the reproductive success of prime females decreased only slightly with annual increases in density, except for the sharp decline during the storm year. (3) The highest reproductive success was that of prime females in low-density harems; however, few prime females were observed in this situation.

If we dissect the young female category into three age groups we find that reproductive success in both the high- and low-density harems was graded according to age. Summing the reproductive success over all years in the high-density

Table II. Proportion and Percentage of Reproductive Success by Young and Prime Females in High- and Low-Density Harems*

Females		Harem density			
		High		Low	
		Proportion	Percentage	Proportion	Percentage
Young	1976	15/32	47	5/7	71
	1977	13/27	48	6/9	67
	1978	1/19	5	11/14	79
	1979	6/31	19	12/20	60
	All years	35/109	32	34/50	68
Prime	1976	17/19	89	2/2	100
	1977	27/28	96	—	—
	1978	8/28	29	4/5	80
	1979	11/14	79	2/2	100
	All years	63/89	71	8/9	89

*The Point harem on Año Nuevo Island was the high-density harem; low-density harems were the Cove and Saddle harems on Año Nuevo Island and up to six harems on the Año Nuevo mainland (see Methods for definition of high- and low-density harems as well as the relative size of each harem).

harem reveals success rates of 13, 33, and 49% for 3-, 4-, and 5-year-olds, respectively. In low-density harems, females in the same age categories had success rates of 47, 78, and 80%.

II. Causes of Variation in Female Reproductive Success

Prime females are superior to young females in protecting and nurturing their pups. This is due in large part to their greater size, ability to dominate in aggressive encounters, early arrival, and greater maternal experience. Each of these factors is highly correlated with the others and calls for multivariate analysis. However, the data are not suitable for this approach, so we treat each factor separately below.

Size. Like many other mammals, female northern elephant seals become reproductively mature before they have attained full size. We quantified the relationship between age and size by measuring the length of females; it was not possible to weigh them. Figure 5 suggests that female length continues to increase rapidly until about 6 to 7 years of age, when the growth rate slows down. This finding corroborates our impression in the field. Trained observers reliably categorize young females, less than 5 years of age, as being smaller, both in length and weight, than other females. A similar relationship between body length and age is reported for the southern elephant seal, *M. leonina*, with the curve levelling off at age 6 (Laws 1953, Figs 19

and 23). Similar growth curves are reported for several other pinnipeds, e.g. the ringed seal, *Pusa hispida*; the ribbon seal, *Histiophoca fasciata*; the common seal, *Phoca vitulina largha*; and the bearded seal, *Erignathus barbatus nauticus*, all of which continue to grow for some time after undergoing puberty (Tikhomirov 1968).

Prime, large females might be expected to wean larger pups than do young, small females because the older females have greater fat, protein, and mineral reserves from which to draw to feed their

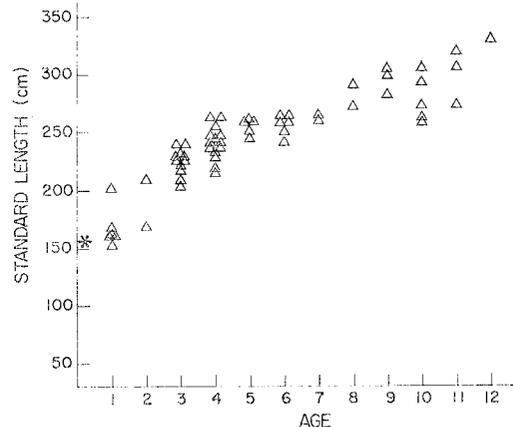


Fig. 5. Female length (nose to tail) as a function of age (in years). The asterisk denotes the mean standard length of 23 female pups measured at 1 month of age.

pups as well as to maintain themselves while fasting. The data in Fig. 6 support the hypothesis that pup weaning weight increases with mother's age. How is this accomplished? Table III shows that the length of females' nursing-fasting period increases with age, suggesting that old, large females are able to remain on the rookery longer and provide more milk before they must wean their pups and return to sea to feed. The hypothesis that a female's size and fat reserves set limits on how long she can fast and feed her pup is further substantiated by the fact that females who lose their pups and do not nurse, or nurse infrequently, remain on the rookery longer than nursing females that successfully wean their pups. For example, in 1976, 24 females who lost their pups remained on the rookery a mean of 30.3 days postpartum. Forty-eight females who nursed their pups in typical fashion remained on the rookery a mean of 27.3 days. This difference in postpartum stay on the rookery is statistically significant ($t = 3.04$, $df = 70$, $P < 0.05$).

Aggression and dominance. Bartholomew & Collias (1962) noted that: (1) most of the stimuli

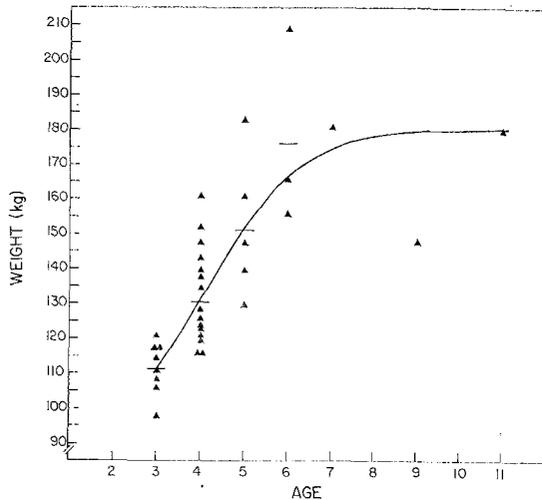


Fig. 6. Weight of pups at weaning in relation to mother's age in years.

that elicit female aggression are potentially dangerous to the female's pup, (2) dominant-subordinate relations exist between cows, (3) females with pups usually dominate pregnant females, and (4) the dominance status of a cow is of great importance in protecting her pup. The last point was confirmed in a study that showed a positive relationship between female aggression and reproductive success (Christensen 1974; Christensen & Le Boeuf 1978). The pups of aggressive (higher-ranking) females were bitten infrequently by other females, and therefore a higher percentage survived than the frequently bitten pups of low-ranking females. Previous studies on Año Nuevo Island showed that female biting of alien pups is a major cause of pup mortality (Le Boeuf et al. 1972; Le Boeuf & Briggs 1977). In these studies, we did not determine the size and age of females.

We observed numerous aggressive episodes between females which influenced parturition sites or pup injury and hence, pup survival. For example, females: threatened another female, causing her to retreat and become separated from her pup; impeded the movements of subordinate females, thereby causing, prolonging, or maintaining mother-pup separations; moved toward a neighbouring female and pup and bit her pup; prevented another female from landing on the beach to give birth; and protected their own pups from potential injury by threatening an approaching female (Le Boeuf et al. 1972; Le Boeuf & Briggs 1977; Reiter et al. 1978). These episodes illustrate that females can enhance their reproductive success by physically dominating other females.

We observed that the older female in a pairwise aggressive encounter dominates the younger one and that there are few exceptions to this generalization. During the 1977 and 1978 breeding seasons, we observed 19 aggressive episodes between known-age females. In 84% of these episodes, the older female dominated the younger one and the latter retreated. Seven- and eight-year-olds were involved in four encounters with younger females, all of which they dominated;

Table III. Mean Number of Nursing Days by Successful Mothers as a Function of Their Age (± 1 SD; N is in parentheses)

Age in years							
2	3	4	5	6	7	8	9
22 \pm 0 (1)	23.7 \pm 1.6 (9)	26.6 \pm 1.6 (24)	26.1 \pm 1.9 (12)	26.5 \pm 2.2 (6)	27.1 \pm 1.2 (8)	28.2 \pm 0.8 (5)	28.5 \pm 0.7 (2)

6-year-olds dominated females younger than themselves in three of five encounters; 5-year-olds won all six encounters we observed with younger females, and 4-year-olds dominated 3-year-olds three of four times. Viewed the other way around, 3-year-olds retreated in 5 of 6 encounters with older females and 4-year-olds retreated in 8 of 10 encounters with older females.

Female dominance status between animals of unequal age appears to be reliably stable within a breeding season provided the dominant individual doesn't lose her pup. In seven pairs of females of unequal age, we observed from two to eight subsequent aggressive encounters during a breeding season. In 20 of 21 episodes, the initially dominant female remained dominant in subsequent encounters.

Date of arrival. The order of arrival of parturient females on the rookery varies with age. Table IV shows that the oldest females tend to breed earliest in the season. This may be a reflection of their greater age, size, and feeding experience, which enables them to put on a large fat store faster than young females. Whatever the proximal cause, early arrival confers numerous advantages that we will enumerate later.

Maternal experience. Since females usually give birth once a year after giving birth for the first time, maternal experience increases with age. Maternal experience alone appears to enhance the probability of weaning a healthy pup. Four-year-old females that gave birth as 3-year-olds weaned a higher proportion of their pups (11/16 = 69%) than primiparous 4-year-old females (19/55 = 35%) ($\chi^2 = 5.94$, $df = 1$, $P < 0.05$). Among the 16 multiparous females, 7 were successful the second year after having failed as primiparous 3-year-olds, 4 were successful in both years, and 5 were unsuccessful in both years. No female in this sample succeeded the first year and failed the second year. However, besides the

postulated benefit of experience, one cannot rule out the possibility that females that bred as 3-year-olds were physically superior to those that did not, and hence they were more likely to succeed at age 4.

Primiparous females were poorer mothers than more experienced females when it came to nurturing and protecting their pups. Support for this statement comes from witnessing events involving known-age females, and from a comparative study of quantifiable aspects of maternal behaviour in seven primiparous 3-year-old females and seven multiparous females, ages 7 to 11 (Table V). Maternal behaviours important for pup survival are: remaining in close proximity to the pup, distinguishing it from alien pups, and feeding it as much as possible.

Three times we saw known-age females abandon their pups immediately after giving birth. Two females were 3 years old and one was 4 years old; all three females were primiparous. Two females returned to sea after giving birth and did not return; the other female gave birth in the crowded Point harem, never turned to face her pup, and subsequently moved away from it. Data in Table V show that primiparous mothers and their pups were more often separated than multiparous mothers and their pups because the mother was often dominated by a neighbouring female, the mother was distracted and moved away from her pup, or the mother was inattentive and allowed her pup to wander.

A variety of situations were observed in which females failed to distinguish their own pup from others. Each breeding season, a few females in the Point harem nursed, attempted to protect, or tolerated all pups, orphans, or recently weaned pups near them in addition to their own pups. At times, these indiscriminant mothers were surrounded by as many as eight pups competing to suckle. Eight of these females were of known age; seven were primiparous 3- or 4-year-olds

Table IV. Mean Day of Parturition as a Function of Female Age (Number of Days from 1 December; ± 1 SD; N is in Parentheses)

	Age in years					
	3	4	5	6	7	8
1976	52.6 \pm 6.1 (4)	54.1 \pm 7.9 (11)	46.1 \pm 10.6 (10)	45.5 \pm 3.5 (4)	44.7 \pm 9.6 (11)	no data
1977	49.2 \pm 6.9 (14)	49.5 \pm 12.8 (10)	46.8 \pm 8.0 (11)	45.6 \pm 10.3 (9)	44.0 \pm 8.7 (5)	44.1 \pm 10.7 (17)

(three of them were in the sample in Table V); and one was a 5-year-old that had not been observed in the several previous years. Two known-age females attempted to feed and protect another pup in addition to their own throughout the nursing period. Both of these females were primiparous 4-year-olds. In three instances, pairs of females switched pups back and forth during the first week of nursing (one pair continued to do this until the pups were weaned). The female pairs consisted of two 3-year-olds, a 3-year-old and a 4-year-old, and a 3-year-old and a female of unknown age but equally small size. Other cases of mistaken identity took the following form. A female who recently gave birth mistakenly claimed the newborn of a neighbour. The two females bickered and fought for several days, competing to nurse and be nearest to the pup. Eventually, the two mothers developed a guarded tolerance towards each other. In three cases, the age of both females and the filial relationship was known with certainty: two were cases of primiparous 3-year-olds nursing or protecting the pups of other primiparous 3-year-olds, and one case involved a primiparous 4-year-old

nursing or protecting the pup of a 6-year-old female.

As a result of the aberrant maternal behaviour of primiparous females, their pups were fed less than those of experienced mothers, and their pups were more frequently injured (Table V).

Time and place of parturition. The location at which and the time in the breeding season when a female gives birth have an important effect on her pup's survival, development, and subsequent reproductive success. The increases in size, aggressiveness, and maternal experience that accrue with age give older females an advantage over younger ones in competition for the most favourable time and place to give birth.

Females that give birth in the centre of a large harem enjoy numerous advantages. The centre of the Point harem was a relatively quiet place to give birth and nurse a pup compared to the harem periphery. There was more space between females in the centre than on the periphery. The area was far less vulnerable to flooding at high tide and too distant to be impacted by high surf, so that mass female aggression and confusion were less

Table V. Importance of Maternal Behaviour for Pup Survival in Seven Primiparous Females and Seven Multiparous Females

	Primiparous 3-year-olds		Multiparous females, age 7 to 11	
	Frequency	Number of females	Frequency	Number of females
Dominance encounters				
Moved by another female	17	4	0	0
Moves another female	0	0	3	2
Mother-pup separations				
Mother moves away	27	7	2	1
Pup moves away	6	4	0	0
Separated by neighbouring female	2	2	0	0
Separated by a male	4	3	0	0
Pup suckles from neighbouring female	4	3	1	1
Separation permanent	6	2	0	0
		3		0
Mother-pup reunion attempts				
Successful	43	6	3	1
Prevented by neighbouring female	22	6	2	1
Prevented by a male	20	4	1	1
	4	2	0	0
Mother's response to orphans or neighbouring weaned pups				
Bites	9	4	5	4
Protects	6	3	0	0
Nurses all		3		0
Nurses unwittingly	3	2	0	0
Pup injuries				
Bitten by neighbouring female	20	5	2	2
Trampled by male	2	1	0	0

frequent. Because it was occupied by one or a few top-ranking dominant bulls, who kept all other males at a distance, nursing females in the harem centre were less frequently disturbed by would-be mates and intermale aggression than females on the periphery (Le Boeuf 1974). Centre-situated mothers were buffered from milk thieves who were aggressively driven out of the harem long before reaching the harem centre (Reiter et al. 1978).

In contrast, the periphery of the Point harem was extremely crowded with females and pups at peak season. Consequently, it was an inhospitable and hazardous place to raise a pup. A variety of forces increased the probability of mother-pup separation and pup injury, which usually resulted in pup mortality (see Le Boeuf & Briggs 1977). At times, density was so high that a female giving birth expelled the foetus onto the back of an adjacent female and had great difficulty turning around to face her pup. High surf crashed on the animals nearest the surf line and flooded the area, causing increases in density that lasted several hours. This flooding was followed by a high level of female movement, aggression, and pup-biting—resulting in many lost or injured pups. Numerous low-ranking or subadult bulls repeatedly attempted to enter the harem or to mate with pregnant or nursing females. They were repeatedly chased out of the harem and around the harem periphery by bulls of higher rank. This activity caused pups to be trampled or separated from their mothers. Orphans and recently weaned pups roamed the area trying to steal milk. Females who had lost their pups searched for them and often stole or bit pups that were not their own. Chaos, confusion, crowding, and numerous pup carcasses characterized this area at peak season.

Prime females formed the centre of the Point harem because they tended to arrive early in the breeding season (Table IV). If they arrived late, they were aggressive and dominant enough to

move toward the harem centre. Once the early-arriving prime females were situated, they prevented young females from approaching and thus restricted them to the periphery of the harem. Table VI shows that the mean age of females on the periphery was less than that of females in the harem centre at various times during the 1977 breeding season. A similar result was found by periodically noting the location of marked known-age females; the older a female, the more time she spent in the centre of the harem.

Females that give birth early in the breeding season on the Point harem, which we have shown tend to be the older females, enjoy additional advantages in rearing their pups that appear to increase their reproductive success (Le Boeuf & Briggs 1977; Reiter et al. 1978): (1) They rear their pups when there are relatively few other females and pups present. Thus, early parturient females are less likely to be separated from their pups as a result of sheer numbers present than females rearing their pups at midseason. (2) Pups weaned early in the breeding season have the option of stealing milk from the multitude of nursing mothers on the rookery at peak season. If successful, they gain a weight advantage over other recently weaned pups, a competitive edge that seems to be particularly important in male pups. Pups weaned late in the breeding season do not have this option since most of the nursing females have already departed from the rookery. (3) Early-weaned pups have more experience in the water and more time to interact socially with peers before leaving the rookery in order to obtain food on their own for the first time. Perhaps this additional experience increases the probability of surviving the first exposure to marine predators (Le Boeuf et al. 1981). (4) A higher proportion of female pups born early in the season survive to reproduce, and they give birth for the first time at an earlier age than female pups born during peak season or late in the breeding season. Table VII shows that a

Table VI. The Mean Age of Females Observed at Harem Periphery and Harem Centre at Various Times in the Breeding Season (± 1 SD; *N* is in parentheses)*

	January				February	
	12	18	28	31	10	14
Periphery	4.6 \pm 2.1 (5)	4.3 \pm 1.1 (7)	4.6 \pm 1.7 (17)	4.7 \pm 1.6 (17)	4.5 \pm 1.7 (12)	4.0 \pm 1.1 (9)
Centre	7.8 \pm 0.8 (6)	6.5 \pm 1.8 (8)	7.0 \pm 1.2 (9)	7.0 \pm 1.3 (7)	7.0 \pm 1.4 (2)	7.5 \pm 0.7 (2)

*All comparisons between the harem periphery and harem centre are statistically significant (*t*-tests, $P < 0.05$).

higher percentage of pups weaned early in the 1974 breeding season (17 January to 4 February) gave birth by ages 3, 4, and 5 years than pups weaned in midseason (5 to 20 February) or late season (21 February to 8 March). Table VIII shows that this trend continued in the 1975 cohort. Although no differences are apparent between groups of primiparous 3-year-olds, the highest proportion of females giving birth for the first time as 4-year-olds were early weaned.

Tables VII and VIII also yield estimates of age at first reproduction for females from the Año Nuevo Island rookery at this particular time. The column totals in both tables show that the modal age of primiparity was age 4 years, with age 3 the next most frequent time of first reproduction. A similar distribution was found in the 1973 cohort ($N = 70$): 8.6% of the cohort gave birth for the first time at age 3, 17.1% at age 4, and 1.4% at age 5. The grand total of 27.5% in Table VII represents the minimum percentage of females born in 1974 that gave birth by their

fifth year. Of the remainder, we assume that: (1) few will give birth for the first time as 7-year-olds or older, (2) a small percentage of them are not identifiable because of lost or unreadable tags, and (3) the majority of them have not survived to age 6.

III. Reproductive Success and Investment in Offspring by Sex

Sex-ratio theory predicts that differential investment in the sex of offspring influences a female's reproductive success (Fisher 1930; Trivers & Willard 1973). Previous work showed that maternal investment in the sexes is not equal in northern elephant seals. Reiter et al. (1978) showed that males weigh more than females at weaning time, and males are nursed 1 full day longer than female pups (mean = 27.8 versus 26.6 days). We made additional observations on Año Nuevo Island in 1978 that support the statement that females invest differentially in their offspring according to sex. Four male newborns

Table VII. The Percentage of Females Born at Various Times (Early, Middle, Late) during the 1974 Breeding Season on Año Nuevo Island that Gave Birth for the First Time in the Indicated Years (N is in Parentheses)

Year and age of primiparity	Early ($N = 32$)	Middle ($N = 92$)	Late ($N = 47$)	Total ($N = 171$)
1976				
2 years old	0	1.1	0	0.6
1977				
3 years old	15.6	7.6	8.5	9.4
1978				
4 years old	21.9	13.0	10.6	14.0
1979				
5 years old	0	2.2	6.4	2.9
1980				
6 years old	3.1	0	0	0.6
Totals	40.6	23.9	25.5	27.5

Table VIII. The Percentage of Females Born at Various Times (Early, Middle, Late) during the 1975 Breeding Season on Año Nuevo Island that Gave Birth for the First Time in the Indicated Years (N is in Parentheses)

Year and age of primiparity	Early ($N = 45$)	Middle ($N = 117$)	Late ($N = 47$)	Total ($N = 209$)
1978				
3 years old	4.4	4.3	2.1	3.8
1979				
4 years old	17.8	6.0	10.6	9.6
1980				
5 years old	0	1.7	2.1	1.4
Totals	22.2	12.0	14.9	14.8

had a mean weight \pm SD of 44.8 ± 4.3 kg compared to a mean weight of 35.2 ± 3.4 kg for seven newborn females. A similar sex difference was found for pups that died within 3 days after birth (seven males, 39.9 ± 4.9 kg versus six females, 32.3 ± 4.3 kg). These data indicate that males were energetically more costly than females in utero. Mothers also invested more energy in male pups after parturition, as indicated by data showing that 17 males had a mean weight of 141.3 ± 28.4 kg at weaning compared to a mean weight of 124.7 ± 20.0 kg for 24 females.

We found no evidence that the sex ratio of offspring varies with the mother's age. Young 3- to 5-year-old females on Año Nuevo Island produced 59 males and 54 female pups; females 6 years of age and older produced 34 males and 35 females ($z = 0.35$, $P > 0.05$). We also found no sex differences in the number of pups weaned during each of the four quarters of the breeding season (cf. Coulson & Hickling 1961; Stirling 1971a).

IV. Reproductive Success and Offspring Genotype

Since male elephant seals provide one-half of the genotype of a female's offspring and nothing else in the way of parental investment, a female might improve her reproductive success by choosing the best mate. Females should compete to mate with adult males of high social rank that have demonstrated their fitness (Selander 1972; Trivers 1972; Cox & Le Boeuf 1977). However, these males are in short supply near harems where the operational sex ratio (Emlen & Oring 1977) may be as high as 30 females to 1 adult male. Prime females might be expected to exhibit a higher frequency of mating with adult, high-ranking males than young females would because circumstances and the respective attributes of adults of both sexes put them in close proximity in the harem centre. Moreover, it is mutually advantageous for high-ranking adult males and females in their prime to mate with each other.

We saw 38 young females in the Point harem copulate for the first time in the breeding season with males of known social rank and approximate age. We assume in this analysis that the first copulation is more likely to result in fertilization than are subsequent copulations (Le Boeuf 1974). Sixty-eight per cent of the young females copulated with adult males who ranked among the top 20 males in the dominance hierarchy. By contrast, 90% of 39 prime females we monitored first copulated with males with a social rank of 20 or higher. During each breeding season in the

study period, the top 20 males occupied a place in the harem or spent a great deal of time in it. Males with a social rank lower than 20 were usually found outside the harem or on its periphery. The majority of the latter were subadults.

The higher incidence of first copulations with low-ranking adult and subadult males by young females in comparison with prime females was most pronounced in 2-, 3-, and 4-year-old females. Forty-five per cent mated with these males. All 10 of the 5-year-old females monitored mated with adult males of high social rank.

Evidently, assortative mating occurred during the study period. Moreover, this study and previous ones suggest that the degree of assortative mating increases with female density. In small harems, and in earlier years when the Point harem was less crowded, adult high-ranking males did virtually all of the mating (Le Boeuf 1974; Cox & Le Boeuf 1977). However, as harem size and female density in the Point harem increased, the monopoly of the adult bulls began to break down. Adult males did over 85% of the mating in the Point harem from 1968 to 1973, in contrast to only 54% in 1979. The increasing copulatory success of young and subordinate males, concomitant with colony growth, resulted mainly from pairings with young females. As Cox & Le Boeuf (1977, page 326) pointed out: 'From the female point of view, an increasing harem size means that the odds of mating with a mature, high-ranking male decreases'. This is especially true for young females.

V. Minimizing Reproductive Failure Early in Life

Since young females are at a great disadvantage when they breed in a crowded harem, we might expect them to reduce reproductive competition by moving to less dense breeding areas or by establishing new ones if space is available. Before we can test this prediction, we must consider the option of emigrating in the context of what elephant seals usually do and have been selected to do. Like most other pinnipeds and many terrestrial mammals, most female elephant seals are both philopatric, giving birth where they were born, and site-tenacious, giving birth in approximately the same location where they gave birth previously. Of 186 females born on Año Nuevo Island during the 1970s, 71.4% gave birth there for the first time. The majority of those that did not demonstrate philopatry gave birth on nearby rookeries in 1978 and 1979, breeding seasons when Año Nuevo Island was very crowded.

To estimate the degree of site tenacity, we examined the records of 150 females that pupped in two successive years within the three major harems on Año Nuevo Island, the Año Nuevo mainland, and Southeast Farallon Island and for which the success or failure in rearing a pup the first year was known. Seventy per cent of the females returned to the same parturition site the second year. Among those females that changed parturition site, 57.8% had failed to wean their pups the first year. This performance was statistically different from that of females who succeeded the first year ($\chi^2 = 4.47$, $df = 1$, $P < 0.05$). Viewed another way, females that failed the first year were more apt to give birth in a different site the second year (38.8%) than females that were initially successful (22.9%).

These data indicate that females display a high degree of site fidelity of both kinds and that females are more likely to break convention in the face of high density (low probability of reproductive success) or following reproductive failure.

Emigration and the establishment of new colonies. Emigration from crowded harems would appear to be the best strategy for young females when a population is growing. The elephant seal population has been reoccupying its former niche since it was reduced by sealers to less than 100 individuals during the 1880s (Townsend 1912; Bartholomew & Hubbs 1960; Bonnell & Selander 1974; Le Boeuf 1977). A population expanding into its former niche finds abundant food and suitable breeding space. These conditions favour the survival of offspring and push the age of first reproduction to the physiological minimum (Cole 1954; Lewontin 1965). Early primiparity was characteristic of females born on Año Nuevo Island in 1973, 1974, and 1975 (Tables VII and VIII), and we suspect that this change was characteristic of all rookeries during most of the recovery phase of the population.

Young females from Año Nuevo Island colonized new breeding areas when harems on Año Nuevo Island became crowded during the mid-1970s (Le Boeuf & Briggs 1977; Le Boeuf 1977). In 1972, breeding began on Southeast Farallon Island, 89 km north of Año Nuevo Island (Le Boeuf et al. 1974). In 1975, a female gave birth on the Año Nuevo mainland, less than a kilometre from the island (Le Boeuf & Panken 1977). Subsequently, both new colonies grew coincidentally with the continued overflow numbers on the Año Nuevo Island Point harem. The greatest increase in females giving birth on the Año Nuevo mainland was in 1978, when bad weather

reduced the effective size of the breeding beaches on the island. In addition, the peak number of females on the Año Nuevo mainland lagged behind the peak number of females on the adjacent island by about 10 days in 1978 and 1979, suggesting that when the island became saturated with females, the overflow simply crossed the channel. Because we tagged weaned pups on Año Nuevo Island annually, and on all other major rookeries approximately every other year since 1968, we were able to determine the age and place of birth of approximately 20% of the pioneers at the new breeding areas, i.e. all of the tagged animals that were present.

The majority of the colonizers in both places were young females (and males) who had been born on Año Nuevo Island. Twenty-six of 34 females, or 76%, that gave birth for the first time on Southeast Farallon Island between 1974 and 1978 had been born on Año Nuevo Island (the few females that bred in 1972 and 1973 were not tagged and, therefore, their age and place of birth were unknown). The remainder of the females came from San Miguel Island (21%) and San Nicolas Island (3%) in southern California. The age distribution was heavily weighted with young females: age 3 years = 9, age 4 = 19, age 5 = 4, age 6 = 1, and age 7 = 1.

Except for two adults, all tagged females were breeding for the first time in their lives. None was observed giving birth elsewhere before breeding on Southeast Farallon Island.

We found similar results at the new breeding site on the Año Nuevo mainland. Thirty different tagged females gave birth there during four breeding seasons between 1976 and 1979. Eighty-seven per cent of these females had been born on Año Nuevo Island, three females were from San Miguel, and one female was from San Nicolas Island. Nearly all females were young and apparently primiparous: 13 females were 3 years old and an equal number were 4 years old. Four multiparous females, aged 4, 5, 9, and 10, had bred on Año Nuevo Island in previous years.

Young females do not breed in new locations strictly by chance. Of 40 females from the 1974 cohort born on Año Nuevo Island, 85% were observed as juveniles on the beach where they later gave birth. Fifteen of the tagged females giving birth on Southeast Farallon Island were sighted there previously as juveniles on one or more occasions. This is a behaviour similar to what Wooler & Coulson (1977) call 'prospecting' in Kittiwake gulls, *Rissa tridactyla*.

Reproductive success of young immigrants.

Data in Table IX show that young females that immigrated to the newly formed rookeries on Southeast Farallon Island and the Año Nuevo mainland were more successful than females of a similar age that bred in the crowded Point harem on Año Nuevo Island. The discrepancy in reproductive success of young females on Año Nuevo Island and in the other two breeding areas was greatest in years of bad storms (1978), high female density (1979), or both (1978). In 1980, we did not monitor young females on Año Nuevo Island; therefore we cannot make comparisons like those in Table IX. However, we determined the pup mortality rate for females of all ages combined in each breeding area. Only 2% of pups born on the Año Nuevo mainland died before weaning, in contrast to 36% of those born in the Point harem at Año Nuevo Island.

The dissimilar success rates in Table IX are directly attributable to differences in harem density and female competition in the old and new breeding locations. For example, harem density was considerably lower in each harem on the Año Nuevo mainland than it was in the Point harem on the island (see Methods) because there was always sufficient space for females to spread out in the former location. Female competition was lower in mainland harems because there were few prime females present. During the period 1976 to 1980, young females outnumbered prime females in mainland harems by 68 to 6, in contrast to 144 to 109 in the crowded Point harem on the island. Consequently, conditions in the new breeding areas were more favourable for rearing pups. Blunders from inexperience were not so severely penalized. If a young mother became separated from her pup, reunion was more likely than on the island's large harem because far fewer females and pups were in the area; conditions were less crowded; there was less noise to mask her pup's call; and fewer older, dominant females were present to prevent her from searching for her pup.

Discussion

Data on the influence of age on reproductive success in wild mammals exists for several ruminants and a few rodents. Most estimates of reproductive success in ruminants are low-order measures such as pregnancy rate or foetuses per animal. For example, in northern Yellowstone elk, *Cervis canadensis*, 2-year-olds show a higher percentage of pregnancies than yearlings (Fowler & Barmore 1978); in pregnant urial wild sheep, *Ovis orientalis*, the mean number of foetuses in yearlings and 2-year-olds is 1.00, in 3-year-olds 1.25, and in ewes older than 3 years 1.53 (Valdez 1976). Data on higher-order estimates of reproductive success, such as number of surviving offspring at the end of the period of parental investment or number of young surviving to maturity, are virtually non-existent. Howard (1979) makes the important point that higher-order estimates of reproductive success are more accurate indices of fitness because more information regarding the potential genetic contribution of the individual is known. In an excellent study, Sherman (1976) showed that litter size at weaning in Belding's ground squirrel, *Spermophilus beldingi*, varies with maternal age; yearlings had three to four offspring, 2- to 5-year-olds had six to eight, and 6- to 8-year-olds had three or four.

Observations of mammals in captivity or in the laboratory suggest what might occur in the wild. Results similar to those of Sherman's were found in a laboratory study of collared lemmings, *Dicrostonyx groenlandicus* (Hasler & Banks 1975). The production of lambs to weaning age increased with the mother's age and then began to drop off after the eighth year in domestic merino sheep (Turner & Dolling 1965) and captive reindeer, *Rangifer tarandus* (Preobrazhenskii 1961). Young ibex females, *Capra aegagrus*, in captivity were less successful in rearing offspring than older females (Nievergelt 1966). Several investigators have observed that primiparous domestic ewes often desert their lambs,

Table IX. The Proportion and Percentage of Young Females, 5 Years of Age or Less, Producing Pups that Survived to Weaning Age in Good Condition and Were Weaned by their Own Mothers

Breeding season	Año Nuevo Island Point harem	Southeast Farallon Island	Año Nuevo Mainland
1976	15/42 = 47%	7/8 = 88%	0/1 = 0
1977	13/27 = 48%	7/12 = 58%	2/4 = 50%
1978	1/19 = 5%	8/17 = 47%	10/12 = 83%
1979	6/31 = 19%	not available	10/17 = 59%

fail to recognize them, or refuse to stand and nurse. Geist (1971) suggests that similar behaviour occurs in wild ruminants.

Elephant seals differ from humans, a few primates that have been studied, and some of the mammals mentioned above in that reproductive success continues to increase with age until death. The oldest females in our sample exhibited the highest success rates in weaning pups (Table I). Old females not only exhibited superior maternal behaviour but preliminary data also suggest that the fecundity rate in 8- to 11-year-old females is as high as in 3- to 5-year-olds. In contrast, reproductive success, measured in various ways, forms a U-shaped function in humans (e.g. Grahn & Kratchman 1963; MacMahon 1974); rhesus monkeys, *Macaca mulatta* (Drickamer 1974); langurs, *Presbytis entellus* (Hrdy 1977); domestic sheep (Turner & Dolling 1965); ground squirrels (Sherman 1976); and lemmings (Hasler & Banks 1975); females are least successful early in life and in extreme age.

The relationship between reproductive success and age has been documented most thoroughly in birds, e.g. the great tit, *Parus major* (Perrins 1965; Perrins & Moss 1974); the European blackbird, *Turdus merula* (Snow 1958); the white stork, *Ciconia ciconia* (Hornberger 1954; Schüz 1957); the yellow-eyed penguin, *Megadyptes antipodes* (Richdale 1957); the kittiwake gull, *Rissa tridactyla* (Coulson 1966); and the Arctic tern, *Sterna paradisaea* (Coulson & Horobin 1976). Older parents produce larger clutches, hatch more eggs, raise larger broods, and fledge more chicks than younger parents.

There are obvious similarities in the manner in which female elephant seals and some of these birds maximize their reproductive success. In addition to the principal finding that reproductive success increases with age, some of these similarities are: (1) older, larger females breed earliest in the breeding season; (2) maternal experience plays an important role in rearing the young; (3) the age of sexual maturity of females varies, i.e. there is deferred maturity; and (4) young females 'prospect' before they emigrate to a new colony. This convergent behaviour is interesting in light of the distant genetic relationships between these animals and the different mating systems involved. All of the birds investigated are monogamous; a female establishes a pair-bond with a male during the breeding season. Some of them retain the same mate in successive years. Males assist in feeding and protecting the chicks. The elephant seal female

gets no help from the polygynous male in feeding and protecting the pup. Sexual dimorphism is extreme in the seal and virtually non-existent in the birds studied.

Variation with age in the reproductive success of female elephant seals results in large part from the fact that they continue to grow for some time after puberty, as do many other long-lived mammals. Because of their inferior size, young adult seals are socially subordinate to individuals in the prime of life, and they lose in competition for the optimal location and time to give birth and nurse their pups. In addition, young females, being smaller than old females, carry smaller fat reserves. Their social and physical inferiority, plus their lack of maternal experience, puts young females at a disadvantage in protecting and feeding their pups. High density compounds the problem by increasing competition and social strife.

Wynne-Edwards (1962) used a similar explanation to account for differential fertility in young and old (prime) birds. He argued that fertility is governed by the interplay of social rank and economic conditions, with the result that newcomers to the breeding caste are liable to be handicapped by their inferior social position. However, he produced no evidence, nor is any to be found in the studies of white storks, kittiwakes, blackbirds, and yellow-eyed penguins. Moreover, these birds do not continue to grow after puberty, as seals do, or continued growth is so small that it is trivial. According to Lack (1954, 1966), reproductive success varies with age in these birds because breeding imposes a strain on the parents that proves too heavy for the youngest individuals. He argues that the greater experience of the older parents in feeding and building up food reserves is the most important variable contributing to the greater reproductive success of old bird parents relative to young ones. If Lack is correct, and the data seem to bear him out, the acquisition of food limits the reproductive success of old bird parents by limiting the number of young that can be fed, and hence fledged. In contrast, competition at the breeding site seems to be the most important variable influencing reproductive success in female elephant seals, and there is evidently a great advantage in being large, as Wynne-Edwards and others have suggested (e.g. Ralls 1976).

Successful reproduction early in the life of an elephant seal female is critical in determining net reproductive success over a lifetime. The

probability that a female will die increases with age, while her reproductive potential decreases annually. The best strategy for a female appears to be to breed whenever she has the opportunity. If she lives long, breeding successfully at an early age enables a female to produce more offspring than females that attempt to reproduce early but fail, or than females in which sexual maturity is delayed. Even if an early-breeding female loses her pup, our data show that she may profit from the experience. Although selection clearly favours early reproduction, many try but few succeed. The greatest variation in reproductive success among females occurs during the first few attempts at reproducing. In contrast, most females that reproduce during their prime years or later successfully wean their pups. Therefore, the time for a female to gain an advantage in reproductive competition with other females is during these early years.

While the benefits of breeding early are obvious, the costs are obscure and more difficult to measure. The simple act of mating involves time and energy costs, predation risks, possible disease transmission, and possible injury (Daly 1978). For example, some female elephant seals die from bites to the head inflicted by over-eager male suitors. The youngest, smallest females appear to be most vulnerable to this type of injury, but systematic data on this phenomenon are difficult to obtain. It is well known that reproductive effort involves mortality risk; however, with few exceptions (e.g. Wooller & Coulson 1977), quantification of this relationship has proved difficult (Pianka & Parker 1975). The risk of mortality appears to be greatest in female seals reproducing for the first time. The energetic drain of breeding early may reduce the ultimate size of a female, and thus lower the probability that her future offspring will survive and reproduce. A pregnant, growing female must nourish herself as well as the developing foetus; during nursing she must maintain herself and her pup while fasting. Meanwhile, non-pregnant females of the same age are at sea feeding and continuing to grow. What is the value of maternal experience gained from reproducing early vis-à-vis the costs incurred?

Female elephant seals that breed earliest in life are probably the largest and healthiest in the cohort (see Darwin 1871, for discussion of mammals in general). Initial ovulation and sexual receptivity are probably contingent on attaining a minimum size. Although we cannot substantiate this hypothesis with direct measurements, the following observations provide indirect sup-

port: (1) Females born early in the breeding season reach reproductive age before females born later in the season; (2) large females in their prime give birth earlier in the breeding season than young, small females; and (3) the size of pups increases with mother's age and size.

Competition is the key to breeding successfully. Early in development, a female elephant seal must either rise to the level of the competition, reduce it, or avoid it altogether. A young female arriving at the rookery minimizes competition by assessing the social and physical environment on the rookery and responding according to prevailing conditions. In contrast to Weddell seals, *Leptonychotes weddelli* (Stirling 1971b), young female elephant seals that emigrate from crowded harems to new or peripheral areas increase their reproductive success. This is due in large part to the absence of former terrestrial predators at breeding sites, such as the grizzly bear, *Ursus horribilis*, on the California mainland.

When all suitable breeding space becomes saturated with mature females and competition with adult females becomes unavoidable, we expect that selection would favour females that postpone breeding until they can compete more effectively. We expect that maturation would be delayed when female density and competition is high and, conversely, that maturation rate would increase when density is reduced. It is well known that maturation rates of some populations of harp seals, *Pagophilus groenlandicus*; northern fur seals, *Callorhinus ursinus*; and southern elephant seals, *M. leonina*, increased after populations were reduced by humans (Sergeant 1973). For example, nearly all southern elephant seal females at South Georgia, an exploited population, gave birth when 3 years old, whereas the average age at first reproduction at Macquarie Island, an unexploited dense population, was 6 years (Carrick et al. 1962). The investigators reasoned that the onset of sexual maturity was inversely related to intrasexual pressures within the population, which stemmed from density in relation to available resources. York (1979) showed that the mean age of first reproduction in northern fur seals declined following commercial harvest of females. Similar results have been found for exploited blue whales, *Balaenoptera musculus*, and fin whales, *B. physalus*, in the Antarctic (Laws 1962; Gambell 1973).

This study underscores the importance of female density to individual reproductive performance and to various measures of colony

reproductive success. This effect is not surprising since female density in elephant seal society translates to number of females competing for optimal birthing and nursing sites. We have shown that the following are density-dependent: (1) female reproductive success and pup mortality on the rookery; (2) assortative mating, and hence genotypic variation in offspring produced annually; and (3) the rate and direction of emigration and the formation of new colonies. Observation of other pinnipeds leads us to suspect that the onset of sexual maturity, fecundity, and longevity also vary with female density. Thus, the degree of reproductive competition influences individual reproductive success, and as a result the size, composition, range, and rate of development of populations, as well as the evolution of the species.

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