Life history consequences of variation in age at primiparity in northern elephant seals

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Summary. The age when female northern elephant seals, *Mirounga angustirostris*, bear their first young varies from 2 to 6 years. At Año Nuevo, California, a group of 77 females, primiparous at age 3, had a lower survivorship rate to each successive year up to age 8 than a group of 98 females that deferred initial pupping until age 4. The difference in survivorship appears to be due to the greater relative energetic costs of gestation and lactation incurred by the earlier breeding females during a period in their development when growth is rapid. An alternate hypothesis for the difference in survivorship that young primiparous females are in poor condition from birth – is untenable; females that pupped early in life were larger at weaning age (a correlate of condition) than females that were primiparous 1 year later.

Models based on the data show that differential survival of seals that vary in age at primiparity has important consequences for population growth and life history strategies. The effect of age at primiparity on the rate of increase of populations varies with colony density and juvenile survivorship. The optimal life history strategy for female elephant seals under most conditions existing today, including those at Año Nuevo during the study period, is to bear the first offspring at age 4. Primiparity at age 3 is projected to be favored when harem density is very low and weaning success and juvenile survivorship are high; postponement of first breeding to age 5 is expected at high harem densities with intense competition for breeding space.

Introduction

Cole (1954) and others (e.g., Lewontin 1965; Hamilton 1966; MacArthur and Wilson 1967; Charnov and Schaffer 1973; Stearns 1976) have argued that selection pushes the age at first reproduction to the physiological minimum in expanding populations. The sooner offspring are born, the sooner they begin reproducing. The advantages to those that reproduce early are substantial (Lewontin 1965). However, many animals postpone reproduction, presumably because there is a cost each time an animal reproduces that either lowers survival or decreases future fecundity (Williams 1966a, b; Gadgil and Bossert 1970; Stearns 1976; Bell 1980). It is assumed that resources directed to reproduction reduce those available for growth and maintenance. This tradeoff may impose a greater strain on young or inexperienced individuals because a higher level of reproductive effort may be needed for a given level of reproductive success (e.g., Lack 1954; Bakker 1959; Charlesworth 1980). Reproduction is assumed to be delayed as long as the expected gains of increasing size, ability or experience offset those lost during the delay (Williams 1966a). Given the putative costs of early reproduction, increases in fecundity or in the quality of offspring may occur with age, making delayed maturation advantageous (Bell 1980; Stearns 1980; Stearns and Crandall 1980; Warner 1984).

We investigate the effects of natural variation in age at primiparity – when a female bears an offspring for the first time – on longevity and lifetime reproductive success in a long-lived mammal, the northern elephant seal, *Mirounga angustirostris*. We stress the effects of age at primiparity on longevity because the costs and benefits are expected to be greater than at any other time in life. Age at primiparity varies from 2 to 6 years with the majority of females bearing their first offspring at age 4 (54%), followed by age 3 (36%), age 5 (6%), age 6 (3%) and age 2 (1%) (Reiter et al. 1981; Le Boeuf and Reiter 1988).

Resources are more limiting for a female of this species bearing the first offspring because of her smaller size, limited blubber reserves, and more rapid growth phase, relative to older females. Mass increases rapidly with age until age 6 and more slowly during the remainder of life. Three-year-old females weigh 35% less than 6-year-old females at the end of lactation (220 vs 340 kg) and less than half as much as females over
Subject growth of hypothetical populations composed of weans her pup by going to sea. One or more males where they give birth and copulate. Varying harem densities, and have different juvenile sur-

By examining age specific fecundity in relation to varying differences in the energetic costs of breeding and

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of age at primiparity on lifetime reproductive success differences in phenotypic vigor; (3) we estimate the effect of age at primiparity and social density in the effects of these variables on population growth. Specifically, (1) we determine the age specific survivorship of females that vary in age at primiparity from field data; (2) upon finding a difference in survivorship among groups of females that give birth for the first time at different ages, we test two hypotheses that might account for this effect, i.e., differences in the energetic costs of breeding and differences in phenotypic vigor; (3) we estimate the effect of age at primiparity on lifetime reproductive success by examining age specific fecundity in relation to varying harem densities; and (4) from cohort lifetables, we project growth of hypothetical populations composed of females that vary in age at primiparity, give birth in varying harem densities, and have different juvenile survivorship rates.

Background information. Northern elephant seals breed annually on islands and headlands along the coast of California and Baja California, Mexico (Le Boeuf and Bonnell 1980). Females gather in harems defended by one or more males where they give birth and copulate. Each female gives birth to a single pup annually that she nurses for 4 weeks while fasting (Le Boeuf et al. 1972; Ortiz et al. 1978). At the end of lactation, a female weans her pup by going to sea.

The northern elephant seal population was decimated in the last century by sealers (Bartholomew 1952; Bartholomew and Hubbs 1960; Bonnell and Selander 1974). Since the turn of the century, the population has been increasing in numbers and continues to extend its breeding range (Le Boeuf and Bonnell 1980). The present study was conducted during a period of population expansion.

Methods

Survivorship. Annual survivorship was calculated for 175 females born on Año Nuevo, California, between 1973 and 1976 for which age at primiparity was known. Post hoc, we divided the sample into two groups: 77 female that were primiparous at age 3 (P3 group) and 98 females that were nulliparous at age 3 and gave birth for the first time at age 4 or died between the age of 3 and 4 (P4 group).

All subjects had been marked with one or two serially numbered tags in the hindflippers at weaning. Each year between 1976 and 1984, when the females were 3 to 8 years old, subjects that appeared on Año Nuevo or on Southeast Farallon Island, 89 km to the north, were identified from their tags and marked with a bleaching agent or dye. By this means, survivorship was determined and observation of the marked animals permitted us to determine individual fecundity and weaning success. Similar searches were made by colleagues at southern California rookeries, however, none of the subjects in our sample were ever observed there.

Juvenile survivorship to age 3 was estimated as 40% from an independent sample of 147 weaned pups born on Año Nuevo and double-tagged at weaning in 1978 and 1980 (Le Boeuf and Reiter 1988).

Adult survival data were corrected for tag loss and the probability that females might have bred unobserved before death (Reiter 1984; Le Boeuf and Reiter 1988). The probability that an adult female lost one tag was estimated at 0.06 each year of life; the probability that a double-tagged female lost both tags in a year was 0.0036 (Reiter 1984). Females not recognized because of lost tags were estimated annually and treated as type one “phantoms” with the same survivorship and reproductive success as females that did not lose their tags.

Type two phantom breeders were those females that retained tags but whose tags were not seen or read during a breeding season. Annual probability estimates of the proportion of type two phan-

To test the hypothesis that young females, 3 to 5 years old, incur a greater relative energetic cost of reproduction (greater percent of reserves or greater weight specific cost)

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