

SEXUAL SELECTION'S EFFECTS ON MALE LIFE HISTORY AND THE PATTERN OF MALE MORTALITY¹

WALTER L. CLINTON² AND BURNEY J. LE BOEUF

Department of Biology, University of California, Santa Cruz, California 95064 USA

Abstract. Modifications of male life history due to sexual selection should be apparent in polygynous species such as elephant seals, in which sexual selection has produced a high degree of sexual dimorphism. In theory, male traits that confer a mating advantage bear survival disadvantages. The aim of this study was to examine the relationship between sexual selection and life history patterns in male northern elephant seals, *Mirounga angustirostris*. A life table, with age-specific estimates of mortality and reproduction, was constructed for male elephant seals from resighting data of tagged seals. Increased age-specific mortality was associated with the period of first reproduction by males, which occurred from 6–10 yr of age. A negative relationship was found between mating success and future survival in males that were beginning to breed. Older males showed no phenotypic costs to reproduction, and a positive, but not significant, relationship was shown between current mating success and future survival and mating success.

Key words: *cost of reproduction; demography; future survival vs. mating success; life history; male life table; male mortality; pinnipeds; Mirounga angustirostris; northern elephant seal; sex differences.*

INTRODUCTION

Modifications of male life history due to sexual selection should be most apparent in polygynous species in which sexual selection has produced a high degree of sexual dimorphism. Many pinnipeds exemplify this association between polygyny and sex differences produced by sexual selection (Nutting 1891, Bartholomew 1970). The most striking sex difference in pinniped morphology is in body size; adult males of some species are 1.2–7.8 times heavier than females (Alexander et al. 1979). The high degree of sexual dimorphism in the polygynous pinnipeds has been attributed primarily to the advantage of large size in male–male combat for access to females that congregate in dense groups on the breeding rookeries. In addition, large size permits long fasts (Bartholomew 1970). Two sex differences in life history are also found in the polygynous pinnipeds: first, males mature sexually and begin breeding much later in life than females, and second, males have higher mortality rates and live shorter lives than females (Stirling 1975).

Sex differences in life history patterns are usually attributed to the operation of sexual selection (Selander 1965, Orians 1969, Charlesworth 1980). In polygynous species large variance in male reproductive success is associated with strong selection pressure on male traits that are important in obtaining mates (Arnold and Wade 1984). Strong sexual selection on males leads to sex differences in morphology and behavior, and these

modifications in males are usually accompanied by differences between the sexes in age-specific mortality and reproductive rates.

Darwin inferred a survival disadvantage to sexually selected male traits because they are sex-limited in their expression and their development is often delayed until after sexual maturity. He reasoned that sexually selected traits must bear some disadvantages since otherwise females would also possess these traits (Darwin 1871). Among vertebrates, sex differences in survival have provided consistent support for Darwin's hypothesis. In polygynous species males generally have lower survivorships than females during most stages in life and lower life expectancies (Carrick and Ingham 1962, Wittenberger 1978, Dittus 1980, Froehlich et al. 1981, Stamps 1983, Sherman and Morton 1984, Clutton-Brock et al. 1985, Wilson and Daly 1985). In monogamous species, either the reverse is true or no sex difference is found (Trivers 1972, Stirling 1975).

Sexual selection on males appears to increase the costs of reproduction, and deferred maturity in males may be a strategy to minimize these costs (Selander 1965, Charlesworth 1980). In many birds and mammals, males produce sperm and are physiologically capable of breeding before the age when they compete for mates, and before the full development of secondary sexual characteristics (Wiley 1974, Wilson 1975). By refraining from reproduction and avoiding the risks and expenses in time and energy of reproductive effort, younger males theoretically reduce the mortality associated with developing sexually selected traits, and thus increase their reproductive value (Trivers 1972, Charlesworth 1980).

On the other hand, traits that confer advantages in

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² Present address: 5844 N.E. 75th Street, Seattle, Washington 98115 USA.

reproductive competition also may have inescapable survival disadvantages. Modifications of male life history associated with larger size, such as higher growth rate, a longer period of growth, and delayed maturity, have been linked to higher male mortality rates (Trivers 1972, Case 1978, Warner 1980, Clutton-Brock et al. 1985). In polygynous mammals a distinct pattern of male mortality may reflect the phenotypic cost of sexually selected traits; age-specific male mortality curves frequently feature a "hump" in the midst of a typical U-shaped mortality curve due to a period of increased male mortality before adulthood (Ralls et al. 1980, Froehlich et al. 1981). In addition to high growth rates, other male traits associated with increased mortality include metabolic characteristics, competition for resources and social status, and emigration (Ralls et al. 1980). Presumably the evolutionary disadvantage of higher pre-reproductive mortality is offset by the value of sexually selected traits in obtaining mates (Trivers 1972). Small, immature males don't reproduce because they are unable to compete effectively for access to mates, and the potentially high reproductive success of a male is realized only by the largest, most vigorous, mature individuals (Darwin 1871, Geist 1971, Le Boeuf 1974, Trivers 1976, O'Donald 1980, Clutton-Brock et al. 1982, Clutton-Brock 1983).

The aim of this study was to examine the effects of sexual selection on the male life history pattern of northern elephant seals, *Mirounga angustirostris*. The life history characteristics investigated include mortality rates, reproductive rates, and age of first reproduction. Previous studies of reproductive behavior in both sexes of northern elephant seals have suggested that sex differences in life history have been produced by strong sexual selection (Le Boeuf and Reiter 1988). A sex difference in age-specific survivorship has not been found, but the maximum life-span differs between the sexes, with an observed maximum age for females of 19 yr, and a maximum for males of 14 yr (B. J. Le Boeuf and J. Reiter 1988 and unpublished data). Because males begin to breed at a later age than females, the probability of survival to breeding age is lower for males than for females. Once males begin breeding they have a relatively brief reproductive life-span compared to females since their maximum life-span is shorter than that of females.

Strong sexual selection is predicted to produce qualitative differences in the pattern of survivorship and mortality of male elephant seals. The curve of age-specific male reproductive value should increase steadily for males that successfully pass through the period of mortality before maturity, following a pattern observed in male red deer (*Cervus elaphus*; Clutton-Brock et al. 1982). In adulthood, reproductive value should rapidly decrease due to high mortality rates associated with reproduction. Although some males are successful for several consecutive seasons (Le Boeuf 1974), a phenotypic cost to reproduction should be found, mea-

surable by the negative effect of current reproduction on subsequent survival and reproductive success. To test the accuracy of our predictions, we constructed a life table and examined the pattern of male life history.

METHODS

The data in this study were obtained during 1978–1990 at Año Nuevo, California from marked male northern elephant seals that ranged in age from 1 mo to 14 yr. We determined survival, phenotypic development, and reproductive success among cohorts of tagged known-age males that were born at Año Nuevo and at two rookeries in the Channel Islands of southern California, San Miguel Island and San Nicolas Island. Known-age males were marked by tagging shortly after weaning with 1 or 2 numbered cattle ear tags attached to the hind flipper webbing (Le Boeuf and Peterson 1969). We also collected data from known-history males that were tagged when immature, between 4 and 7 yr of age, at Año Nuevo; these males' ages were estimatable from body size and physical features to within 1 yr. We attached additional tags to tagged males later in life to minimize the loss of identifying marks. In order to recognize males easily during behavioral observations, we marked males with names and numbers by application of black hair dye or hair bleach to their pelage during molting and breeding haul-out periods at Año Nuevo.

We calculated estimates of mortality from records of returning tagged seals obtained from observers at Año Nuevo, Southeast Farallon Island, the Channel Islands, and the northern coast of California and Oregon (Clinton 1990). A total of 1840 male elephant seal weanlings were tagged at Año Nuevo from 1978 through 1984. After their initial departure to sea, 684 of these males were resighted at 7 mo of age or older. Not all the 1156 males that were never resighted had died. Elephant seals are seldom observed dead, and during this study only 8 moribund male seals were found. Tagged weanlings that lived past 7 mo of age may have been overlooked during surveys for tagged seals on rookeries, they may have dispersed to remote areas, or they may have disappeared because they lost their tags. To adjust the estimates of male mortality, we estimated the number of seals that were alive but not resighted, and the number of seals that lost their tags (Clinton 1990).

Data for known-age males were also obtained from 25 males tagged as weanlings in 1978 at the Channel Islands that survived past 6 yr of age and permanently immigrated to Año Nuevo. We collected data from 37 estimated-age males tagged as subadults between 1984 and 1985; we estimated these males were 6–7 yr of age at tagging, and thus born in 1977–1979. Due to the low survival of males to 11 yr of age—only one known-age and two estimated-age males—we included data for the oldest males present during the period between 1983 and 1987 at Año Nuevo. This group included 1

known-age and 8 estimated-age males that lived to 11–14 yr of age during the study period.

Mortality estimation and life table calculations

We estimated age-specific mortality rates from resightings of tagged and marked males, then calculated the other parameters in the life table from the mortality rates. Our resighting data included both complete life-spans and partial life-spans for males that were lost for reasons other than dying. We handled partial records of life-spans, in other words life-spans that were "censored" before the individual died, by using an actuarial method for estimating life table parameters from data with right-censored observations (Miller 1981, Cox and Oakes 1984). We censored the life-spans of males that permanently emigrated from Año Nuevo, were overlooked while present, lost all tags, or survived past the end of the study period. We calculated mortality rates and survivorship from these resighting data with the SAS LIFETEST procedure (SAS Institute 1985).

We analyzed the 1978–1984 Año Nuevo cohorts by combining these data to form one sample that we treated as a single cohort (e.g., Caughley 1977). We grouped the resighting data by age intervals. Males reached successive age intervals as they were sighted during the fall haul-out and the following molt haul-outs. We assumed that when seals disappeared from the sample they disappeared during the age interval in which they were last seen, which means that mortality rates were calculated from one fall–winter haul-out to the next.

We analyzed separately the 1978 known-age Channel Island cohort and the estimated-age males to estimate their mortality rates from 6–14 yr of age. To construct a complete mortality curve for males, we estimated age-specific mortality rates from a pooled cohort that contained all four groups of males: Año Nuevo cohorts, Channel Island cohort, estimated-age males, and the oldest males. We calculated age-specific life expectancy, which is the age-specific mean future life-span, from the age-specific survivorships by the standard demographic methods (Krebs 1989). We used age-specific fecundity rates and survivorship to calculate reproductive value by Pianka's simplified method, which assumes a stable population that is not increasing in size (Pianka and Parker 1975).

Tag loss, missed resights, and emigration

To determine how many males to censor at each age interval, we estimated the rate of tag loss, the proportion of seals overlooked in surveys, and the number of emigrants. Annual tag loss rates were 11%/yr for 1–2 yr old seals and 6%/yr for 3–6 yr old seals (Le Boeuf and Reiter 1988). We calculated expected tag loss separately for single tagged and doubly tagged seals (Clinton 1990).

After seals reached 6 yr of age we determined censoring due to tag loss by observing actual tag loss by

males with pelage marks. Marks were lost annually when the pelage molted, so from 1985 through 1988 we marked 7–14 yr old tagged males on their new pelage with black hair dye during the summer molt. We classified males that disappeared at these ages as dead if we last observed them during the breeding season with clear marks. If males were last observed during the molt with a mark but no tags, we censored them during that age interval.

At rookeries elephant seals congregate in large groups, which makes reading tag numbers difficult, so we missed resighting some tagged seals during the last age interval they survived. We estimated the proportion resighted in each age interval from the number of males resighted divided by the total number alive at that age interval, which included males not resighted, but sighted at a later age. The percentage of resightings of live seals dropped from 78% for yearlings to 60–70% for 2–4 yr olds, then rose to $\approx 90\%$ for 5–6 yr olds. Beginning at 7 yr of age, males' tags are much easier to read because males disperse widely on the beach during the breeding season, and we resighted 100% of males known to be alive from 7–14 yr of age.

Emigration outside the study area may have changed the probability of annually resighting living subjects, and for this reason we censored emigrants from Año Nuevo. We determined emigration of seals by analyzing resightings obtained by observers at other rookeries. Sightings at the Southeast Farallon Island and the California–Oregon coast to the north of Año Nuevo were common for 1–3 yr old males. Elephant seals seasonally migrate northward as they forage at sea (Condit and Le Boeuf 1984), and these sightings do not necessarily indicate emigration; however, an extended series of resightings at other rookeries indicated that certain seals were staying away from Año Nuevo, and we classified these males as emigrants. Of the 250 males observed at locations to the north, 65 permanently returned to Año Nuevo during their later years and were not classified as emigrants. We classified the remaining 185 males as emigrants to northern rookeries. Southward movement of elephant seals was not common, and only 13 males were sighted in the Channel Islands. Of these males, 2 returned to Año Nuevo later in life, and the other 11 males emigrated.

Mating success and reproductive rates

Mating success was measured by tallying copulations by males in female groups on the beaches during the breeding season. All copulations by males were recorded during behavioral observation periods. A male's copulatory success was derived from the copulation counts by calculating the proportion of copulations obtained by the male in each female group, then multiplying this proportion by the total number of females in the group, giving an Estimate of the Number of Females Inseminated (ENFI, Le Boeuf 1974). We made two important assumptions to equate mating success

TABLE 1. Age-specific mortality rates in four groups of male northern elephant seals at Año Nuevo, California, and the overall estimated lifetime mortality rates. Cohort mortality rate estimates are given as means \pm 1 SE.

Age (yr)	Año Nuevo cohorts	Channel Island cohort	Known-history males	Oldest males	Pooled mortality rates
W*	0.510 \pm 0.012				0.510
1	0.193 \pm 0.016				0.193
2	0.180 \pm 0.021				0.180
3	0.128 \pm 0.023				0.128
4	0.064 \pm 0.020				0.064
5	0.237 \pm 0.041				0.237
6	0.301 \pm 0.061	0.333 \pm 0.103			0.310
7	0.469 \pm 0.088	0.200 \pm 0.126	0.139 \pm 0.058		0.253
8	0.552 \pm 0.131	0.500 \pm 0.177	0.281 \pm 0.084		0.333
9	0.545 \pm 0.212	0.250 \pm 0.216	0.571 \pm 0.118		0.411
10	0.667 \pm 0.385	0.667 \pm 0.272	0.667 \pm 0.192		0.667
11		0.000	0.667 \pm 0.385	0.111 \pm 0.105	0.174
12				0.267 \pm 0.162	0.267
13				0.800 \pm 0.179	0.800
14				1.000	1.000

* W = weanling.

with reproductive success: first, that male reproductive success was reflected by matings obtained in the female breeding groups, and the matings obtained outside breeding groups did not substantially increase a male's reproductive success, and second, that each mating has an equal probability of inseminating a female, regardless of the male's and female's prior mating activities.

Mean ENFIs for each age from 5 to 14 yr of age were calculated for known-age and estimated-age males. Estimated-age males tagged as subadults and all known-age males present at Año Nuevo during 1983-1989 were included in the estimate of mean ENFI by age. Known-age males and estimated-age males had similar mean ENFIs ($F_{1, 229} = 3.50$, $P = .0625$; the effect of age on ENFI was controlled). We pooled the data from both groups to estimate age-specific ENFIs.

To calculate age-specific fecundity for the life table, we estimated the number of offspring surviving to weaning. The number of offspring sired in the subsequent season was calculated by multiplying each male's ENFI by the probability of the female surviving to the next season (0.77, Reiter and Le Boeuf 1991), the birth rate of females (0.97, Le Boeuf and Reiter 1988), and the survival rate of pups born in the following season. Age-specific fecundity rates of males were calculated as one half the mean number of offspring surviving to weaning because each offspring a male fathered added one half to fecundity, with the other half of the genetic credit going to the mother (Fisher 1930).

The distributions of mating success at each age included a large proportion of ENFIs at or near zero, and the variances were high and correlated with the mean, therefore non-parametric rank methods were used for statistical tests, or parametric methods were performed using square-root-transformed ENFI (Zar 1984).

Longitudinal records of individual males

To examine lifetime reproductive success and life-span we compiled yearly records for individual males

that had complete histories up to their deaths (Clinton 1990). At each year of life an individual measure of future life-span and future ENFI was calculated for each male based on the longitudinal records. Future life-span was the number of years a male survived past the current haul-out. Life-spans increased by a half year for each resighting of a male during the subsequent semi-annual haul-outs.

We also collected individual longitudinal histories between 1984 and 1986 for the 102 tagged adult males and compared their mean adult life-span with the age-specific life expectancy of adults calculated from the life table. A small number of these males were tagged because their dominance rank was high, but most of the tagging of adults was done opportunistically. Although this method of selecting subjects is properly called haphazard sampling (Martin and Bateson 1986), this large number of tagged adults was essentially a random sample of the adult males present.

RESULTS

Male mortality rates

Age-specific mortality rates of the Año Nuevo males decreased from weaning to 4 yr of age, then mortality rose steadily until 10 yr of age. From 6-10 yr of age, age-specific mortality rates for the Channel Island males and the estimated-age males were similar to the mortality rates of the Año Nuevo-born cohort. The most variation between these groups occurred from 7-9 yr of age, when the age-specific mortality rates were sometimes lower for the Channel Island and estimated-age males. All three groups had an overall trend of increasing mortality rate toward a peak of 0.667 at 10 yr of age (Table 1).

From 11 through 14 yr of age, mortality was estimated for the three males surviving from the previous samples plus nine older males at Año Nuevo during the study. Mortality rates at 11 yr of age were much

TABLE 2. Age-specific mating success of males.*

Age (yr)	Mean	Standard deviation	n
4	0	0	22
5	0.04	0.289	48
6	0.10	0.495	90
7	0.36	0.995	92
8	1.72	2.882	66
9	5.86	9.134	40
10	6.30	8.303	24
11	7.75	9.841	13
12	15.89	13.367	9
13	12.13	10.305	4
14	0		1

* Mating success was measured as the estimated number of females inseminated (ENFI) per breeding season. These data included seasonal ENFIs of both known-age males and estimated-age males whose ages were estimatable to within 1 yr of age.

lower than at 10 yr of age. Mortality at 12 yr of age was also low in comparison to the high mortality rates from 7–10 yr of age. At 13 yr of age mortality was high again, and no males survived past 14 yr.

The complete age-specific mortality curve from weaning to 14 yr of age featured two periods of reduced mortality. Pre-reproductive mortality rates were lowest at 4 yr of age, and after reproductive maturity another decrease in mortality rates occurred at 11–12 yr of age. From weaning to 5 yr of age these mortality rates were based solely on Año Nuevo born males, but from 6–14 yr of age two or more of the groups of tagged males contributed to the estimates of mortality at each age interval.

Age and reproductive success

Age of first observed mating by known-age males ranged from 5 to 12 yr of age. The mean age of first reproduction was ≈ 8 yr of age (mean ± 1 SD = 7.7 ± 1.46 yr, median = 8 yr, $n = 23$). No males younger than 5 yr of age were observed copulating with females. Of the known-age males in the 1978 Año Nuevo and Channel Island cohorts, six males reached 9 yr of age, and three of these males disappeared before they mated.

A male's mating success in each season depended strongly on the male's age (Table 2). The proportion of males with zero mating success in each age class also depended on age. At 5 yr of age only 1 of 46 males mated. From 6–8 yr of age 6–39% of males obtained matings. We observed matings by a majority of males in each age class from 9–13 yr of age; from 9–12 yr of age 60–75% of males mated, and all four of the 13-yr-old males mated.

Reproductive value and life expectancy of males

We constructed a complete life table for males, including estimates for age-specific survivorship, reproductive value, and life expectancy (Table 3), which

were calculated from the estimates of age-specific mortality and age-specific fecundity over the life-span of males. Reproductive value steadily increased as males became older. The principal reason for increasing reproductive value was the steady increase of the chances a male would survive to the ages when male fecundity was highest. According to the estimates of survivorship, about three quarters of males born died by 5 yr of age, and by 9 yr of age only 7% of the males remained alive. Clearly, the longer a male lived the better his chance of reproducing, since males had to reach between 9 and 13 yr of age to realize high mating success.

Age-specific reproductive value and fecundity were plotted together to illustrate how they changed with age (Fig. 1). This graph also shows the proportion of reproductive value represented by reproduction beyond the present age, or residual reproductive value. For ages before peak fecundity, a large proportion of age-specific reproductive value consisted of offspring at future ages instead of current fecundity. Reproductive value increased rapidly between 6 and 9 yr of age since males that survived each of these years of increasing mortality were more likely to survive to an age of high fecundity. Once male fecundity increased at 9–10 yr of age, the climb in reproductive value slowed because of the increasing proportion that was current fecundity. Finally, at 11 yr of age reproductive value sharply increased to its peak level; the drop in mortality rate at 11 yr of age produced this peak since low mortality meant males were not only at an age of high fecundity, but also they had a high probability of reaching 12–13 yr of age, which were the years of highest male fecundity. The pattern of age-specific male reproductive value reflects two periods in male life history: first, a long period of steadily increasing reproductive value as surviving males pass through the ages before male fecundity rises at 8–9 yr of age, and second, a short period of rapid increase, and then fall in reproductive value during a brief reproductive life-span.

TABLE 3. Life table for male northern elephant seals at Año Nuevo, California.

Age (yr)	Survivorship (l _x)	Mortality (q _x)	Fecundity (m _x)	Reproductive value	Life expectancy
W*	1.000	0.510	0	0.503	2.848
1	0.490	0.193	0	1.026	4.287
2	0.396	0.180	0	1.272	4.193
3	0.324	0.128	0	1.552	4.006
4	0.283	0.064	0	1.781	3.523
5	0.264	0.237	0.016	1.903	2.730
6	0.202	0.310	0.038	2.475	2.425
7	0.139	0.253	0.134	3.531	2.288
8	0.104	0.333	0.642	4.546	1.894
9	0.069	0.411	2.413	5.857	1.590
10	0.041	0.667	2.345	5.847	1.351
11	0.014	0.174	2.886	10.506	2.053
12	0.011	0.267	5.914	9.224	1.380
13	0.008	0.800	4.513	4.513	0.700
14	0.002	1.000	0	0	0.500

*W = weanling.

Male life expectancy was low throughout life because mortality rates were high at most ages (Table 3). The highest life expectancies occurred from 1–3 yr of age, which was the period when the mortality rate steadily decreased until the low point at 4 yr of age. The highest life expectancy among adults was found at 11 yr of age, which was the age when adult mortality rates dropped to low levels.

These estimates of adult life expectancy were checked by comparison with adult life-spans of tagged males of unknown age. The mean age-specific life expectancy from 8–14 yr of age, weighted by survivorship, was 1.66 yr of life. By comparison, the mean adult life-span of 102 adult males of unknown ages was 1.63 yr, indicating that the life table accurately reflects adult survival probabilities. An average expectation of >1 yr of additional life was produced by the mortality rates below 50% at 8–9 yr of age and the low mortality of 11–12 yr of age, and meant that the majority of adults could expect to live at least to the next season.

Consequences of reproduction

Longitudinal histories of individual males indicated that mating success early in life had an immediate adverse affect on survival of young males. Among males 7–8 yr of age, mating success was associated with poor prospects of survival to the next season (Table 4). From 9–11 yr of age the relationship between current reproduction and survival was weakly negative and near zero, with probabilities that were not significant. At 12 yr of age the relationship was positive, but not significant.

The total lifetime mating success of males was positively correlated with both the maximum age that males reached and the number of seasons that males bred. Among males that mated during their lifetimes, the independent effects of age and the number of seasons of mating success were analyzed by multiple regression, using the square root of total lifetime ENFI as the dependent variable. Both variables had positive and

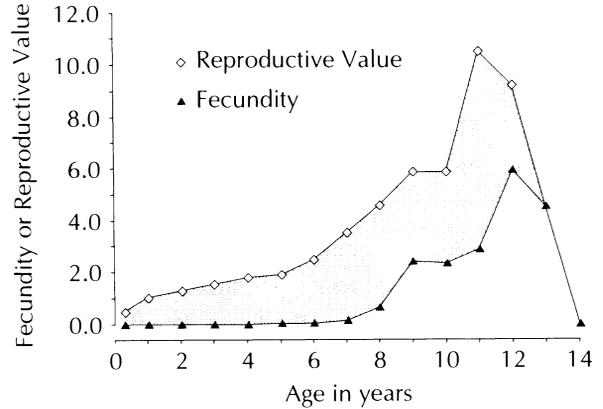


FIG. 1. Reproductive value and fecundity for male northern elephant seals from 1 to 14 yr of age. The difference between the curves (the gray area) is residual reproductive value.

significant relationships with lifetime ENFI (for maximum age the slope $b = 0.459$, $t = 3.659$, $P < .01$; for the number of seasons the slope $b = 0.996$, $t = 4.989$, $P < .01$). The partial correlation between maximum age and lifetime mating success was 0.436, which was somewhat lower than the partial correlation of 0.551 for the number of seasons of mating and lifetime mating success. Each variable was important to the total mating success over the lifetime of males, and together they accounted for two-thirds of the variance in lifetime mating success of the males that mated ($F_{2, 57} = 50.482$, $P < .001$, $R^2 = 0.627$).

DISCUSSION

As a result of strong sexual selection, the life history of male northern elephant seals is geared toward high mating success late in life. But the chance of living to an age of high mating success is low, and only a small proportion of males live long enough to reproduce at all. Most males reproduced for the first time at 8 yr of age when survivorship was $\approx 10\%$ of the initial cohort.

TABLE 4. The association between mortality and mating success (=ENFI, estimated number of females inseminated).

Age (yr)	Survival to next season	Mating success		Correlation coefficient	Fisher's exact test*
		ENFI = 0	ENFI > 0		
7	Died	2	5	$\phi = -0.497$	$P = 0.006$
	Survived	29	5		
8	Died	0	8	$\phi = -0.511$	$P = 0.002$
	Survived	18	11		
9	Died	3	9	$\phi = -0.031$	$P = 1.000$
	Survived	5	13		
10	Died	2	6	$\phi = -0.121$	$P = 1.000$
	Survived	4	7		
11	Died	0	2	$\phi = -0.289$	$P = 1.000$
	Survived	3	6		
12	Died	2	2	$\phi = +0.598$	$P = 0.167$
	Survived	0	5		

* Fisher's exact test probabilities are two-tailed tests of the null hypothesis of no association. Bold numbers in data arrays for each age indicate the cells contributing to the direction of the significant associations.

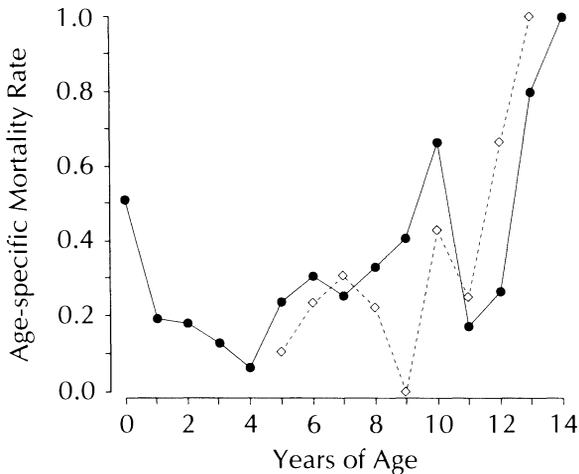


FIG. 2. Mortality curves for male northern elephant seals in this study (●) and males from the 1964–1967 Año Nuevo (California) cohorts (◇).

On average, the highest mating success occurred at 12–13 yr of age, and male survivorship to these ages was $\approx 1\%$ of males born.

These results were nearly identical to those found in the 1964–1967 Año Nuevo-born male cohorts (Le Boeuf and Reiter 1988). To compare our current mortality rates with the mortality rates of previous Año Nuevo cohorts, resighting data for the 1964–1967 male cohorts were pooled to calculate age-specific mortality rates for these males from 5–13 yr of age, and the curves were plotted together for comparison (Fig. 2). Mortality rates from 5–10 yr of age appear to have increased since the 1970s, when these earlier data were obtained. Average male lifetime reproductive success in the earlier study was 2.95 offspring surviving to weaning, which reflected an increasing elephant seal population; however, based on the male life table we constructed for this paper, the net reproductive rate (R_0) of males was 0.5034, which indicated a declining population. Our estimate of the rate of increase (r) was -0.071 , which was within the range of -0.160 to -0.061 estimated for females at Año Nuevo (Reiter and Le Boeuf 1991). The recent growth of the colony at Año Nuevo has been produced by recruitment of immigrants from rookeries to the south (Reiter 1984, Le Boeuf and Reiter 1988). Since the population across the entire range of northern elephant seals has been increasing at a rate of $\approx 15\%/yr$ (Cooper and Stewart 1983), estimates of male survivorship obtained at rookeries with stable or increasing rates of increase should be higher than our estimates of survivorship. The males in both studies at Año Nuevo had similar patterns of male mortality and reproductive success, and we expect that similar patterns of male mortality and reproductive success would be found elsewhere because male social behavior does not vary between elephant seal rookeries.

Both curves of age-specific mortality in males had two periods of increasing mortality rates, producing a

U-shaped curve with a hump roughly in the middle. Ralls et al. (1980) proposed that this pattern of mortality in males was caused by sexual selection, and our study supports this hypothesis, adding another species to the list cited in Ralls et al. (1980) of polygynous species with similar shapes in male mortality curves, including toque monkeys (*Macaca sinica*, Dittus 1980), impalas (*Aepyceros melampus*, Jarman and Jarman 1973), and humans (*Homo sapiens*, Ralls et al. 1980, Wilson and Daly 1985). Similar mortality curves were also found subsequently in two more polygynous monkeys, howler monkeys (*Alouatta palliata*, Froehlich et al. 1981), and vervet monkeys (*Cercopithecus aethiops*, Cheney et al. 1988).

Suggestions for causes of the increase in male mortality include nutritional stress during periods of high growth rate, energy expenditure and risk associated with emigration, social stress due to integration into new social groups, and social stress and risks to young, inexperienced males during initial entry into male-male competition (Ralls et al. 1980, Froehlich et al. 1981, Trivers 1985, Wilson and Daly 1985). The increased mortality of males that mated while 7–8 yr of age indicates that higher mortality was associated with competition for mates. On the other hand, 11–12 yr old males showed no costs from mating; those that were successful in mating not only survived to subsequent seasons, but also had similar levels of mating success in subsequent seasons (Fig. 3). Both longer life and a longer breeding life-span contributed to higher lifetime mating success. Some males with only one

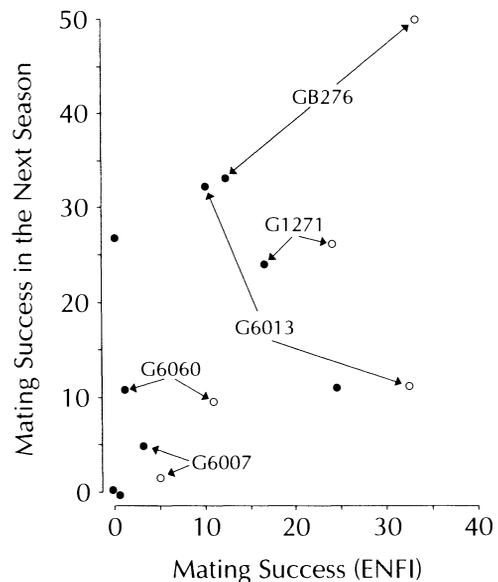


FIG. 3. The relationship between mating success in successive seasons for 11-yr-old (●) and 12-yr-old (○) male northern elephant seals. Five males with data from 11 through 13 yr of age are labeled. Spearman rank order correlations for 11-yr-olds: $r_s = 0.511$, $n = 9$, $P = .074$; 12-yr-olds: $r_s = 0.900$, $n = 6$, $P = .036$. Probabilities are for one-tailed tests.

season of reproduction achieved higher lifetime mating success in that season than other males that breed in > 1 yr, but males that mated over several seasons were usually more successful, and the most successful males mated for the highest number of seasons. Although mating had an immediate negative effect on future survival, some males that mated at 8 yr of age also survived to old age, and they had high mating success in later years.

The interval of high mortality in subadults and young adults was the second period when natural selection could operate strongly. The first period of strong selection was after weaning, when elephant seals began a 6–7 mo pelagic trip to sea from which only half of them returned. In this study, the mortality rate at 10 yr of age was higher than the mortality after independence. The traits favored during this second period of strong selection could be traits that are opposed by sexual selection, but it is also possible that traits that favor survival are also advantageous in intrasexual competition for mates. The return to relatively low levels of mortality at 11–12 yr of age may indicate that the males of these ages were phenotypically different from the males that failed to survive.

Positive correlations between reproductive success and subsequent survival and reproduction have been frequently found in other species, especially in field studies (Reznick 1985, Clutton-Brock 1988). The premise of such studies has been to measure the phenotypic costs of current reproductive effort to subsequent survival and reproduction. Reproduction was expected to require the expenditure of limited resources and the taking of risks beyond those required for survival. The positive correlations found in field studies of free-living subjects have been attributed to higher resource intake during breeding to compensate for the energy costs (Tuomi et al. 1983), and to factors that affect the “quality” of different individuals, such as age and previous experience, that are not measured or considered in the analysis of the data (Clutton-Brock 1988, Clutton-Brock et al. 1989). By focusing on the effects of age at primiparity, reproductive costs were found in female northern elephant seals (Reiter and Le Boeuf 1991). In this study, we controlled for the effects of age, which was the most obvious variable that influenced potential reproductive performance and survival. By restricting the analysis of the relationship between survival and reproduction to males of the same age, we found a significant cost to reproduction in young males.

Costs to reproduction were not measurable in the older males, and the likely reason is that factors associated with age determined the “quality” of the males, such as their size, experience, or ability to forage at sea. Because they survived the period of high mortality as subadults and young adults, the older males were probably the type of male phenotypically better able to maintain the high level of energy expenditure as-

sociated with high social rank and high mating success, and to forage effectively after breeding and recover from the long fast that males undergo during breeding. Older males were more experienced socially and competitively, and probably possessed a lower likelihood of suffering the debilitating effects of stress and injury from competition for social rank and access to females. In retrospect, the absence of reproductive costs in fully mature, experienced individuals indicates that the phenotypic traits that are important for reproduction may also be important for survival, at least in adults.

The disadvantages of sexually selected traits such as higher growth rates, which delay reproduction and increase mortality rates, are probably experienced most strongly by young, immature males, and by the time males are fully mature the costs of these traits already have been “paid” (Case 1978). The traits associated with higher mortality of young males may have unavoidable survival disadvantages. If the development of sexually selected traits is viewed as part of male reproductive strategy, the long-term consequences of such traits could be best interpreted as a cost of preparation for breeding, and functionally similar to the preparations for breeding found in females or in males of monogamous species, such as defending a territory, nest building, and increased foraging rates, which are easily recognized as a part of reproductive costs. In northern elephant seals, fully mature males seem to be phenotypically more fit for survival than the males that did not survive to maturity. If the most fit males are also the most successful in male–male competition, we would predict that the males of other polygynous species that do most of the breeding should also be the most able to recover from the stresses of reproduction. If our hypothesis is correct, then males in polygynous species would be poor subjects for measuring the phenotypic costs of reproduction, but good subjects for studies of physiological processes and other adaptations that minimize the costs of reproduction.

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