Male-male Competition and Reproductive Success in Elephant Seals

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synopsis. Male-male competition and reproductive success of northern elephant seals, *Mirounga angustirostris*, was studied for six consecutive breeding seasons at Año Nuevo Island, California. The conclusions were as follows: (i) Less than one third of the males in residence copulate during a breeding season. A few males are responsible for the majority of copulations. (ii) The number and age of males copulating varies with: (a) harem location and topography, (b) the number of estrous females in the harem, and (c) the number of males competing for females. (iii) Copulation frequency is related directly to success in male-male competition, i.e., social rank. (iv) The same individuals may dominate breeding for three consecutive breeding seasons. (v) Successful males die within a year or two after their reproductive peak. (vi) The reproductive success of most males is nil or low because many die before reaching breeding age and some of those that reach maturity are prevented from mating by the highest ranking males. (vii) Individual strategies have important consequences for reproductive success. (viii) Male-male competition is a major cause of pup mortality prior to weaning.

The potential reproductive success of males is much greater than that of females. Changes in colony number and composition affect the reproductive success of males as well as females.

Darwin (1871) observed that male animals compete with each other to inseminate females while females do not compete for males but are choosy in selecting a mate. Darwin argued that these behaviors helped each sex produce the largest possible number of offspring.

To understand how natural selection acts differently on males and females we must know whether "males which conquer other males" leave a greater number of offspring than the conquered and whether "females that choose" leave more offspring than less discriminating females. That is, we must determine how and why reproductive success varies between the sexes and within each sex.

To estimate reproductive success in females, one simply counts the number of eggs hatched or records the number of young born. The problem is considerably more complicated for males since in most species they simply inseminate the female in a brief pairing and then depart. Under natural conditions, male reproductive success is usually estimated by counting copulations with different females. But many species present problems such as difficulty in identifying individuals and in observing animals that are highly mobile or that breed at night. In species where there is female choice, the analysis of male reproductive success is further complicated. The difficulty of studying reproductive success in males is reflected by the paucity of naturalistic studies in this area.

Naturalistic studies or observations of male reproductive success have been done on lizards (Trivers, 1972), polygynous birds (e.g., Scott, 1942; Robel, 1966; Kruijt and Hogan, 1967), a few primates (Altmann, 1962; DeVore, 1965), and a pinniped (Le Boeuf and Peterson, 1969a). Few studies have covered more than one breeding season.

The present paper reports a 6-year study

of the reproductive success of male elephant seals, *Mirounga angustirostris,* a polygynous species which is exceptionally well suited to studies of this kind for the following reasons: (i) These seals breed once a year on remote islands that are relatively free of human disturbance. The preferred breeding areas are sandy beaches which afford virtually unobstructed vision to the observer. Thus, one can anticipate the arrival of the animals and make advance preparations for studying them. (ii) Females clump together in space and time, a situation which focuses the competition among males and facilitates observations. (iii) There is no choice of males exerted by estrous females to complicate the analysis of male performance (Le Boeuf, 1972). (iv) The large size and slow movements of the animals makes it easy to record male competition, and matings with insertion can be readily distinguished from incomplete matings. (v) The aggressiveness of elephant seals makes it possible to mark or tag individuals (while they sleep) without causing a mass exodus into the water as is the case with sea lions. Marks and tags permit identification from day to day and from year to year.

Biology of the elephant seal

Elephant seals spend most of the year in the water, hauling out on land once a year to breed and once a year to moult. The breeding season haul-out begins in early December and lasts until mid-March. Adult males arrive first on the traditional beaches and immediately begin fighting and threatening each other. A stable dominance hierarchy is established quickly. Dominance is expressed by threatening gestures which are usually accompanied by a loud, low frequency vocalization (Le Boeuf and Peterson, 1969*b*). If a threatened male is subordinate to the aggressor, he moves away. If he does not move away or moves away too slowly he is attacked and bitten. If the threatened male responds with a threat vocalization of his own, a fight usually ensues in which each male delivers blows to the neck of the other and attempts to bite the other on the neck or proboscis. The loser in a fight flees from the winner. When the pair next meet, the winner need only threaten the loser to displace him. Nearly all fights involve pairs of males. The sum of all these encounters defines the social hierarchy (Le Boeuf and Peterson, 1969*a;* Le Boeuf, 1971).

A social hierarchy is evident before females begin arriving on the rookery in mid-December. Pregnant females form dense aggregations called harems. The proximity of males to the female harem is determined by social rank, the higher ranking males being closest to the females. The top ranking bull, or alpha bull, is always in or near the harem but, depending on the number of females present, other high ranking bulls may also occupy an area in the harem. More males come to occupy the harem as the number of females in it increases. Even sub-adult males sneak in from time to time. However, the lower a male's rank the more difficult it is for him to penetrate the defense of higher ranking males and to gain entrance into the harem. Each bull keeps males lower in rank than himself from approaching females.

Females deliver one pup about 6 days after they arrive. She nurses her pup for 28 days, then departs for the sea, thus weaning her pup. During the last 4 days of nursing, the female is in estrus and may copulate several times (Le Boeuf, 1972).

Males are approximately three times larger than adult females and they undergo puberty at 5 to 6 years of age. Females may copulate as early as age two and give birth the following year, although the average age of first birth is more frequently 4 or 5 years (Le Boeuf et al., 1972). Females apparently give birth to a single pup every year. Both males and females appear to die by age 14 years. The present breeding range of the Northern elephant seal is along the Western coast of North America from Isla Cedros in Baja California, Mexico, to the Farallon Islands in Central California.

STUDY AREA AND METHODS

The observations making up this study were made during six breeding seasons dating from 1968 to 1973. The study area was Año Nuevo Island, an 8-acre island ½ mile offshore and 19 miles north of Santa Cruz, California.

Elephant seals utilized two sandy beaches on Año Nuevo Island for breeding (see Fig. 1 in Le Boeuf et al., 1972). An exposed point on the mainland side of the island incorporated the Point harem each breeding season. The quasi-circular harem, which contained as many as 427 females in 1973, was located near the center of the beach and thus males could approach from all sides. During the last three years of the study, the harem took up so much space that it fissioned into two parts when the number of females declined rapidly towards the end of each season. The smaller of the fissioned harems was controlled by the beta bull, but the alpha bull still commanded the entire area at will. The Cove harem was located on a sandy beach on the seaward side of the island. Because of steep banks of sand and rock on the landward side, males could enter the harem only from the sea. In 1973, a third small harem formed on the sandy elevated saddle separating the above two beaches.

The elephant seal population at Año Nuevo Island was expanding throughout the study period. The first pups born on the island since the decimation of the population by sealers in the last century was in 1961 (Radford et al., 1965). Since then the number of pups born annually has increased and followed a sigmoid curve of growth. In 1973 386 pups were born on Año Nuevo Island. The adult female population increased from 193 females in 1968 to 470 females in 1973. The relative increase in males was slightly smaller: from 103 males in 1968 to 180 males in 1973.

Each year all males in the Año Nuevo population were marked and tagged so as to permit identification from day to day and year to year. At the beginning of each season names were bleached into the pelage of males on the dorsolateral surface of their backs (Le Boeuf and Peterson, 1969a). These marks could be read easily from the observation blinds and lasted throughout the breeding season but were lost during the mid-summer moult. Beginning in 1968, numbered plastic cattle-ear tags were attached to the interdigital webbing of the hind flippers of all males. Since then all untagged males sighted each breeding season were promptly tagged. These tags last for several years and permit individual identification from one year to the next. Approximately 20% of the females in residence each year were marked and tagged and all pups born each year were tagged.

In addition, elephant seals of both sexes and various age categories were tagged on all major rookeries where they bred during the course of the study period. These rookeries, and the year in which tagging was done, were: San Miguel Island (1968 through 1972), San Nicolas Island (1968, 1969, and 1971), Isla de Guadalupe (1969, 1970, 1971, and 1973), Islas San Benito (1970 and 1971), and Isla Cedros (1970). The tagging program provides a data base yielding information concerning dispersion, seasonal movements, immigration, emigration, ontogeny, and annual mortality.

Observations of both breeding areas at Año Nuevo Island were made from blinds overlooking the beaches and were continuous during the daylight hours for the Point harem throughout the breeding season. The Cove harem was observed during approximately 20% of the daylight hours. Aggressive encounters and copulation frequency was recorded to determine the relationship between the social rank of an individual and his reproductive success.

RESULTS

The most important results can be summarized in several general points.

1) *Less than one third of the males in residence during a season copulate. A few males are responsible for the majority of the copulations observed.* Table 1 shows

TABLE 1. *The number and per cent of males copulating during consecutive seasons.*

	1968	1969	1970	1971	1972	1973
Number of males present	103	120	125	136	146	180
Number of males copulating	14	17	32	41	51	62
Per cent of males copulating	14	14	26	30	35	34
Per cent copulations by the five most active males	83	92	69	65	53	48
Number of females present	193	243	311	352	408	470

that 14 to 35% of the males in residence each season accounted for all copulations observed. Mating was restricted to a few males as indicated by the fact that the five most active males accounted for approximately 50% or more of the copulations during each breeding season.

2) *The number of males copulating, or the reproductive success of a particular male, is limited by several characteristics of the harem: (i) the number of estrous females present, (ii) the number of competing males, and (iii) its location and topographic setting.* Table 1 shows that the number of males copulating increased as the male and female population increased. Similarly, the monopolization of breeding by a few top ranking males became less extreme with an increase in the population. It is difficult to determine which was the most important variable affecting changes in male reproductive success, the number of females in the harem or the number of males competing, since both varied from one breeding season to the next. One approach to this dilemma is to examine a single breeding season since the male population is relatively constant throughout this period while the number of females is either increasing or decreasing (see Le Boeuf, 1972). Table 2 shows that more males copulated during the 1971 breeding season when the greatest number of females were in estrus and con-

versely, the alpha male's percentage of all copulations observed was lowest when the greatest number of females were in estrus. Thus, in this situation, it is clear that the reproductive success of males varied with harem size alone.

Table 3 shows that the percentage of copulations by the alpha bull associated with the Cove harem was always higher than that of the alpha bull associated with the Point harem. This difference was due in part to the restricted access of the Cove harem resulting from its topographic setting. The alpha male in the Cove harem did not have to work as hard to keep other males from entering the harem since he was protected by high banks for 180° and could concentrate on intruders entering from the sea. The Point harem was more difficult to defend since males could enter from all directions. Additionally, the Cove harem was easier to defend because it held fewer females and took up less space. Normally, an energetic alpha male can keep other males out of a tightly packed aggregation of females if the latter number 40 or less (Le Boeuf, 1972).

In summary, the reproductive success of males can be expected to vary with the defensibility of the harem. The larger the harem size, the more area it covers and the more vulnerable it is to infiltration by males. Exposed harems are harder to defend than those which afford restricted

TABLE 2. *Changes in the reproductive success of males associated with the Point harem during the 1971 breeding season.*

	Jan. 22-31	Feb. 1-10	Feb. 11-20	Feb.-Mar. 21-2	March 3-12
Number of males copulating	19	22	24	12	2
Number of copulations (approximate number of females in estrus)	79	180	256	99	8
Alpha male's percentage of total copulations	34	27	21	40	88

TABLE 3. *Percentage of copulations by alpha bulls in their respective harems. The number of females present during each breeding season is in parentheses.*

	1968	1969	1970	1971	1972	1973
Cove harem	73	100	100	59	100	100
	(81)	(58)	(40)	(53)	(53)	(26)
Point harem	37	49	28	28	14	12
	(112)	(185)	(271)	(299)	(355)	(427)

access to males. The importance of the number of competing males is not clear.

3) *As harem size increases, younger males begin to copulate.* Poulter and Jennings (1962-1966) tagged pups born on Año Nuevo Island from 1964 to 1967. Thus, known age males up to 8 years old were available for direct observation as well as for serving as standards in estimating the age of unmarked seals. Each breeding season all males were put into one of four categories according to their: (i) overall length, (ii) degree of neck shield cornification, and (iii) proboscis development. Development of each of these structures correlates with advancing age. For example, 6-year old males are approximately 12 ft in length, have only a rudimentary neck shield and their nose is just beginning to dangle. Full grown males are longer than 14 ft and have fully developed neck shields and probosces.

Table 4 shows changes in the reproductive success of males by age category throughout the study period. As population size increased, younger males began to copulate. For example, in 1968, all copulations observed were performed by 10 of the 23 adult males in residence, i.e., 43% of the males in the adult category

copulated. In 1969, three SA^4 males and one SA^3 male copulated in addition to adult males. From 1970 to 1973, SA^4 males accounted for 7 to 16% of the copulations observed and SA^3 males accounted for a little less than 5% of the copulations observed. Although adult males were responsible for the majority of the copulations throughout the study period, it is clear that the reproductive success of subadults increased as the population grew. The variability in reproductive success in each category may be due, in part, to error in categorizing the males.

The success of younger males was not due to a differential increase in the size of this category over the course of the study period since the percentage of SA^3 males to total males present was 44% in 1968 and 40% in 1973, an insignificant change. The success of younger, smaller males seems to have been due to easier access to females as harem size and the area it covered increased. Top ranking bulls simply reached a point where they could not keep young males away from females.

4) *Copulation frequency is roughly proportional to social rank; the higher a male's social rank, the more frequently he*

TABLE 4. *The percentage of the total copulations per season by males in the Point harem is shown in the top figure for each age category. The lower figure represents the number and percentage (in parentheses) of males in each age category that copulated at least once each season.*

Age category (SA = subadult)	Approximate age	1968	1969	1970	1971	1972	1973
Adult	8-14+	100	97	79	88	86	89
		10(43)	13(46)	17(81)	18(72)	18(69)	35(73)
SA^4	7-8	—	2	16	8	10	7
			3(17)	5(17)	6(23)	15(62)	9(35)
SA^3	6-7	—	1	5	4	4	4
			1(2)	6(12)	9(18)	15(25)	8(12)
SA^2	5	—	—	—	—	—	1
							1(4)
Total copulations observed per season		128	146	420	627	1004	914

TABLE 5. *The percentage of copulations per season by the 10 top-ranked males associated with the Point harem. Males were assigned the social rank they held for the longest period of time during the six-week period that females were in estrus.*

Social rank	1968	1969	1970	1971	1972	1973
1	37	49	28	28	13	12
2	31	22	18	19	10	8
3	14	14	11	8	14	13
4	4	4	9	13	9	4
5	6	1	5	4	8	6
6	0	4	1	4	10	4
7	2	1	4	4	4	8
8	1	1	5	2	4	8
9	1	1	1	2	5	4
10	1	1	1	1	2	3
Spearman rank—difference correlation coefficient	.86	.90	.90	.97	.87	.66

copulates. Table 5 shows the relationship between the percentage of copulations by successful males associated with the Point harem each breeding season and the social rank held when females were in estrus. The relationship between these two variables is high and positive but decreased notably as harem size increased. All Spearman rank-difference correlation coefficients are significant ($P < .05$, df = 10).

Table 5 provides further support for the earlier point that the monopoly of a few males declines with increases in harem size.

5) *Individual males may copulate in three or four different years and an exceptional bull may even dominate breeding for three consecutive seasons. Males die within a year or two after their most successful year.* One can compare the performance of males from one season to the next and arrive at an estimation of the number of females inseminated by multiplying a male's percentage of the total copulations observed in one breeding season times the number of females that were present. This index (ENFI) was computed for the most successful males associated

TABLE 6. *Estimated number of females inseminated (ENFI) by the most successful males associated with the point harem.*

Males	1968	1969	1970	1971	1972	1973	Totals
GL	40 (1)	0 (low)	1 (low)	+	+	+	41
GLS	16 (3)	90 (1)	6 (low)	+	+	+	112
BO	1 (7)	41 (2)	78 (1)	+	+	+	120
ADR	AB	0 (low)	3 (low)	81 (1)	37 (1-2)	50 (1)	171
RAT	AB	0 (low)	0 (low)	1*	48 (1-2)	18 (4)	67
CLS	34 (2)	2 (low)	+	+	+	+	36
2STP	0 (low)	2 (6)	50 (2)	1+ (low)	+	+	53
59S	AB	0 (low)	10 (low)	54 (2)	+	+	64
OB	0 (low)	0 (low)	14 (8)	**	50 (2-3)	2 (low)	66

* One copulation in the Cove harem.
** Arrived late and did not copulate.
ENFI = the percentage of a male's copulations observed in a season to the total observed × the number of females present during the breeding season. Social rank is in parentheses. Low = social rank below 10. + = absent and assumed dead. AB = absent.

with the Point harem and the results are shown in Table 6.

Five males listed in the table copulated in three or more seasons and three of them might return for an additional season. GLS, BO, and ADR each inseminated over 100 females in two consecutive seasons. The latter achieved the alpha or beta position for three consecutive years and easily dominated breeding during that period. (See p. 176.)

In the Cove harem, a different male was in the alpha position each year and as a result, no single male monopolized breeding on this beach for more than one season. Some males competed in one harem one year and changed to the other in the next year, e.g., RAT in 1971 and 1972.

Five out of six males listed in Table 6 did not return within 1 or 2 years after their most successful year and I assume they died. This assumption is based on two observations: (i) Males absent in one year on Año Nuevo Island were never observed on this island the following year. (ii) Although 661 puberal males (6 years of age or more) were tagged on five major rookeries during the study period—Año Nuevo Island (274), San Miguel Island (72), San Nicolas Island (30), Isla de Guadalupe (225), and Islas San Benito (59)—not a single one was ever observed on a rookery other than the one where it was tagged during the season of tagging or in subsequent breeding seasons. Thus, it appears that once males reach puberty and appear on a rookery during the breeding season, they hold allegiance to this same rookery and reappear there in subsequent breeding seasons until they die.

Less successful males than those listed in Table 6 showed a similar pattern. Seven of nine males that attained full growth and who were observed for at least 3 years did not return after their best year; the other two males survived for an additional year.

6) *The reproductive success of most males is nil or low because many die before reaching breeding age and some of those that survive to maturity are prevented from mating by higher ranking males.*

Since Poulter and Jennings (1962-1966) attached metal tags to 151 male pups born on Año Nuevo Island during the years 1964 to 1967, and since males begin to appear on rookeries during the breeding season of their fifth or sixth year, some of these animals were observed in 1970 and in subsequent years. Mortality prior to participation in breeding can be estimated if one assumes that tag loss was neglible and that males born on Año Nuevo Island returned there to breed when they reached puberty.

I assume that tag loss was neglible because: (i) The tags used in 1965 and 1966 were attached to the interdigital webbing of the hindflippers where the connective tissue is tough, bleeding is minimal and the wound heals quickly (the tags were attached to the axilla of the foreflippers in 1964). (ii) The tag is concealed and unlikely to snag when attached to the hindflippers since the latter are closed except when the seal is swimming. (iii) The tags are made of non-corrosive monel and have been shown to last for as long as 21 years on Alaska fur seals (Anonymous, 1962). (iv) I observed few animals bearing scars indicative of lost tags even though over 1700 elephant seals were single-tagged on several rookeries between the years 1968 and 1972 (Le Boeuf et al., 1974) in addition to those tagged by Poulter and Jennings. (v) Out of 13 yearlings double-tagged on the Farallones in 1968, three were observed within 6 months to 3 years later with both tags intact. No reports of animals with one tag missing have been received to date.

I assume that males born on Año Nuevo Island during the mid-sixties returned to their birth place to breed because Año Nuevo-tagged males were not observed on other rookeries during the study period even though approximately 400 male pups born on Año Nuevo Island were tagged between 1964 and 1969 (Poulter and Jennings, 1962-1966; Le Boeuf, unpublished). If these males had been present on other rookeries during breeding seasons in the study period, it is likely that they would have been seen since the tags for each

TABLE 7. *The number of males tagged as pups on Año Nuevo Island and the number of those sighted there five to nine years later. The per cent return are in parentheses. Tagging was done by Poulter and Jennings (1962-1966).*

Year	Number of male pups tagged	Number present and (per cent return)				Age in years
		1970	1971	1972	1973	
1964	29	2^d (6.9)	2^c (6.9)	1^b (3.4)	0^a	a = 9
1965	35	1^e (2.9)	5^d (14.3)	5^c (14.3)	5^b (14.3)	b = 8
1966	43	0	3^e (7.0)	4^d (9.3)	3^c (7.0)	c = 7
1967	44	0	0	3^e (6.8)	3^d (6.8)	d = 6
						e = 5

rookery are color-coded and my associates and I visited all major elephant seal rookeries at one time or another (see study area and methods) for the specific purpose of reading tags. In addition, colleagues visiting these islands read tags and forwarded the information to me.

In summary, I am confident that tag loss was less than 5% and that males born on Año Nuevo Island in the mid-sixties returned to this island to breed when they reached puberty since they were not seen elsewhere.

Table 7 shows the number of males, aged 5 to 9 years, observed during the latter part of the study period. These data show that none of the males tagged in 1964 lived to age nine! Furthermore, mortality may have been as high as 97% prior to reaching age eight and as high as 86 to 93% prior to reaching ages six or seven. The low returns for 5-year olds is not due to mortality alone since some males do not make their first breeding season appearance until their sixth year. Similarly, the returns for the 1964 cohort must also be considered with caution because pups born in this year were tagged on the foreflippers. Tags in this location are more readily overlooked than those attached to the hindflippers. Thus, although the present sample is limited in size, the data indicate strongly that male mortality prior to reaching early breeding age can be very high.

Data were obtained on the related question of annual mortality among males. Since virtually all males were marked and tagged individually each season it was a simple matter to record which of them did not return each year by age category. These data are shown in Table 8. Although annual mortality clearly fluctuated from one breeding season to the next in each age category, averaging across years reveals a probability of approximately .45 that a male present in one breeding season will not return in the next breeding season, i.e., die. Annual mortality varied across age categories and was evidently slightly higher for the oldest males. Figures for the SA^2 category are no doubt less reliable than those for other categories due to the small sample size. Finally, the upper age limit reached by males of this species appears to be about 14 years as judged from preliminary tooth sectioning studies by Kenneth Briggs in my laboratory.

If a male survives to breeding age, what are his chances of mating? We can consider first the males treated in Table 7 keeping in mind that they were not fully mature. Only 5 of the 16 returning males listed in Table 7 copulated (nine males were observed in two or more seasons). In 1971, both 7-year old males and one of the 6-year old males copulated. The best performance was by a 7-year old who achieved 1.1% of the total copulations in that year; this male did not return in 1972. In 1972, the 8-year old male copulated six times, two 7-year old males copulated twice and five times, respectively, and one 6-year old copulated once. None of these males achieved more than 1% of the total copu-

TABLE 8. Annual mortality: proportion and per cent of tagged males that did not return from one breeding season to the next.

Age category	1968-69	1969-70	1970-71	1971-72	1972-73	Totals proportion per cent
Adult	6/19 = 31.6	14/25 = 56.0	13/20 = 65.0	13/25 = 52.0	11/26 = 42.3	57/115 = 49.6
SA[4]	11/18 = 61.0	9/14 = 64.3	13/27 = 48.1	10/25 = 40.0	5/21 = 23.8	48/105 = 45.7
SA[3]	17/30 = 58.6	13/36 = 36.1	19/33 = 57.6	15/37 = 40.5	15/54 = 27.7	79/190 = 41.6
SA[2]	0/1 = 0	4/8 = 50.0	6/8 = 75.0	3/9 = 33.0	6/14 = 42.9	19/40 = 47.5
Totals	34/68 = 50.0	40/83 = 48.2	51/88 = 58.0	41/96 = 42.7	37/115 = 32.2	203/450 = 45.1

lations observed in 1972. In 1973, four 8-year olds and one 7-year old accounted for 3% of the copulations observed; one 8-year old achieved 1.6% of the total. The most successful marked male was born in 1964; he failed to copulate at age six, copulated six times at age seven, six times at age eight and then he died, apparently, since he did not return for the 1973 season. Five-year old males were never observed mating, although they attempted to do so.

Another approach to the matter of mating among the surviving males is to consider the percentage of males in each age category that *did not* copulate. These data are presented in Table 9 for the entire study period. Evidently, the older and larger males were as a group much more successful than younger males but even in the adult category many individuals failed to mate. Note also the trend for a higher percentage of males in each category to copulate as the size of the population increased over the course of the study period.

Finally, several males were observed to mature, peak, decline and then disappear without ever having been observed copulating.

Lack of mating in surviving males was due primarily to the fact that males prevented those lower in rank from copulating by overt attack or by the threat of it (Le Boeuf, 1971). The higher a male's rank the more males he prevented from copulating and the less likely it was that he was treated in a similar fashion (Le Boeuf and Peterson, 1969a). Only the alpha male mated without interruption. The result was that low ranking males were either prevented from entering the harem in the first place or once in proximity to females they were prevented from copulating even though they and the female were willing. For example, 76% of mounts attempted by males having a social rank lower than the top five ranking bulls were interrupted by threatening males in 1968. Copulations in progress were interrupted in a similar manner. Over the entire study period, 5 to 10% of copulations each breeding sea-

TABLE 9. *Number and per cent (in parentheses) of marked males in each age category that did* not *copulate.*

	1968	1969	1970	1971	1972	1973
Adult	13	15	9	8	7	11
	(56.5)	(53.6)	(42.9)	(32.0)	(26.9)	(22.4)
SA⁴	14	16	21	18	13	19
	(77.8)	(88.9)	(72.4)	(69.2)	(54.2)	(67.9)
SA³	39	41	42	42	43	61
	(100.0)	(95.3)	(87.5)	(84.0)	(71.7)	(85.9)
SA²	9	13	16	10	17	31
	(100.0)	(100.0)	(100.0)	(100.0)	(100.0)	(96.9)

son were interrupted in less than 1½ min after insertion occurred. The period of insertion averages 5 min (Le Boeuf, 1972).

The threat of attack in the harem is so likely that it appears to intimidate some males from competing; some of them retreated from the harem areas and spent most of their time sleeping in non-breeding areas. After several days of this non-activity, they might timidly check the action in one of the harems only to be turned away by the vocal threats of dominant males, whereupon they returned to the resting areas. Interestingly, even after a male gave up competing, he remained in the vicinity of the island until all females departed.

7) *Individual strategy has important consequences for reproductive success.* In using the term "strategy" I don't wish to imply that male seals deliberately choose among alternatives for maximizing their reproductive success but rather that certain behaviors are more apt to lead to copulation than others and that these would be subjected to natural selection. Time of arrival on the rookery is a good example of this kind of behavior.

Breeding age males may arrive on the rookery as early as the first week in November or as late as the last week in February. Those who arrive earliest and those that arrive very late are not likely to be successful at mating. Although the earliest males to arrive have the advantage of securing a high rank from the start, this is usually offset by the likelihood of being deposed before females begin coming into estrus around the middle of January. For example, only in one year, 1969, did the male who was alpha in the Point harem at the beginning of the season remain alpha until all females had been inseminated around the first week in March. In all other years the initial alpha male was deposed before the season ended—in 3 of 5 years before the first females came into estrus! Initial alpha males expend much energy early in the season chasing subordinates out of the harem and their decline in rank is in part due to exhaustion.

Males that are most successful at mating arrive during the first two weeks in December. For example, in the Point harem, males that arrived during this period did 89% of the breeding in 1969, 70% in 1970, and 73% in 1971. Full grown males arriving after this period ended were far less successful and no male arriving later than 31 December achieved more than 1% of the copulations observed in any one season in the Point harem.

Males arriving later than mid-December are unsuccessful at mating because they must compete for social rank in a dominance hierarchy that is already established. Since dominance is established between individuals, a male cannot gain control of a harem by simply beating the alpha male. He must fight all males that he cannot bluff or that he has not dominated in previous seasons. Thus, the later a male arrives, the more males he must fight and in effect the more difficult it is for him to rise to a high rank. Only high-ranking males dominate breeding. Interestingly, late-arriving males are likely to spend much of their time sleeping instead of competing around the female harems.

With respect to time of arrival on the rookery, the best general strategy for maximizing reproductive success would appear

to be for a male to arrive in early December, obtain one of the top five social ranks, spend as much time as he can resting until mid-January and then when females begin to come into estrus, attempt to move up in rank to the alpha position. Some successful males adopted this strategy.

A few other successful strategies observed during the course of the study were as follows: (i) Copulate in the harem. A poor strategy appears to be waiting to mate with females as they depart from the harem into the sea. Although some of these females are still in estrus, they have been copulating in the harem for four or more days prior to departure and presumably have already been fertilized. For example, the adult male, PIN, adopted this strategy of waiting in the shallow water near the Point harem in 1968. He was observed copulating with eight different females but each one of them had copulated previously with a high ranking male in the harem. Although this would seem to be a poor strategy, a few low ranking adults and young males adopted this strategy each breeding season. (ii) On several occasions males were observed challenging and fighting a male dominant to them after the latter had just finished a long fight and was exhausted. Under these circumstances, the challenger is more apt to win and thus elevate his social rank. This strategy brought about the downfall of two alpha bulls. (iii) Young and low ranking males move frequently from one harem to another in an apparent attempt to settle in a harem which will offer them the highest possibility of mating. These movements were particularly noticeable on rookeries such as San Miguel Island where several harems were located adjacent to each other on a large sandy beach. A case illustrating the benefit of moving when the probability of mating is low occurred in 1968 at Año Nuevo Island. For the first six weeks of the season RNK was alpha and CLS was beta in the Cove harem. In mid-January CLS challenged RNK and was defeated in a long, bloody fight. After a short rest he swam around the island, hauled out near the Point harem, and boldly threatened the resident alpha bull who retreated immediately. But CLS was challenged by other high ranking males near the Point harem and he eventually settled into the beta position for the rest of the season. The benefit to CLS of moving to the other harem after the losing fight can be calculated. RNK finished the season with 73% of the copulations observed with 50 females for an ENFI of 36 females. Had CLS remained near the Cove harem he could have inseminated no more than 14 females, at best. In the Point harem, he achieved 31% of the copulations observed with 112 females for an ENFI of 35 females, almost as high a score as RNK, the alpha bull that beat him! (iv) Lastly, some young males sneak into the harem and occasionally succeed in copulating with females who are almost as large as they are by apparently passing for females. These males have small noses, keep their head low and refrain from threatening others. Perhaps it is because of this "low profile" strategy and their resemblance to females that some of these young males were often more successful at mating than larger adult males.

8) *Male-male competition is a major cause of pup mortality prior to weaning.* In their effort to achieve high social rank and copulate with females, males trample and crush young pups in their paths. Males are impervious to a pup's presence and neither its shrill cries nor its mother's aggressiveness persuades a 2 to 3 ton bull to move when he has come to rest on a pup. Newborns less than 1 week old are the most frequent victims and death results from ruptured organs and internal hemorrhage. Each season, except 1973, 13% to 14% of the pups born on Año Nuevo Island died before they were 28 days old, the time when they are usually weaned. Pup mortality doubled in the exceptional year due to inclement weather. Necropsies performed in 1971 and 1972 revealed that 39% and 43% of the pup mortality each year, respectively, could be attributed to the competition among males (Le Boeuf et al., 1972).

Is a male likely to kill a pup he sired in

a previous year? Clearly, this behavior would be antagonistic to his reproductive success. The likelihood of this happening must be low since most males do not return and secure a high position in the same harem following their best performance. But there are exceptions and one will be considered. The male most likely to have killed his own offspring was ADR who inseminated 81 females in 1971 and was active in the same harem the following year (Table 6). Fourteen percent of the pups he sired in 1971 (11 pups) would have died on the rookery from various causes in 1972 and 43% of these, or five of his pups, would have been crushed by males. Even if ADR killed all five of these pups (an unlikely event since he was one of at least 10 high ranking males present in the harem throughout the 1972 season, not to mention 115 other males that entered the harem from time to time), this loss would have been offset by the benefit he accrued from inseminating 37 females in 1972. In other words, if ignoring pups in his path enabled a male to inseminate more females, then this behavior would be selected even if it meant that he sometimes killed his own offspring.

DISCUSSION

I've summarized the extent and circumstances under which reproductive success has varied among male elephant seals at Año Nuevo Island. The conclusion is clear: "males which conquer other males" do indeed leave a greater number of offspring than the conquered and the differential in reproductive success between victor and vanquished is immense. Male attributes which bear directly on reproductive success—such as great size and fighting ability, long life, and the ability to fast throughout the breeding season—have no doubt been subjected to great selection pressure.

The factors which determine a female's success in leaving progeny have not been studied systematically; however, it is clear that the reproductive potential of the two sexes is of a different order of magnitude.

The most successful female can produce about ten pups in a lifetime if she gives birth every year starting at age four and ending at age 14. The outstanding male—having first survived to old age and bested his cohorts—can sire at least 17 times this number of offspring (see ADR in Table 6). The factors that limit the reproductive success of each sex in other animals and the consequences of these differences on behavior is given excellent treatment by Trivers (1972).

Colony structure and dynamics influence the reproductive success of both males and females. One important variable, the size of the colony with respect to suitable breeding areas, i.e., the degree of crowding, will be considered. This paper has shown that a higher percentage of resident males begin to mate as breeding beaches become more crowded. The reproductive success of females changes, too, for it is intimately associated with that of males.

McLaren (1967) and Bartholomew (1970) pointed out the importance of female gregariousness for reproductive success in female pinnipeds. Females that congregate near the most successful territorial males, or those with the highest social ranks, enhance their "inclusive fitness" through their offspring (Hamilton, 1964) since they are inseminated by the "most fit" males (insofar as territorial acquisition and high social status are genetically based). Conversely, females that breed with subordinate "marginal males" should ultimately produce fewer offspring and this behavior should be selected against. Bartholomew (1970) concluded that "gregariousness in females should be positively reinforced just as long as the territorial behavior of the males results in the exclusion of some males" and further that ". . . the mutual reinforcement between female gregariousness and male territoriality will persist as long as the level of reproductive performance does not fall below some critical value."

As the Año Nuevo colony grew, fewer and fewer males were excluded from breeding. With continued increases in the population, accompanied by the trend for a higher percentage of copulating males each

year, a point should be reached where all or nearly all males will have an equal opportunity to mate. As panmictic mating among males is approached, the mutual reinforcement between female gregariousness and male dominance should diminish and ultimately break down. Then it would no longer be advantageous for females to mate in crowded harems since the harem would contain males of varying ages and fitness. Moreover, since pup mortality is greatest in crowded harems (Le Boeuf et al., 1972) one would expect females to begin utilizing peripheral beaches and to begin breeding with "marginal males." In this way, decreasing variation in male reproductive success could influence the tendency of females to disperse to different rookeries or to begin breeding in new places.

Females have been observed giving birth and mating in new areas with immature males. In 1972, elephant seals began breeding on Southeast Farallon Island, 89 km north of Año Nuevo Island (Le Boeuf et al., 1974). The two males that mated with the Farallon females in both 1972 and 1973 were unquestionably "marginal." Both had been observed, marked, and identified at Año Nuevo Island. One was a SA^2 and the other a SA^3. The latter was probably 7 years of age or less. Unfortunately, the origin and age of the females could not be determined.

However, data collected by L. Petrinovich, M. Bonnell, and me on a crowded beach at Isla de Guadalupe suggest that before the point is reached where all males stand an equal chance of mating, the composition of resident males changes such that the full-grown male category increases in size and adults outnumber individuals in all other age categories. Censuses taken in early February 1973 on Pilot Rock beach, one of the two large congested beaches on Isla de Guadalupe where most of the breeding takes place, revealed that 60% of the resident males were full grown adults, 20% were SA^4, 17% were SA^3, and 3% were SA^2. In contrast, at Año Nuevo Island in 1973, 29% were adults, 16% were SA^4, 40% were SA^3, and 15% were SA^2.

This difference in colony composition is in part due to the fact that Año Nuevo Island is a colony of recent origin, its population is expanding, and it receives immigrants from southern rookeries annually. Nearly all male immigrants observed during the breeding season are SA^2 and SA^3, which explains why these age categories are so large relative to Pilot Rock beach. On the other hand, Isla de Guadalupe is the oldest and largest northern elephant seal rookery. The size of the breeding population has been relatively constant during the last several years and the rookery receives no immigrants (Le Boeuf, unpublished). Pups and prepuberal young disperse annually to rookeries to the east and to the north. Very likely, the inability of young puberal males to gain entry on breeding beaches congested with older, more dominant males causes them to migrate to less crowded, peripheral colonies to the north, such as Año Nuevo Island. Christian (1970) has pointed out that population density and intraspecific competition (particularly in the form of social hierarchies) combine to bring about dispersion: "Low-ranking individuals are generally forced to emigrate from their birthplace and to find space in suitable habitat unoccupied by higher-ranking members of the same species or by members of dominant competing species." These subordinate individuals suffer high mortality but some of them become dominant in the new area.

In other words, once crowding gets extreme most junior males don't even get to land on the breeding beaches. This is the typical breeding situation in territorial sea lions, particularly early in the season, with only adult males possessing territories (e.g., Peterson and Bartholomew, 1967; Rand, 1967; Gentry, 1970). The consequence of this arrangement is that adult males predominate both in number and in monopolizing mating. During an 11-day study period at Pilot Rock beach, adults did 91% of the copulations observed, even though 47% of the males present mated (see Tables 1 and 4 for comparisons with

Año Nuevo Island). Many males copulated but nearly all of them were adults. This form of exclusion should continue to benefit females that congregate and breed in congested harems and this behavior should continue to be reinforced.

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* Note added in proof: The alpha male and most frequent copulator associated with the Point harem in 1974 was none other than ADR. Thus, he has dominated breeding at this location for 4 consecutive years and has apparently inseminated over 200 females!