I. INTRODUCTION

Northern elephant seals have been expanding their breeding range and increasing in number every year since sealers reduced the world population to less than 100 individuals during the 1880's. At present, these seals breed on 12 islands or island groups from central Baja California, Mexico, to the Farallon Islands near San Francisco in central California (Fig. 1). This is virtually the same range the species occupied before exploitation began in the last century. Present population size is estimated to be over 60,000 animals (Le Boeuf, 1977). No other large mammal has made such a remarkable recovery from near extinction. However, the population continues to increase and crowding is evident in certain parts of the range. From 1968 to 1981, my students and I monitored dispersal of individuals within the population and fluctuations in the size of colonies. This facilitated the study of colony dynamics on Ano Nuevo Island, a rookery we studied intensively. Early in the study period, Ano Nuevo was a small new colony of elephant seals with low female density in harems. Pup production increased annually. By 1980, the colony had become very large and crowded. This chapter will document the increase in density on this rookery, report observations made during the colony's growth, and address problems inherent in studying changes that occur with increasing density.
II. POPULATION GROWTH

The population of northern elephant seals more than quadrupled in the last 21 years. A plot of total northern elephant seals censused periodically since 1890 reveals that the population is still in the exponential phase of growth (Fig. 2). The curve fits the equation $Y = ae^{bx}$ with $a = 29.35$ and $b = 0.09$. At the colony level, four new island rookeries were established during the 1970's and one breeding site was established on the continental mainland.
Fig. 2. Exponential growth of northern elephant seals since the nadir of the population in 1890.

A. Colony Changes Associated with Increasing Density.

During the recovery phase of the elephant seal population, some rookeries reached their carrying capacity and sent off immigrants to form new colonies. Ano Nuevo Island was colonized in 1961 by immigrants from southern California rookeries. Pup production rose annually so that by 1980 over 1,200 pups were born on the two beaches on this tiny 8-acre island. By the early 1970's signs of crowding began to appear. First, the pup mortality rate began to increase (Le Boeuf and Briggs, 1977). Fig. 3 shows that the increase was gradual at first, but the pup mortality rate began to skyrocket in bad storm years so that in 1978, 40% of the pups born died before reaching weaning age. Storms did not kill pups directly so much as indirectly by increasing density. Secondly, some Ano Nuevo-born seals began establishing new breeding sites in the vicinity of Ano Nuevo Island. In 1972 breeding began on Southeast Farallon Island, 89 km north of Ano Nuevo (Le Boeuf et al., 1974). Eight years later, pup production was up to 250 pups
Fig. 3. Variation in pup mortality and annual pup production on Ano Nuevo Island during the period 1968 to 1980. The mortality rate is calculated from pups that died prior to weaning. S denotes storms which struck the rookery at peak season when the maximum number of females and pups were present. Adapted from Le Boeuf and Briggs (1977) and Reiter et al. (1981).

per year. Seventy-six percent of the tagged seals that gave birth here during the period 1972 to 1978 were born on Ano Nuevo Island. Ninety-two percent were young females, five years of age or less. Similarly, the male pioneers were also young and Ano Nuevo-born. In 1975 breeding began on the mainland less than 1 km across the channel from Ano Nuevo Island. Pup production increased annually; 150 pups were born here in 1980. Eighty-seven percent of the females were Ano Nuevo-born and very young.

B. Causes of Pup Mortality and Emigration of Young Females

Young females began to breed in new locations because they could not compete effectively with older females in the high density conditions that prevailed (and continues to prevail) on
Año Nuevo Island (Fig. 4). A study of reproductive success as a function of female age (Reiter et al., 1981) revealed that the probability of a female producing a pup that survives to weaning increases with age (Table I). Young females were least successful under high density conditions. The low reproductive success of young females was due in large part to their inferiority to older females in size, dominance, and maternal experience. Young females gave birth at a poor time for rearing pups, at peak season or later, and in the poorest location, the periphery of the harem where conditions led to a high probability of mother/pup separation and pup injury.

The reproductive success of young females that gave birth in the low-density harem on the Año Nuevo mainland (Fig. 5) or on Southeast Farallon Island was higher than that of their counterparts who remained on Año Nuevo Island and gave birth in the crowded harem (Table II).

C. Other Indicators of Crowding

As the number of females in a harem increases, the area unoccupied by the females spreads out because the aggressiveness of females tends to maintain inter-individual spacing. When a beach occupied by a harem becomes fully utilized in this way, the arrival of additional animals leads to an increase in density. On the Point Harem on Año Nuevo Island, a stage was reached where landing became so difficult that females began to breed in marginal areas, formerly unoccupied beaches with a rocky rather than a sandy substrate. Thus, a fully utilized beach and use of marginal areas is a sign of crowding.

High density in a harem is indicated by a high frequency of mother/pup separation, the presence of many orphaned pups, a high frequency of milk stealing, disruption of nursing, trampling of pups by males, female biting of pups, and finally, high pup mortality. Several females may gang up on an orphan and in a frenzy, bite it repeatedly and kill it. These chaotic conditions -- exacerbated further by bad weather -- make for a high level of arousal and bickering among females. This would appear to cause them to expend their limited fat reserve (their only source of food and water for themselves and their pups because females do not eat or drink while nursing) in activities other than nursing. Consequently, I predict lower weaning weights for pups nursed in high-density harems as opposed to low-density harems, as well as a shorter nursing period for females (the female's nursing period and stay on land is limited by her fat store).

In crowded harems the age composition of males is heavily weighted to adult bulls. For example, on Pilot Rock Beach at Isla de Guadalupe, which was extremely crowded at peak season
Fig. 4. Part of a crowded harem on Ano Nuevo Island during the 1980 breeding season.

Fig. 5. A small low-density harem of young females.
TABLE I. The Percentage of Females in Various Age Categories That Produced Pups Which Survived to Weaning Age on Ano Nuevo Islanda

<table>
<thead>
<tr>
<th>Breeding season</th>
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<th>Age 4</th>
<th>Age 5</th>
<th>Age 6</th>
<th>Age 7</th>
<th>Age 8</th>
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<th>Age 10</th>
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aN is in parenthesis. From Reiter et al. (1981).
in 1973, 60% of the males on the beach were full grown and over eight years of age. In contrast, at Año Nuevo Island, then a low-density peripheral rookery, only 29% of the males were adults; 55% of the colony was composed of pubertal males six years of age or less (Le Boeuf, 1974). As the number of animals breeding on Año Nuevo Island increased and crowding set in, the age composition of males has approached the proportions observed earlier at Isla de Guadalupe. I suspect that a similar change in age composition occurs among females.

Although there are relatively few young males near crowded harems, compared to older males, the former can copulate more frequently in this setting than in lower-density harems because it is easier for them to sneak into a chaotic crowded harem undetected than into a small low-density one. In the latter, one adult male usually prevents all males from approaching the females and he alone does all of the mating. Thus, copulations by young pubertal males are a sign that the harem is crowded. In the vicinity of crowded rookeries it is common to observe single males hauling out on isolated beaches or coves. During the last ten years, subadult males have been observed frequently on mainland beaches north and south of Año Nuevo Island.

D. Immigration and Recruitment During Crowding

The Año Nuevo colony has grown through immigration and recruitment. Every year new females and males from southern rookeries have bred here (Fig. 6). Elephant seals are site tenacious; once they breed in a certain place, over 70% of them return to the same place to breed. Elephant seals are also
Fig. 6. The major routes of dispersion and immigration of northern elephant seals based on tagging studies of pups conducted during the 1970's. The following abbreviations are used: FAR = Southeast Farallon Island, ANI = Año Nuevo Island, SMI = San Miguel Island, SNI = San Nicolas Island, COR = Los Coronados, GPL = Isla de Guadalupe, and SBI = Islas San Benito.
philopatric; over 70% that survive to breeding age return to give birth at their birthplace. It is interesting that immigration of animals from southern rookeries to Año Nuevo did not stop once the latter began to show signs of crowding. Rather, young females from the southern rookeries (San Miguel and San Nicolas Islands) began to appear on Año Nuevo Island as well as on the new breeding areas (Southeast Farallon Island and the Año Nuevo mainland).

III. METHODOLOGICAL PROBLEMS

What I have summarized thus far about signals and symptoms of crowding on a rookery must be liberally salted before ingestion. There are serious problems in studying and measuring changes with increasing density in field studies on long-lived pinnipeds. First, the changes occur over a number of years. During this time there may be changes in personnel, fluctuation in motivation by the observers, and changing priorities in research (not to mention lapses of funding and difficulties in acquiring the necessary permits). One does not usually set out with the single-minded purpose of studying changes that occur with density over the course of a 14-year longitudinal study. Second, there is the problem that one does not know what to look for. Because of the time factor, the changes are slight, subtle, and easily overlooked. One must collect data consistently through the years so that appropriate statistical procedures can be applied. Finally, there is the most serious problem of all — the difficulty of measuring some of the most important variables increases with density! Assessing the annual pup mortality rate is a good example. When the Año Nuevo Island colony was small, we removed each dead pup to avoid the bias of it being buried or washed away and thus underestimating the count or overestimating by counting one corpse twice. Early counts were not so much estimates as absolute values of pup mortality. But as the harems grew in area and number, it was no longer possible to approach the dead pups, let alone pull them out. It became necessary to estimate more and more using various methods applied by various observers over the years. The irony is that at a time when it was most important to know precisely what was happening to the pup mortality rate, i.e., at high densities, the measure was most suspect. Thus, the natural inclination of the scientist to be conservative in the face of uncertainty results in softening our conclusions about the effect of density.
During the last few years, the number of elephant seals breeding on Ano Nuevo Island and the Ano Nuevo mainland has increased to such a point that elephant seals have become a tourist attraction in the state park and a common sight on other beaches in the area. An increasing number of seal/people confrontations have occurred, some with good endings and others with disastrous consequences (usually for the seals). Given the present rate of increase in the seal population, one can anticipate conflicts between seals and people in the future. The conflict is not likely to be over food but over beach space. Before this time comes we must ponder the question: How far will we allow a species like the northern elephant seal to come back from near extinction? How many individuals will we tolerate on mainland beaches before people begin to consider the comeback-success species of the last few decades a cancerous growth in the present decade, a threat to people, a menace?

REFERENCES


