

The Northern Elephant Seal (*Mirounga angustirostris*) Rookery at Año Nuevo: A Case Study in Colonization

Burney J. Le Boeuf,¹ Richard Condit,² Patricia A. Morris,¹ and Joanne Reiter¹

¹*Institute for Marine Science, University of California at Santa Cruz, Santa Cruz, CA 95064*

E-mail: leboeuf@ucsc.edu

²*Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, USA*

Abstract

Our aim was to examine the colonization process in a large mammal, documenting the development of a breeding colony from its inception to reaching equilibrium numbers. We describe the development of a colony of northern elephant seals (*Mirounga angustirostris*) at Año Nuevo in central California from initial colonization in 1961 to 2010, a period when the worldwide population was expanding rapidly. We recorded pup production and pup mortality prior to weaning from censuses of animals by sex and age categories. Colony growth was rapid initially, and pup production reached approximately 2,700 births during the period 1995 to 2006. Pups born declined subsequently. The pattern of colony growth and decline is explained by species-specific seal behavior; population variables that influence immigration rates; and local environmental factors such as breeding space, animal density, and tidal and surf conditions at peak season that increase pup mortality. Colony growth was driven primarily by external recruitment of young females from large southern rookeries rather than internal recruitment. Births on the island segment of the colony, where breeding space was limited, peaked in 1980 then declined subsequently by 50% in association with increased density and pup mortality. Births on the adjacent mainland stabilized from 1995 to 2006, despite ample breeding space and low pup mortality; cessation of growth here was associated with reduced external recruitment of females. Primiparous females pioneer the establishment of new colonies, settling new sites to avoid low weaning success in crowded natal rookeries where they are dominated by older females. We conclude that the long-term study of the development of a single colony provides vital information on colony and population processes that have wide applicability to other mammals. The colonization of Año Nuevo recapitulated the process employed at other colonies during the recent growth and

expansion of the population and signals the pattern to be expected in future colonies.

Key Words: northern elephant seals, *Mirounga angustirostris*, colonization process, density-dependence, dispersion, immigration, recruitment

Introduction

The development of a mammalian breeding colony reveals vital information about the form and pattern of individual reproductive success, the operation of variables that control colony growth, and the influence of fluctuations in population numbers on peripheral colony development. Northern elephant seals (*Mirounga angustirostris*) offer practical, economic, and scientific advantages for long-term monitoring of the colonization process in a large predator. Elephant seals breed annually at predictable times; colonies are discrete and accessible; and individuals can be identified and easily counted. Consequently, colony development can be documented more reliably than in many other marine and terrestrial mammals. The growth of the population since near extinction in 1884 and the subsequent recolonization of California from the mother colony in Baja California, Mexico, in the 20th and 21st centuries is a model of recovering and expanding mammal populations that is exceptionally well-documented (Townsend, 1885; Huey, 1930; Bartholomew & Hubbs, 1960; Le Boeuf, 1977; Cooper & Stewart, 1983; Allen et al., 1989; Stewart et al., 1994). Moreover, as apex predators, elephant seals may regulate the abundance and population growth rates of many prey species and thus have important consequences for ecosystem conservation and management (Sinclair & Krebs, 2002).

Our aim is to describe the origin, development, and present status of a peripheral colony, Año Nuevo, California, in the northern part of the breeding range, and to examine its growth in relation to developments in the general population. In

doing so, we make extensive reference to earlier studies that document behavior of the animals at this site. This long-term baseline dataset helps us understand the natural history of this species, reveals general principles of colony and population growth for comparison with other animals, and facilitates identification of potential natural and human-generated changes that are of interest to wildlife managers, other investigators, and the general public.

Background

Population—The outstanding fact about the history of the northern elephant seal over the last 200 y is that its population was reduced by sealers from thousands in Baja California, Mexico, and California at the beginning of the 19th century to a few survivors in the late 1880s on Isla de Guadalupe, Mexico (Scammon, 1874; Townsend, 1885; Bartholomew & Hubbs, 1960). The effective population size in 1884 may have

been as low as 20 elephant seals (Hoelzel et al., 1993). Since this time, the animals have made a remarkable recovery; they have increased in number to 166,000, and they have reestablished what is thought to be their former breeding range from central Baja California, Mexico, to central California (Le Boeuf, 1977; Barlow et al., 1993; Hoelzel et al., 1993, 2002; Le Boeuf & Laws, 1994a; Weber et al., 2000).

Presently, elephant seals breed at 21 locations along the west coast of the United States and Mexico (Figure 1). Approximately 83% of the population is found in California, with most of it in southern California (Figure 1). Knowing the date that each rookery was colonized and colony growth helps address the factors that control population growth (Stewart et al., 1994).

Colony Location and Origins—The elephant seal rookery at Año Nuevo (N. 37.1086° latitude, W. 122.3378° longitude) is 31 km north of Santa Cruz, California (Figure 1). Seals were

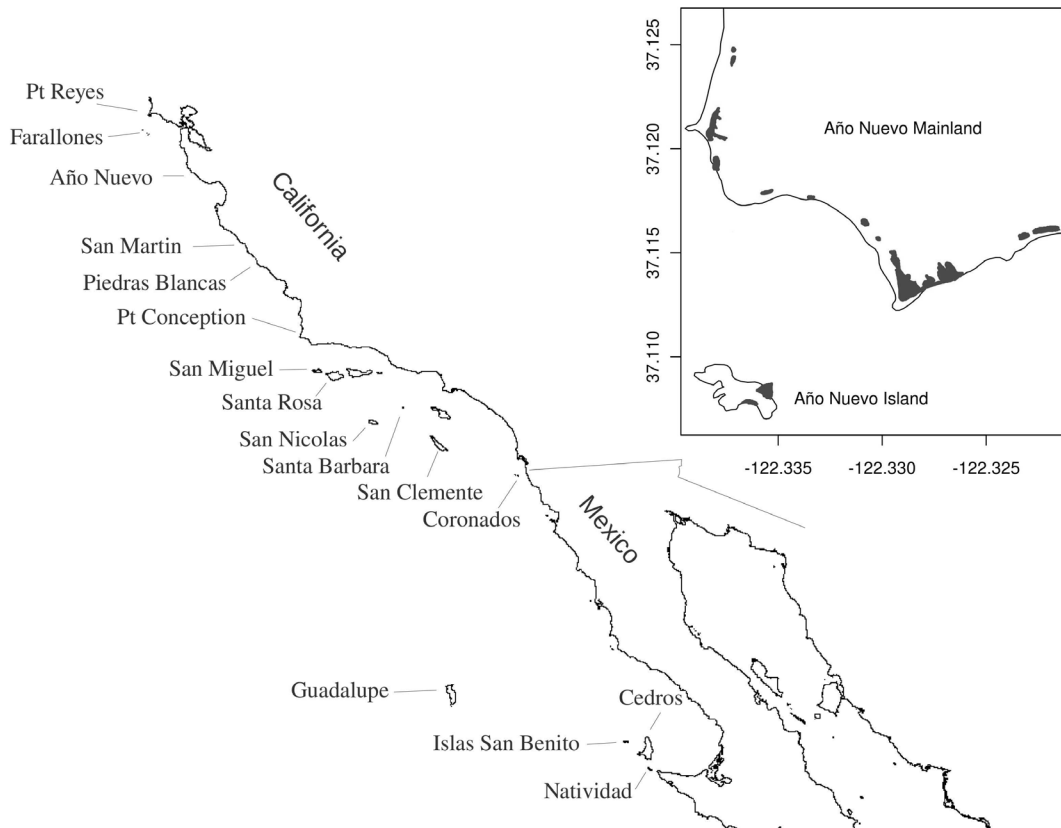


Figure 1. The principal rookeries of the northern elephant seal (*Mirounga angustirostris*) are shown for 2010. A few animals breed in Oregon and Washington (not shown) in years when the weather and sea condition are moderate. The inset shows the Año Nuevo colony, which encompasses the island and mainland portions separated by a channel measuring approximately 500 m at high tide. Harem locations at peak season are indicated as dark areas.

first recorded on the island in 1955, but the first pup was not recorded until 1961 (Orr & Poulter, 1965; Radford et al., 1965). Since 12 pups were observed in 1961, it is likely that breeding began a year or two earlier. There are no records to indicate whether breeding occurred at this site prior to sealing in the early 1800s. The first birth on the adjacent mainland, across a 500-m channel from the island, occurred in 1975 (Le Boeuf & Panken, 1977). Access to the area encompassing the seal rookeries is controlled by the California Department of Parks and Recreation.

Natural History—The breeding season begins in early December with the arrival of adult males. Pregnant females begin arriving in mid-December and reach their peak in numbers between 28 January and 2 February; thereafter, their numbers decline steadily until all females have returned to sea by mid-March. Nearly all females in residence during the breeding season (96.5% or higher; Crocker et al., 2006) are pregnant and give birth an average of 6 d after arrival (Le Boeuf et al., 1972). Each female nurses her pup daily for a mean of 25 d, while fasting from food and water, and then weans the pup by returning to sea. Since early-arriving females depart the rookery, weaning their pups, before late arriving pregnant females come ashore, the peak female count is less than the total females using the colony (Condit et al., 2007). The rookery contains both suckling and weaned pups from mid-December until early March (Le Boeuf et al., 1972; Le Boeuf & Laws, 1994b).

In addressing the history of the colony, we emphasize pup production as it provides a good estimate of population status and growth. We present two metrics of pup production: (1) the number born and (2) the number weaned (1 mo old). We use pup production to assess population growth rate—the key unifying variable linking various facets of population ecology (Sibly & Hone, 2002). Our census data cover the period 1968 to 2010. For completeness, we add counts made by others from 1961 to 1967, the first 7 y of the rookery's history (Orr & Poulter, 1965; Radford et al., 1965).

Our specific aim was to document the origin, development, and present status of the rookery by tracking pup production, including births, deaths, and successful weaning. We put the results in perspective by reference to previous studies addressing the causative variables limiting growth such as breeding space, inclement weather and ocean warming, and intraspecific competition, and we discuss changes in the colony relative to events at other colonies and developmental changes in the entire population.

Materials and Methods

Censuses

Data reported are based on direct counts of northern elephant seals categorized by age and sex. Counts were made with binoculars from an abandoned lighthouse tower on the island from 1968 to 1976. Thereafter, when the tower was dismantled, counts on both the island and the mainland were made from elevated vantage points on dunes near harems. Censuses were conducted opportunistically at various times during the year. During the breeding season, census frequency ranged from daily to two to three times per week in early years but was reduced in later years because biweekly counts were deemed adequate. Census categories included adult males (8 to 14 y of age), subadult males (4 to 7 y of age), adult females (3 y or more), suckling pups, weaned pups, dead pups, and juveniles. Additional details on census methods are provided in Condit et al. (2007).

Pup Production

The number of pups born during a breeding season was estimated by direct counts of pups and by estimates of parous females in the colony.

Direct Counts of Pups Born—We counted all suckling pups, weaned pups, and dead pups, the sum of which yielded total pups born in that year. Direct counts, such as these, were possible only in harems of approximately 200 females or less.

Estimating Pups Born from Parous Females Present—In larger harems, we first estimated the number of females in attendance during the breeding season using the model described by Condit et al. (2007), which acknowledges that the total females that give birth on site must be estimated because all females are not present at once. On average, the number of females using the colony exceeded the peak female census in late January by 18% on the island and by 10% on the mainland. To estimate the number of pups born, we assumed a natality rate of 97.5%—the percentage of females that were resident at the rookery during the breeding season and gave birth—and multiplied this number by the total number of females estimated from the model that were present.

Resident Female Natality

Two sets of observations from years of intensive study were used to estimate the proportion of females arriving at the colony that were pregnant and gave birth (i.e., resident female natality). In 1969, when the island harem included 250 females at peak season, all dead pups were counted by directly removing them from harems daily throughout the entire breeding season. This procedure reduced the error of missing dead pups

because they were buried in sand or washed out to sea or of counting the same dead pup twice. Summing living and dead pups provided the best estimate of females that were present and gave birth. The second method was based on observations of 215 females identified by bleach-marks soon after their arrival in 1990. Of those, 202 were closely observed for 3 wks or more, and observations of pregnancy, birth, and maternal behavior were recorded, resulting in the estimate of natality. We assume that twinning did not occur as we have never observed twin births in this species (twins do occur rarely in southern elephant seals [*M. leonina*]; see McMahon et al., 2003). We assumed that a female exhibiting maternal behavior (nursing it or lying next to it) had given birth, although not necessarily to the pup with which she was associated (Reiter et al., 1981). We observed few or no nonpregnant females each year of the study period. These nonparous females were seen at the very beginning of the breeding season; they were usually repulsed vigorously from harems and pups by pregnant or parous females. These estimates of natality match closely the 95% natality estimates by Crocker et al. (2006) averaged over 14 breeding seasons; in only 1 y did natality drop below 95% and that was following the major 1998 El Niño Southern Oscillation (ENSO).

Adjustments to the Model for Low Sample Size and Female Movements

We used the model of Condit et al. (2007) to produce a mean ratio $r(T) = C(T)/N$, where $C(T)$ is the count on date T and N is the total number of females using the colony—that is, $r(T)$ is the proportion of the population present on T . We applied this ratio to estimate the number of females in 1985, 1986, 1997, and 2002 because too few counts were made in those years to use the model of Condit et al. (2007). In two other years, 1983 and 2010, females moved from the island to the mainland *en masse* in response to bad weather. In both years, we used counts before and after the storms, along with the correcting ratio $r(D)$, to estimate the number of females that moved and the number of pups born in each location. For example, in 1983, the storm occurred on 27 January, so we assumed that all females that moved had given birth; in 2010, a series of storms occurred during the period 16 to 19 January, and we assumed that 20% of the females that moved had already given birth.

Pups Weaned

All pups were counted on or near 1 March every year. This is the optimal time for censusing weaned pups because 95% of them are weaned (the remaining 5% are still suckling), but they

have not yet begun to depart from the rookery (Reiter et al., 1978). Because most breeding females have returned to sea to feed, weaned pups are easily counted because they are conspicuous, unlikely to be confused with other age classes, and they are approachable. Total pup counts, weaned plus suckling pups, were generally stable from 20 February to 10 March (Figure 2). We averaged all counts made in a single year to generate a mean and variance. High and low outliers (more than 20% above or below the mean of 1 y) were excluded; there were 11 such outliers out of a total of 460 such censuses over the entire census period.

Pup Mortality

Since obtaining accurate counts of dead pups directly in large harems is subject to error, we estimated pup mortality as the difference between the number of pups born and the number of pups weaned. In small harems, we validated this method with direct counts as described above. Pup survival was estimated each year by dividing the number of pups alive on 1 March by the estimated number of parous females that were present during the breeding season.

Males

Counts of all subadult and adult males between 15 January and 15 March were used to estimate the population of breeding males in attendance. Censuses prior to 15 January were excluded because large numbers of juvenile males present were not easily distinguished from the youngest subadult males. After 15 January, the number of males was fairly stable and included no juveniles because they had returned to sea. We report the mean of all counts each year except for 3 y when no censuses were taken. The proportion of the total male population that these daily counts represent is unclear because of the considerable movements of males in the nearshore waters to and from the breeding areas.

Census Database

All counts of individual locations and animal categories from 20 September 1967 to 2004 were recorded in the field and later transcribed into a normalized *MySQL* database (Widenius & Axmark, 2002). After 2004, new censuses were entered directly into the database. We report results from 2,095 female censuses, 911 male censuses, and 519 pup censuses, where one census is the summed daily counts covering the entire island or mainland during the specified time interval.

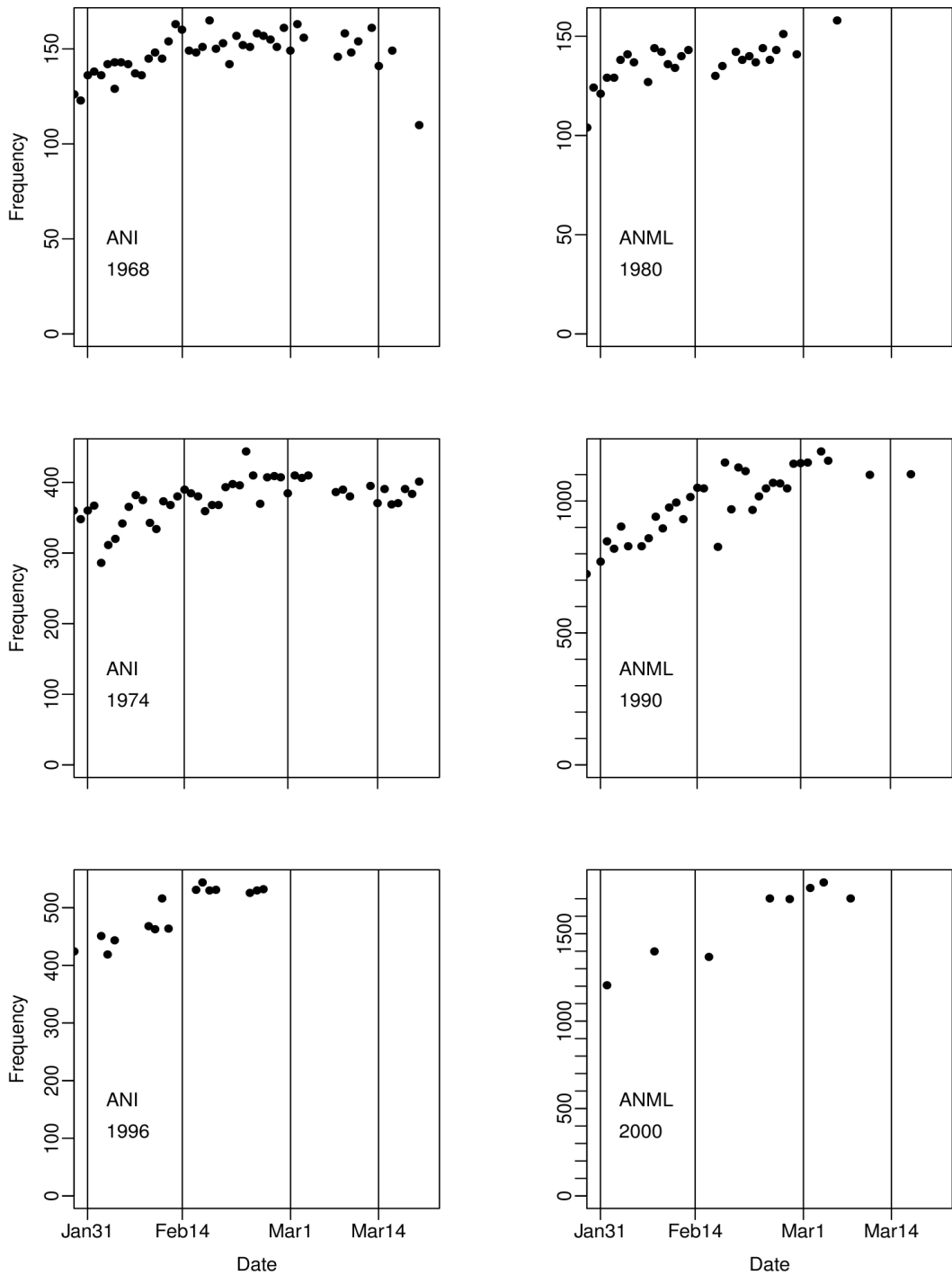


Figure 2. Northern elephant seal pup counts (suckling and weaned) at Año Nuevo Island (ANI) and mainland (ANML) in selected years; the period covered is from late January, the peak of the breeding season when females are most numerous, to mid-March when all females have departed the rookery to return to sea and all pups are weaned.

Confidence Intervals

The model for female population size includes an estimate of variance that incorporates errors in counting and in the model. Call f the estimated female population, $s^2(f)$ its variance, and $CV(f) = s(f)/f$ the coefficient of variation. The number of pups weaned, w , has a variance $s^2(w)$ and $CV(w)$ from multiple counts. In years with fewer than five counts of weaned pups near the beginning of March (17 times for the island colony; 11 for the mainland), we used the mean $CV(w)$ from other years (island mean $CV = 0.054$; mainland 0.064). The fecundity rate, $p = 0.975$, had a variance $s^2(p) = 0.025^2$ and thus $CV(p) = 0.052$ as estimated by two different methods.

The pup survival rate is $\theta = w/(fp)$, with fp the number of pups born. We estimated the error of θ by summing squares of the coefficients of variation,

$$CV^2(\theta) = CV^2(f) + CV^2(w) + CV^2(p) \quad \text{Eq. 1}$$

(Meyer, 1975). Since the CVs for f , w , and p are known, this produces an estimate of $CV(\theta)$ and thus $s^2(\theta)$. For each parameter, 95% confidence intervals were taken as $\pm 1.96 s$; intervals for the mortality rate were simply one minus those for survival. In some years, the lower mortality limit was < 0 , so we simply took it as zero. In those cases, the upper confidence bound for w , the number weaned, exceeded the lower bound for fp , the number born. For all estimates, we assumed statistically significant differences when the 95% confidence limits did not overlap.

To compare the mean and variance in annual mortality on the island and at the mainland, we used a bootstrap. One thousand samples, with replacement, of all annual rates were used to calculate the standard deviation. Confidence limits were percentiles 2.5 and 97.5.

Validation of Counts from Aerial Censuses

During the 1970s and 1980s, ground counts at peak season were compared with counts from photographs taken from aircraft flying 150 m above the rookery. We present comparisons where aerial and ground counts were on the same day.

Rate of Colony Growth

The rate of colony change was estimated from successive estimates of the number of females using the colony. The growth rate r is $\ln N_2 - \ln N_1$, where N_2 and N_1 are colony sizes in successive years.

Graphical Display

For scatter plots of survival rates and colony growth rates through time, we displayed smoothed curves using local polynomial regression. For each point,

a second-order polynomial was fitted through the N nearest points (measured along the x -axis), not including the focal point. N was set to 65% of all the points. In the polynomial fit, points were weighted in proportion to $(1 - (D/D_{max})^3)^3$, where D is the x -distance from focal to neighboring point and D_{max} the distance to the furthest point in the neighborhood. The smoothing was programmed with the *Loess* function in the computer programming language R, Version 2.9.2 (R Development Core Team, 2009). The smoothed curves are presented for visual comparison; they were not used in statistical tests.

Results

Pup Production

Island—The number of pups born each year on the island since breeding began in 1961 increased rapidly until reaching a peak of 1,216 in 1980 (Figure 3; Table 1). Thereafter, pup production on the island declined to 751 births in 1987, and a downward trend continued, reaching a low of 410 pups born in 2010.

Mainland—Breeding was initiated on the mainland in 1975 with the birth of a single pup (Le Boeuf & Panken, 1977). Thereafter, pup production increased rapidly until 1995 when 2,041 pups were born (Figure 3; Table 2). By 1987, more pups were born on the mainland than the island. From 1995 to 2005, the number of pups born on the mainland stabilized at about 2,000, but in the ensuing years, the number decreased, falling to 1,735 in 2010.

Colony—Pups born in the entire region, island and mainland combined, increased steadily from initial colonization up to a high of 2,731 in 1995; there were only brief reversals of the steady increase in 1981, 1985 through 1988, and 1993–1994 (Figure 3). Numbers stabilized at approximately 2,500 over the next decade but declined after 2005. The annual rate of pups born was high immediately after colonization on both the island and the mainland. For instance, the number of pups born on the mainland in 1975 through 1978 was 1, 7, 16, and 81, respectively. Subsequently, the annual rates declined steadily at both sites, approaching zero around 1995 and slightly below zero since 2005 (Figure 4).

Breeding Males

The number of breeding males did not increase proportionally to breeding females and pups (Figure 5a). Up to 1985, the number of males rose steadily, as did females, but after 1985, with the number of breeding females continuing to increase above 1,500 females (Figure 5b), the male count stabilized at around 500 (i.e., the positive

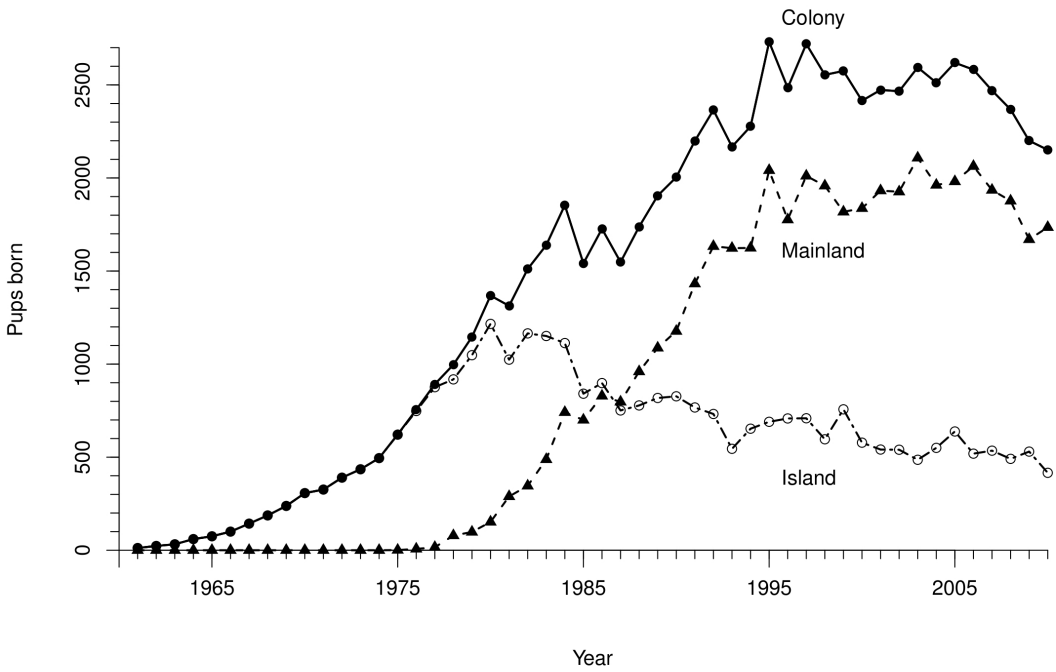


Figure 3. The number of northern elephant seal pups born at the Año Nuevo rookery since 1961 (filled circles and solid line); also shown are pup births on the island (open circles and dotted line) and on the mainland (filled triangles and dashed line). Data from 1961 through 1967 are number of pups weaned (Orr & Poulter, 1965); data for pups born for that time period are not available.

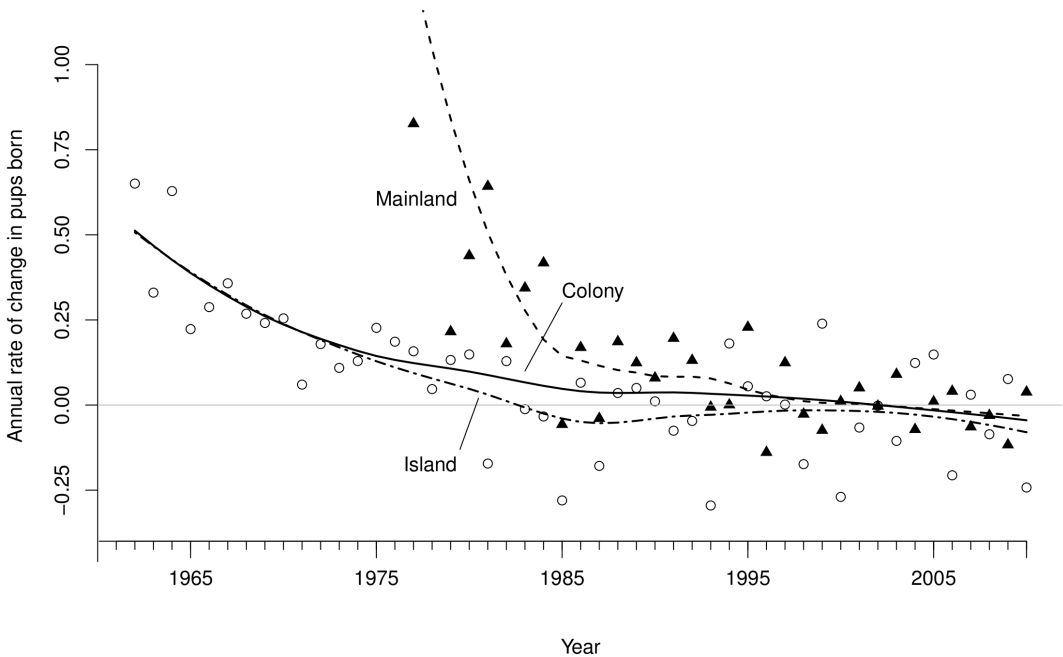


Figure 4. The annual rate of change in northern elephant seal pup births on ANI (open circles and dotted line) and ANML (filled triangles and dashed line) from 1961 to 2010; the entire colony, island and mainland combined, is shown by a solid black line. For 1961 through 1967, the rate of change is based on the number of pups weaned rather than pups born.

Table 1. Northern elephant seal (*Mirounga angustirostris*) pup statistics from the Año Nuevo colony collected during the period 1961 to 2010, showing pups born, pups weaned, and the annual survival rate; pups born were not available for the period 1961 through 1967.

Year	Island			Mainland			Total		
	Born	Weaned	% Survival	Born	Weaned	% Survival	Born	Weaned	% Survival
1961	--	12	--	0	0	--	--	12	--
1962	--	23	--	0	0	--	--	23	--
1963	--	32	--	0	0	--	--	32	--
1964	--	60	--	0	0	--	--	60	--
1965	--	75	--	0	0	--	--	75	--
1966	--	100	--	0	0	--	--	100	--
1967	--	143	--	0	0	--	--	143	--
1968	187	153	82.0	0	0	--	187	153	82.0
1969	238	203	85.5	0	0	--	238	203	85.5
1970	307	238	77.3	0	0	--	307	238	77.3
1971	326	253	77.8	0	0	--	326	253	77.8
1972	390	303	77.5	0	0	--	390	303	77.5
1973	435	282	64.8	0	0	--	435	282	64.8
1974	495	395	79.8	0	0	--	495	395	79.8
1975	621	487	78.4	1	1	100.0	622	488	78.4
1976	748	585	78.2	7	7	100.0	755	592	78.4
1977	876	589	67.2	16	16	98.7	891	604	67.8
1978	918	455	49.6	79	59	74.1	998	514	51.5
1979	1,048	627	59.8	98	76	77.3	1,146	702	61.3
1980	1,216	637	52.4	152	143	94.5	1,368	780	57.0
1981	1,024	516	50.3	289	238	82.4	1,313	754	57.4
1982	1,165	804	69.0	346	311	89.7	1,511	1,114	73.7
1983	1,151	273	23.8	488	477	97.8	1,639	751	45.8
1984	1,113	720	64.7	741	682	92.1	1,854	1,401	75.6
1985	841	600	71.3	700	634	90.5	1,541	1,233	80.0
1986	898	579	64.5	829	753	90.9	1,726	1,332	77.2
1987	751	583	77.6	797	707	88.7	1,548	1,290	83.3
1988	778	492	63.3	960	861	89.6	1,738	1,353	77.9
1989	818	684	83.6	1,087	942	86.6	1,905	1,626	85.3
1990	827	691	83.6	1,177	1,095	93.0	2,004	1,786	89.1
1991	767	727	94.7	1,432	1,330	92.9	2,200	2,057	93.5
1992	732	513	70.0	1,633	1,555	95.2	2,366	2,068	87.4
1993	545	445	81.6	1,623	1,484	91.4	2,168	1,929	88.9
1994	653	544	83.3	1,624	1,506	92.7	2,276	2,049	90.0
1995	690	230	33.3	2,041	2,002	98.1	2,731	2,232	81.7
1996	708	532	75.1	1,776	1,714	96.5	2,484	2,246	90.4
1997	709	636	89.6	2,011	1,684	83.7	2,720	2,320	85.3
1998	596	314	52.7	1,958	1,942	99.2	2,554	2,256	88.3
1999	757	556	73.5	1,818	1,643	90.4	2,575	2,199	85.4
2000	578	485	83.9	1,837	1,732	94.2	2,416	2,217	91.8
2001	541	359	66.3	1,932	1,762	91.2	2,473	2,121	85.8
2002	540	439	81.3	1,926	1,809	93.9	2,466	2,248	91.1
2003	486	384	79.1	2,108	2,019	95.8	2,594	2,403	92.6
2004	550	209	38.0	1,962	1,812	92.3	2,512	2,020	80.4
2005	638	484	75.9	1,981	1,959	98.9	2,619	2,443	93.3
2006	519	413	79.6	2,063	1,988	96.4	2,582	2,402	93.0
2007	535	465	87.0	1,935	1,858	96.0	2,470	2,322	94.0
2008	491	341	69.5	1,877	1,804	96.1	2,368	2,144	90.6
2009	530	468	88.4	1,670	1,544	92.4	2,199	2,012	91.5
2010	410	305	74.4	1,735	1,538	88.7	2,144	1,843	86.0

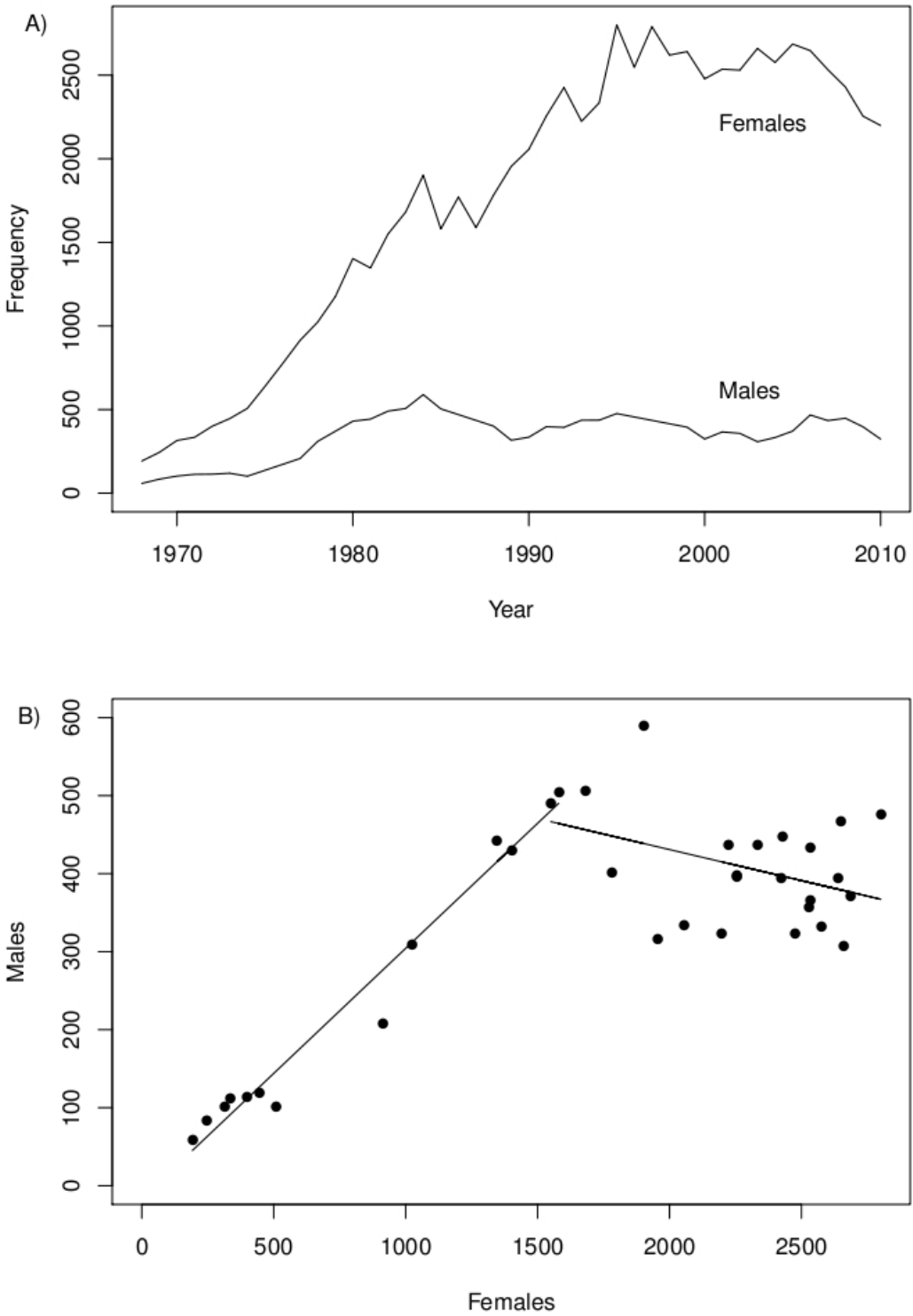


Figure 5. The number of males recorded annually at the Año Nuevo rookery from 1968 to 2010 in relation to the total number of females in attendance: (A) male and female numbers by year and (B) males in relation to females by year

correlation between male and female numbers broke down when 1,500 or more females were in attendance whereupon male numbers reached equilibrium numbers).

Pups Weaned

Changes in the total number of pups weaned over the study period matched rather closely the changes in the number of pups born, increasing steadily up to 1997 and 2005 (Table 1; Figure 6). The number of pups weaned and the weaning rate, however, were significantly different on the mainland than on the island (Figure 7). The mean annual survival rate on the mainland was 91.8% (confidence limits: 90.0 to 93.6%), significantly higher than the island mean of 71.2% (66.3 to 75.9%). Moreover, the year-to-year standard deviation in survival on the island (15.3%) was significantly higher than on the mainland (5.6%).

Pup Mortality

Pup survival was especially low on the island in 1983, 1995, 1998, and 2004 (Figure 7; Table 3), all years with severe winter El Niño conditions (Smith & Sardeshmukh 2000; www.esrl.noaa.gov/psd/people/cathy.smith/best). We made extensive observations of the effect of winter storms on pup survival in 1983 and 2010. In 1983, the entire breeding beach was inundated by high surf on

27 January, and most pups were separated from their mothers (Le Boeuf & Condit, 1983). High surf also impacted the rookery in mid-January 2010, but fewer females had given birth at the time of the storm, and pup mortality was not nearly as high as in 1983 or 1998. The major mainland beaches, having ample space above the high surf line, were relatively immune to storm effects, but several of the smaller mainland harems were awash at high surf; and in 2010, three of these beaches had high pup loss.

The high pup mortality in 2004 on the island was not due to surf as there were no major storms that year in January. Over 200 pups died after 13 February in 2004, when many were already weaned, and 80 moribund pups were counted in a pile at the base of the beach on 1 March. Moreover, on 1 March, five freshly dead weaned pups were observed. In most years, few dead weaned pups were observed. We had no direct observations of the cause of those 2004 pup deaths.

Validity of Female Counts

Censuses of breeding females from the air and the ground near peak season were within 5% of each other. For example, on 25 January 1986, an aerial count of the mainland harem yielded 680 females, and the ground count was 655 females. On three dates, aerial and ground counts of the largest

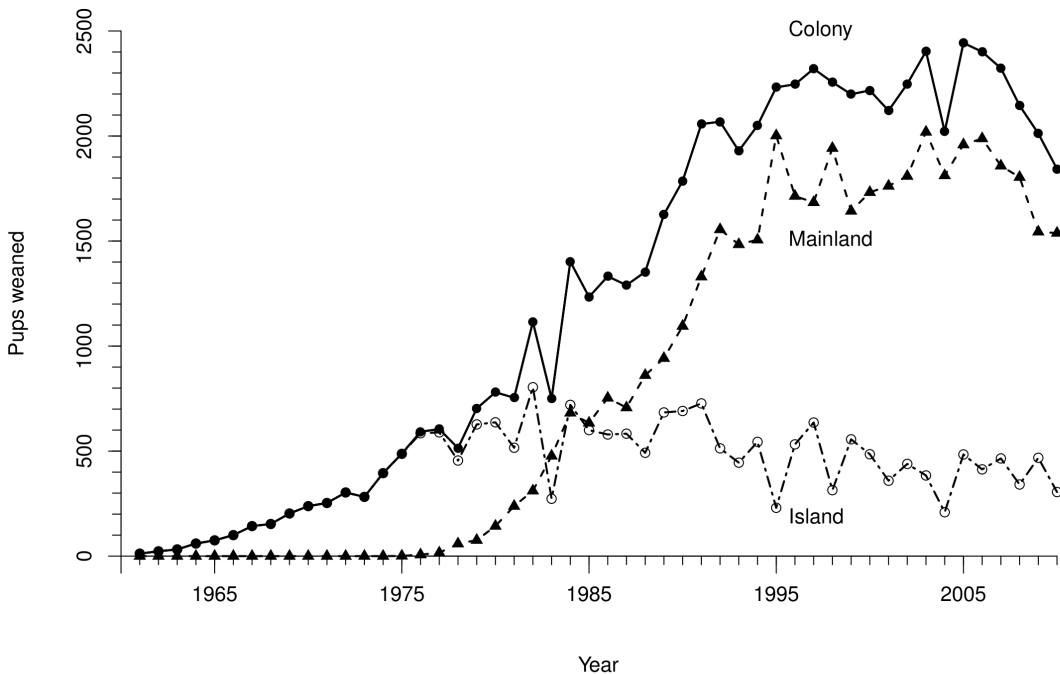


Figure 6. The total number of pups weaned on the Año Nuevo colony (filled circles and solid line), the island portion of the colony (open circles and dotted line), and the mainland (filled triangles and dotted line)

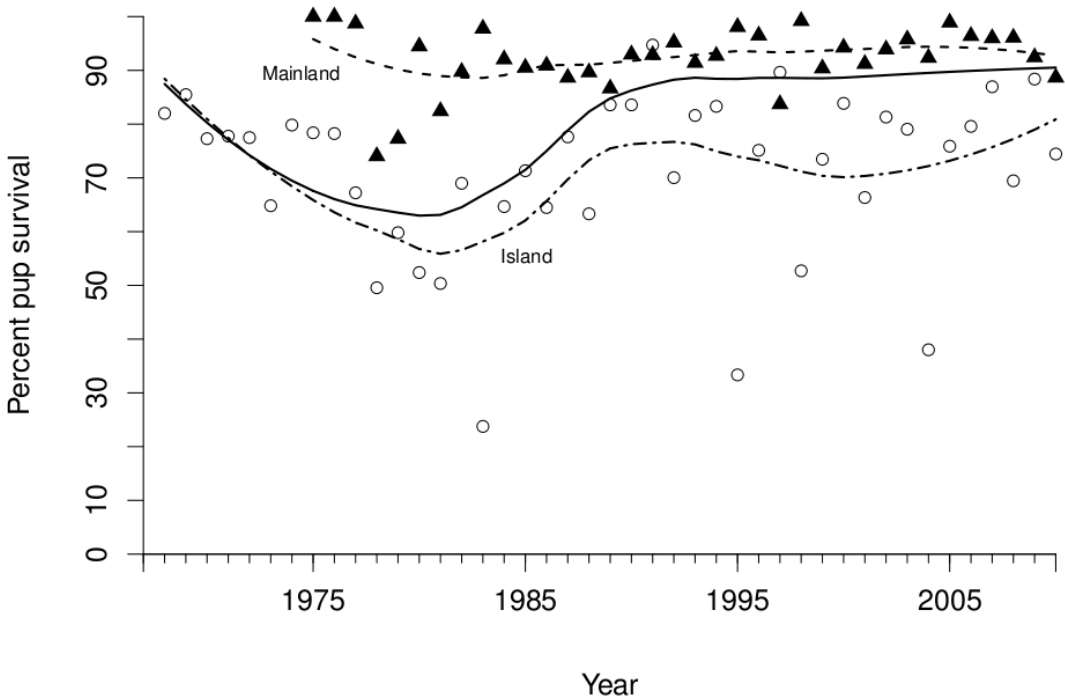


Figure 7. Percent pups surviving to weaning at the Año Nuevo rookery during the period 1968 to 2010; rates are shown for the island (open circles and dotted line), the mainland (closed triangles and dashed line), and the entire rookery (solid black line).

island harem were 512 and 524 (4 February 1976), 533 and 554 (20 January 1976), and 776 and 698 (29 January 1983), respectively.

Natality

In 1969, the number of females estimated to use the colony was 244, with 95% confidence limits of 236 to 251. Thirty-five dead pups were dragged from the harem prior to mid-February, and 203 living pups were counted at the end of February. Thus, 97.5% of the females had pups (238 of 244) with confidence limits of 95 to 100%. In 1990, 191 of 202 dye-marked females were observed exhibiting routine maternal behavior: 176 of those were observed near a single pup, and 15 others were seen near one or more pups. On the other hand, one of the 202 was recorded as nonpregnant upon arrival, and four others were never seen near a pup in many observations. Six females were seen once or twice near a pup. Assuming that only parous females exhibit maternal behavior, a minimum, 191 of 202 females were maternal, and most likely 197 of 202 were maternal, supporting a fecundity rate of 97.5% with confidence limits of 95 to 99%.

Discussion

The Año Nuevo colony of northern elephant seals grew rapidly, reaching peak numbers of over 2,700 pups born approximately 35 y after colonization was initiated in 1961. This is a growth rate of 16.2%/y. The number of pups born annually was relatively stable between 1995 and 2006 but then declined steadily after this to a low of 2,144 in 2010. The trend in pups weaned was similar to that of pups born. The Año Nuevo colony is evidently mature as evidenced by cessation of growth and the recent downward trend in pup production.

The expansion and leveling off of pup production at this colony is explained by factors operating at both the population and the local level. We address both of these topics in turn.

Population Factors

We argue here that the pattern of pups born annually at Año Nuevo was determined primarily by the influx of young breeding females dispersing from larger colonies to the south, a general pattern that has been observed throughout the growth of the population. Internal recruitment at Año Nuevo was less important in colony growth than external recruitment.

The growth and dispersal pattern of the population in breeding range and number of animals since the 1890s provides the context for understanding the development of the Año Nuevo colony. Initially, survivors were observed only on Isla de Guadalupe, Mexico (Bartholomew & Hubbs, 1960). Subsequently, the population expanded in number and breeding range, and the prevailing direction of expansion was northward. In the 1930s, new colonies were formed on the Mexican Islands of Islas San Benito and Coronados along the coast of Baja California and, thereafter, to the north at San Miguel, San Nicolas, and Santa Barbara Islands in southern California in the early 1950s, to central California at Año Nuevo in 1961, Southeast Farallon in 1972, and Point Reyes in 1981 (Stewart et al., 1994). In 1960, 91% of the entire population was concentrated at Guadalupe and included 3,500 pups born. Growth, however, ceased at the Mexican colonies in the 1970s. By 1991, pup production had increased to 28,000 (Stewart et al., 1994); and in 2005, 42,000 pups were produced, and the total population was estimated at 165,000 (M. Lowry, pers. comm., 2009; B. J. Le Boeuf & R. Condit, unpub. data, 2009-2010). Presently, 83% of pup production in the population is from U.S. rookeries in California: 81% of the total from southern California (San Clemente, Santa Barbara, San Nicolas, and San Miguel), 11% from the Big Sur coast (Point Conception, Piedras Blancas, and Cape San Martin), and 8.6% from central California (Año Nuevo, Southeast Farallon, and Point Reyes).

Tagging studies confirmed that San Miguel and San Nicolas Islands in southern California were colonized by northern elephant seals from Guadalupe (Bonnell et al., 1979). During the 1970s, elephant seals born at San Miguel and San Nicolas Islands became the major source of the colonization and subsequent growth at Año Nuevo, Southeast Farallon Island, and Point Reyes (Le Boeuf et al., 1974; Le Boeuf & Panken, 1977; Allen et al., 1989). During the 1990s, San Miguel, the largest colony in California, reached carrying capacity; it had become crowded with breeding females at peak season, and the population leveled off at approximately 14,000 pups (Lowry, 2002). During this period, new colonies were established at nearby Santa Rosa Island and Piedras Blancas on the adjacent mainland, most likely by females born at San Miguel Island.

The growth and dispersal pattern of the population at the Año Nuevo colony was determined mainly by external recruitment of females from San Miguel Island and, to a lesser extent, from San Nicolas Island. Indeed, the estimates of the

low survival rate of pups born at Año Nuevo during the first 30 y of the colony indicate that total colony numbers would have declined from internal recruitment alone (Le Boeuf & Reiter, 1988; Le Boeuf et al., 1994). A similar case has been made for Southeast Farallon Island (Huber et al., 1991). Moreover, the cessation of growth and then decline of pups born at Año Nuevo since 1995 was coincident with the explosive growth of the new colonies at Santa Rosa Island and Piedras Blancas (Lowry, 2002; B. Hatfield, pers. comm., 2010). This suggests that the explanation for the leveling off and decline in pups born at Año Nuevo is that young females from San Miguel and San Nicolas dispersed instead to the newly formed more proximal colonies at Santa Rosa Island and Piedras Blancas. Loss of recruitment from San Miguel and San Nicolas Islands to Año Nuevo during this period is confirmed from observation of tagged animals. In 1971 and 1972, 43% of the males and females in residence during the breeding season at Año Nuevo were born in southern California (Le Boeuf & Petrinovich, 1974). Two decades later, 1989 to 1998, the percentage of breeding females at Año Nuevo that were immigrants from San Miguel and San Nicolas had declined to 30%. The immigration rate was further reduced to 13% in 1999 through 2005, and then to 6% in 2006 through 2009. The decreasing influx of immigrants to Año Nuevo was associated temporally with the decline in pups born.

Behavior and Local Factors

Species-specific behavior of northern elephant seals and local factors associated with the Año Nuevo colony also exerted a strong influence on pup production, especially on pups weaned. The proportion of pups weaned to pups born varies with the age composition of females in the colony and intraspecific competition between females (Reiter et al., 1981). Pup survival depends on a close association of mother and pup. This depends to a large extent on the availability of suitable space for females to give birth and nurse their pups, especially at peak season when numbers and density are highest. High tides and high surf associated with inclement weather at peak season, and ardent males attempting to mate with females cause mother-pup separation and increase pup mortality.

Weaning success is positively correlated with increasing age and size of females (Le Boeuf & Briggs, 1977; Reiter et al., 1978, 1981; Riedman & Le Boeuf, 1982). Young females, especially primiparous females, have lower weaning success than older females because (1) they lack mothering experience and make mistakes such as confusing their newborn with a neighbor's pup; (2) they are subordinate to older, larger females which

makes them prone to being physically separated from their pups, and they cannot protect their pups from neighboring females; and (3) they are shunted to the periphery of harems where they are exposed to aggressive male mating attempts while nursing and to high surf conditions at high tide. Moreover, the pups of young mothers receive less milk energy and weigh less at birth and at weaning than pups of older mothers (Deutsch et al., 1994; Crocker et al., 2001). In effect, the higher the density among breeding females, the more difficult it is for a young female to maintain contact with her pup, nurse it, and wean it in a healthy condition. Once females give birth at a particular location, they tend to return to the same place to give birth the following year; those that fail to wean their pups at the natal site, however, more readily move to a new site to give birth. They are the pioneers in the colonization process, and most of them are primiparous (Reiter et al., 1981).

How do dispersing young females settle on new breeding sites? Yearlings and juveniles, like adults, go to sea to feed twice a year. The feeding trip lasts 2 to 5 mo in duration during which the elephant seals move north to northwest (Le Boeuf et al., 1996). Some elephant seals appear at island or mainland sites along the migratory route during or after the migration. When they come of breeding age, young females breed in new locations where they were observed previously (Reiter et al., 1981); for example, in 1974, 15 tagged Año Nuevo-born females giving birth on Southeast Farallon Island had been sighted there previously on one or more occasions. This behavior is similar to "prospecting" in Kittiwake gulls (*Rissa tridactyla*; Wooller & Coulson, 1977). Once females give birth in a new site, males follow; later, arriving females join females in attendance to reduce harassment from male suitors (Le Boeuf & Mesnick, 1991).

This behavior pattern of females provides the underlying basis for density dependent dispersal, the establishment and growth of new colonies, and, ultimately, population growth. This is illustrated by comparison of the growth patterns of the island and mainland portions of the Año Nuevo colony. Initially, pup production on the island increased rapidly, but as available breeding space became crowded and carrying capacity was reached by the early 1980s, some young females began dispersing to nearby Southeast Farallon Island in 1972 (Le Boeuf et al., 1974), to the adjacent mainland in 1975 (Le Boeuf & Panken, 1977), and to Point Reyes in 1981 (Allen et al., 1989). These movements were driven by crowding of females and pups on the island at peak season and was reflected by pup mortality soaring to over 50% of pups born and up 76% in years in which high tides and surf coincided with peak season (Le Boeuf & Briggs,

1977; Reiter et al., 1981; Le Boeuf & Condit, 1983). Under these conditions, young females were at a great disadvantage in reproducing locally and, consequently, more likely to disperse than older females (Le Boeuf et al., 1974; Le Boeuf & Panken, 1977). It is notable that seals dispersed to sites less dense with breeding females than the rookeries from which they were coming, and that emigration began well before the maximum density of breeding females was reached, a pattern observed with tagged animals from Guadalupe, San Miguel, San Nicolas, and Año Nuevo. This behavior accords with observations of dispersal in many mammals—for example, crabeater seals (*Lobodon carcinophaga*; Caughley, 1960), pocket gophers (*Thomomys bottae*; Howard & Childs, 1959), and field voles (*Microtus pennsylvanicus* and *M. ochrogaster*; Myers & Krebs, 1971). Moreover, our data on the island shows that once the maximum number of females was reached and stabilized or even declined (around 1980 in Table 1 & Figure 3), the pup mortality rate in subsequent years fluctuated widely depending on tidal and surf conditions at peak season (Le Boeuf & Condit, 1983; Le Boeuf & Reiter, 1991).

In contrast, the mainland part of the colony had lower and less variable pup mortality rates than the island. The main difference between the two sites is that breeding space was virtually unlimited on the mainland; arriving females could come ashore easily to secure a place to give birth and nurse their pups and, when threatened by high surf, mothers and pups could move away from danger to higher ground. This was not possible on the island; females in residence were limited by available breeding, which led to high pup mortality, which is a classic example of density-dependence. Nevertheless, the number of pups born on the mainland ceased to increase in the mid-1990s, and numbers declined in the following years. Obviously, the check on pup growth on the mainland requires a different explanation. Circumstances suggest strongly that the cause was lowered external recruitment from southern rookeries as argued above. If so, pup production on the mainland may increase again when carrying capacity is reached at the Santa Rosa Island and Piedras Blancas colonies and young animals disperse northward.

Evidently, both population and local factors, working in synergy with the geographical environment, weather and sea conditions, and intraspecific competition and density, affect pup production at the Año Nuevo colony. These processes are likely the same ones that operated from colony to colony as the population expanded while recovering from near extinction. That is, viewed over the course of the last 110 y, the northern elephant seal

population as a whole has exhibited range-wide density dependence that is evident as each colony was established and matured, and which caused young females to colonize new sites. This regulatory progression is expected to continue until all optimal habitat is occupied or until the elephant seals come into conflict with humans over beach space as is occurring on the California coast near Piedras Blancas (C. Skinder, pers. comm., 2009). The extent to which food and predation limit growth is unknown. Ocean warming affects foraging and reduces resource accrual in gestating females, which is correlated with weaning smaller pups (Le Boeuf & Crocker, 2005; Crocker et al., 2006), but the effect on survival and colony growth on northern elephant seals is unknown; a positive link between maternal foraging and first-year survival of pups is reported in southern elephant seals (McMahon & Burton, 2005). White sharks (*Carcharodon carcharias*) prey on elephant seals near their rookeries (Le Boeuf et al., 1982; Le Boeuf, 2004), but the impact on the population is uncertain. We conclude that documenting the growth of a single colony like Año Nuevo, from initial colonization to reaching equilibrium numbers, focuses attention on several of the key factors that affect pup production and the pattern of population growth.

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Literature Cited

- Allen, S. G., Peaslee, S. C., & Huber, H. R. (1989). Colonization by northern elephant seals of the Point Reyes Peninsula, California. *Marine Mammal Science*, 5, 298-302. <http://dx.doi.org/10.1111/j.1748-7692.1989.tb00342.x>
- Barlow, J., Boveng, P., Lowry, M. S., Stewart, B. S., Le Boeuf, B. J., Sydeman, W. J., . . . Oliver, C. W. (1993). *Status of the northern elephant seal population along the U.S. West Coast in 1992*. La Jolla, CA: Southwest Fisheries Science Center.
- Bartholomew, G. A., & Hubbs, C. L. (1960). Population growth and seasonal movements of the northern elephant seal, *Mirounga angustirostris*. *Mammalia*, 24, 313-324.
- Bonnell, M. L., Le Boeuf, B. J., Pierson, M. O., Dettman, D. H., & Farrens, G. D. (1979). *Summary report 1975-1978. Marine mammal and seabird surveys of the Southern California Bight Area: Vol. III. Pinnipeds* (Contract AA550-CT7-36, 535). Washington, DC: Bureau of Land Management, Department of the Interior.
- Caughley, G. (1960). Dead seals inland. *Antarctica*, 2, 270-271.
- Condit, R., Le Boeuf, B. J., Morris, P. A., & Sylvan, M. (2007). Estimating population size in asynchronous aggregations: A model and test with elephant seal counts. *Marine Mammal Science*, 23(4), 834-855. <http://dx.doi.org/10.1111/j.1748-7692.2007.00141.x>
- Cooper, C. F., & Stewart, B. S. (1983). Demography of northern elephant seals, 1911-1982. *Science*, 210, 969-971. <http://dx.doi.org/10.1126/science.219.4587.969>
- Crocker, D. E., Williams, J. D., Costa, D. P., & Le Boeuf, B. J. (2001). Maternal traits and reproductive effort in northern elephant seals. *Ecology*, 82(12), 3541-3555. [http://dx.doi.org/10.1890/0012-9658\(2001\)082\[3541:MTAREI\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2001)082[3541:MTAREI]2.0.CO;2)
- Crocker, D. E., Costa, D. P., Le Boeuf, B. J., Webb, P. M., & Houser, D. S. (2006). Impact of El Niño on the foraging behavior of female northern elephant seals. *Marine Ecology Progress Series*, 309, 1-10. <http://dx.doi.org/10.3354/meps309001>
- Deutsch, C. J., Crocker, D. E., Costa, D. P., & Le Boeuf, B. J. (1994). Sex- and age-related variation in reproductive effort of northern elephant seals. In B. J. Le Boeuf & R. M. Laws (Eds.), *Elephant seals: Population ecology, behavior, and physiology* (pp. 169-210). Berkeley: University of California Press.
- Hoelzel, A. R., Fleischer, R. C., Campagna, C., Le Boeuf, B. J., & Alvard, G. (2002). Impact of a population bottleneck on symmetry and genetic diversity in the northern elephant seal. *Journal of Evolutionary Biology*, 15(4), 567-575. <http://dx.doi.org/10.1046/j.1420-9101.2002.00419.x>
- Hoelzel, A. R., Halley, J., O'Brien, S. J., Campagna, C., Arnborn, T., Le Boeuf, B. J., . . . Dover, G. A. (1993). Elephant seal genetic variation and the use of simulation models to investigate historical population bottlenecks. *Journal of Heredity*, 84, 443-449.
- Howard, W. E., & Childs, H. E. (1959). Ecology of pocket gophers with emphasis on *Thomomys bottae mewa*. *Hilgardia*, 29, 277-358.
- Huber, H. R., Beckham, C., & Nisbet, J. (Eds.). (1991). Effects of the 1982-83 El Niño on northern elephant seals on the South Farallon Islands, California. In F. Trillmich & K. A. Ono (Eds.), *Pinnipeds and El Niño: Responses to environmental stress* (pp. 219-233). Berlin: Springer-Verlag.
- Huey, L. M. (1930). Past and present status of the northern elephant seal with a note on the Guadalupe fur seal. *Journal of Mammalogy*, 11, 188-194. <http://dx.doi.org/10.2307/1374066>

- Le Boeuf, B. J. (1977). Back from extation? *Pacific Discovery*, 30, 1-9.
- Le Boeuf, B. J. (2004). Hunting and migratory movements of white sharks in the eastern North Pacific. *Memoirs of the National Institute of Polar Research*, 58, 89-100.
- Le Boeuf, B. J., & Briggs, K. T. (1977). The cost of living in a seal harem. *Mammalia*, 41, 167-195. <http://dx.doi.org/10.1515/mamm.1977.41.2.167>
- Le Boeuf, B. J., & Condit, R. S. (1983). The high cost of living on the beach. *Pacific Discovery*, 36, 12-14.
- Le Boeuf, B. J., & Crocker, D. E. (2005). Ocean climate and seal condition. *BMC Biology*, 3, 1-9. <http://dx.doi.org/10.1186/1741-7007-3-1>; <http://dx.doi.org/10.1186/1741-7007-3-9>
- Le Boeuf, B. J., & Laws, R. M. (1994a). Elephant seals: An introduction to the genus. In B. J. Le Boeuf & R. M. Laws (Eds.), *Elephant seals: Population ecology, behavior and physiology* (pp. 1-26). Berkeley: University of California Press.
- Le Boeuf, B. J., & Laws, R. M. (Eds.). (1994b). *Elephant seals: Population ecology, behavior, and physiology*. Berkeley: University of California Press.
- Le Boeuf, B. J., & Mesnick, S. (1991). Sexual behavior of male northern elephant seals: I. Lethal injuries to adult females. *Behaviour*, 116, 143-162. <http://dx.doi.org/10.1163/156853990X00400>
- Le Boeuf, B. J., & Panken, K. J. (1977). Elephant seals breeding on the California mainland. *Proceedings of the California Academy of Sciences*, 41, 267-280.
- Le Boeuf, B. J., & Petrino, L. F. (1974). Dialects of northern elephant seals, *Mirounga angustirostris*: Origin and reliability. *Animal Behavior*, 22, 656-663. [http://dx.doi.org/10.1016/S0003-3472\(74\)80013-8](http://dx.doi.org/10.1016/S0003-3472(74)80013-8)
- Le Boeuf, B. J., & Reiter, J. (1988). Lifetime reproductive success in northern elephant seals. In T. H. Clutton-Brock (Ed.), *Reproductive success: Studies of individual variation in contrasting breeding systems* (pp. 344-362). Chicago: University of Chicago Press.
- Le Boeuf, B. J., & Reiter, J. (1991). Biological effects associated with El Niño, Southern Oscillation 1982-83, on northern elephant seals breeding at Año Nuevo, California. In F. Trillmich & K. A. Ono (Eds.), *Pinnipeds and El Niño: Responses to environmental stress: Vol. 88. Ecological studies* (pp. 206-218). Berlin: Springer-Verlag.
- Le Boeuf, B. J., Ainley, D. G., & Lewis, T. J. (1974). Elephant seals on the Farallones: Population dynamics of an incipient colony. *Journal of Mammalogy*, 55, 370-385. <http://dx.doi.org/10.2307/1379005>
- Le Boeuf, B. J., Morris, P., & Reiter, J. (1994). Juvenile survivorship of northern elephant seals from Año Nuevo. In B. J. Le Boeuf & R. M. Laws (Eds.), *Elephant seals: Population ecology, behavior, and physiology* (pp. 121-136). Berkeley: University of California Press.
- Le Boeuf, B. J., Riedman, M., & Keyes, R. S. (1982). Shark predation on pinnipeds in California coastal waters. *Fisheries Bulletin*, 80, 891-895.
- Le Boeuf, B. J., Whiting, R. J., & Gantt, R. F. (1972). Perinatal behavior of northern elephant seal females and their young. *Behaviour*, XLIII, 121-156.
- Le Boeuf, B. J., Morris, P. A., Blackwell, S. A., Crocker, D. E., & Costa, D. P. (1996). Diving behavior of juvenile northern elephant seals. *Canadian Journal of Zoology*, 74, 1632-1644. <http://dx.doi.org/10.1139/z96-181>
- Lowry, M. S. (2002). *Counts of northern elephant seals at rookeries in the Southern California Bight: 1981-2001* (NOAA-TM-NMFS-SWFSC-345). Washington, DC: U.S. Department of Commerce.
- McMahon, C. R., & Burton, H. R. (2005). Climate change and seal survival: Evidence for environmentally mediated changes in elephant seal, *Mirounga leonina*, pup survival. *Proceedings of the Royal Society B*, 272, 923-928. <http://dx.doi.org/10.1098/rspb.2004.3038>
- McMahon, C. R., Burton, H. R., & Bester, M. N. (2003). A demographic comparison of two southern elephant seal populations. *Journal of Animal Ecology*, 72, 61-74. <http://dx.doi.org/10.1046/j.1365-2656.2003.00685.x>
- Meyer, S. L. (1975). *Data analysis for scientists and engineers*. New York: John Wiley & Sons.
- Myers, J. H., & Krebs, C. J. (1971). Genetic, behavioral and reproductive attributes of dispersing field voles, *Microtus pennsylvanicus* and *Microtus ochrogaster*. *Ecological Monographs*, 41, 53-78. <http://dx.doi.org/10.2307/1942435>
- Orr, R. T., & Poulter, T. C. (1965). The pinniped population of Año Nuevo Island, California. *Proceedings of the California Academy of Sciences*, 32, 377-404.
- Radford, K. W., Orr, R. T., & Hubbs, C. L. (1965). Reestablishment of the northern elephant seal (*Mirounga angustirostris*) off Central California. *Proceedings of the California Academy of Sciences*, 31, 601-612.
- R Development Core Team. (2009). *R: A language and environment for statistical computing*. Retrieved 12 October 2011, from www.R-project.org.
- Reiter, J., Panken, K. J., & Le Boeuf, B. J. (1981). Female competition and reproductive success in northern elephant seals. *Animal Behavior*, 29, 670-687. [http://dx.doi.org/10.1016/S0003-3472\(81\)80002-4](http://dx.doi.org/10.1016/S0003-3472(81)80002-4)
- Reiter, J., Stinson, N. L., & Le Boeuf, B. J. (1978). Northern elephant seal development: The transition from weaning to nutritional independence. *Behavioral Ecology and Sociobiology*, 3, 337-367. <http://dx.doi.org/10.1007/BF00303199>
- Riedman, M. L., & Le Boeuf, B. J. (1982). Mother-pup separation and adoption in northern elephant seals. *Behavioral Ecology and Sociobiology*, 11, 203-215. <http://dx.doi.org/10.1007/BF00300063>
- Scammon, C. M. (1874). *The marine mammals of the northwestern coast of North America*. San Francisco: J. H. Carmany and Co.
- Sibly, R., & Hone, J. (2002). Population growth rate and its determinants: An overview. *Philosophical Transactions of the Royal Society of London, Series B—Biological Sciences*, 357(1425), 1153-1170. <http://dx.doi.org/10.1098/rstb.2002.1117>

- Sinclair, A., & Krebs, C. (2002). Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *Philosophical Transactions of the Royal Society of London, Series B—Biological Sciences*, 357(1425), 1221-1231. <http://dx.doi.org/10.1098/rstb.2002.1123>
- Smith, C. A., & Sardeshmukh, P. (2000). The effect of ENSO on the intraseasonal variance of surface temperature in winter. *International Journal of Climatology*, 20, 1543-1557. [http://dx.doi.org/10.1002/1097-0088\(20001115\)20:13<1543::AID-JOC579>3.0.CO;2-A](http://dx.doi.org/10.1002/1097-0088(20001115)20:13<1543::AID-JOC579>3.0.CO;2-A)
- Stewart, B. S., Yochem, P. K., Huber, H. R., DeLong, R. L., Jameson, R., Sydeman, W., . . . Le Boeuf, B. J. (1994). Population recovery and status of the northern elephant seal, *Mirounga angustirostris*. In B. J. Le Boeuf & R. M. Laws (Eds.), *Elephant seals: Population ecology, behavior, and physiology* (pp. 29-48). Berkeley: University of California Press.
- Townsend, C. H. (1885). An account of recent captures of the California sea-elephant and statistics relating to the present abundance of the species. *Proceedings of the U.S. National Museum*, 8, 90-94.
- Weber, D. S., Stewart, B. S., Garza, J. C., & Lehman, N. (2000). An empirical genetic assessment of the severity of the northern elephant seal population bottleneck. *Current Biology*, 10(20), 1287-1290. [http://dx.doi.org/10.1016/S0960-9822\(00\)00759-4](http://dx.doi.org/10.1016/S0960-9822(00)00759-4)
- Widenius, M., & Axmark, D. (2002). *MySQL reference manual*. Sebastopol, CA: O'Reilly & Associates, Inc.
- Wooller, R. D., & Coulson, J. C. (1977). Factors affecting the age of first breeding of the Kittiwake, *Rissa tridactyla*. *Ibis*, 119, 339-349. <http://dx.doi.org/10.1111/j.1474-919X.1977.tb08252.x>