Breeding Biology of the Northern Elephant Seal (*Mirounga angustirostris*) at the Isla San Benito del Oeste, Eastern Pacific, Mexico

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Abstract

The reproduction of the northern elephant seal (Mirounga angustirostris) has been studied within the colonies of California, but little information exists for the colonies of the Pacific coast of Mexico. Here, I present information for two consecutive breeding seasons (2001-2002 and 2002-2003) collected at one of the San Benito Islands, close to the southern limit of the distribution of the species. The number of females that arrived at the island was higher in 2002-2003, but this did not indicate that the colony is increasing in population. The principle reproductive parameters (the length of stay on land and the duration of lactation), and the birth and death rates were similar for both years. The breeding season was estimated to begin in early December and end in early March, lasting for 100 days or more, and the peak of the season, with the greatest number of females, occurred on January 19 in both years. There were some differences between San Benito and information reported from other northern colonies: the duration of the breeding season is longer in San Benito, the peak of the season occurred earliest, and the preweaning pup mortality was less.

Key Words: Mexican Pacific, *Mirounga angustirostris*, reproductive biology, Rothery & McCann model

Introduction

The northern elephant seal (*Mirounga angustiro-stris*) has areas of breeding, molting, and resting extending from Point Reyes, California, to Isla Natividad, Baja California, México (King, 1983; Stewart et al., 1994). The Islas San Benito had an important role in the recovery of the northern elephant seal. The history of the species includes intensive hunting during the 19th century, and the species being declared extinct in the early 20th century. In the early 1910s, a reduced group

was found at Isla Guadalupe (less than 150 individuals), and some years later, in 1918, a group was found at Islas San Benito (Bartholomew & Hubbs, 1960). During 1938, the first evidence of reproduction out of Isla Guadalupe was reported in those islands (Bartholomew & Hubbs, 1960; Le Boeuf & Laws, 1994). The total population size in 1957 was estimated at 13,000 individual residents at Isla Guadalupe, Islas San Benito, and the Channel Islands (Bartholomew & Hubbs, 1960). Unfortunately, little of the biology of the species has been studied at these Mexican colonies, apart from a few isolated censuses. Nothing is known, therefore, about its demography and reproductive biology, which could serve to evaluate the present state of the population.

The San Benito Islands are located to the west of the central portion of the Baja California peninsula, northwest of Cedros Island. The island complex is made up of three islands whose names agree with their longitudinal relationship: San Benito del Oeste, San Benito del Centro, and San Benito del Este. Because the distances between the islands are well within the swimming capacity of these animals, I assume that the San Benito del Oeste colony forms part of a single stock, which would include the three Islas San Benito and Isla Cedros. The stock is situated at the southern limit of the distribution of the species and, at these latitudes, may present differences in the timing of reproductive events compared to those reported for central California, as has been observed for other pinniped species (Boyd, 1991; Temte & Temte, 1993). The present study describes the reproductive biology of the elephant seal at San Benito del Oeste compared to colonies located further north.

Materials and Methods

Fieldwork

The study area embraces 14 beaches of the northeastern region of San Benito del Oeste $(28^{\circ}18'N, 115^{\circ}22'W)$, the westernmost island in the San Benito complex (Figure 1). Fieldwork was carried out during two consecutive breeding seasons, from 19 December 2001 to 18 February 2002 (hereafter termed the 2001-2002 season), and from 21 December 2002 to 21 February 2003 (the 2002-2003 season). Daily counts were made by walking the 14 beaches, noting all categories of age and sex. There were 62 and 63 censuses carried out during the 2001-2002 and 2002-2003 seasons, respectively. Most females at the study area were marked on both flanks with an individual code using hair dye (Le Boeuf & Peterson, 1969): 350 females in the 2001-2002 season and 486 in 2002-2003. The marking began at the start of the field season and continued until no more females were encountered. I tried to mark each female on the day of arrival to follow each individual systematically throughout its stay on the island.

The marked females were inventoried, recording the beach at which they were observed, their dates of arrival, births, acts of copulation, and the last day they were seen. It was also recorded if the females lost their pups or if these had died. The pups of known females were marked with plastic Jumbo Rototags (Dalton I.D. Systems) on both posterior flippers (the first before weaning, and the second after weaning). During 2001-2002, 263 pups were marked, and during 2002-2003, 310. After being weaned, the presence of the pups and their sex were recorded on a daily basis.



Figure 1. Location of the San Benito Islands, Eastern Pacific, México; the rectangle shows the study area at San Benito del Oeste.

Data Analysis

The parameters most important for their reproductive biology were estimated from the individual records of the females. These included date of arrival and parturition, interval between arrival and parturition, length of stay on land, duration of lactation, date of departure, mean date of copulation, and the interval between parturition and copulation.

The total number of females that arrived at each beach was estimated using the model of Rothery & McCann (1987). The model assumes that the time at which females arrive follows a normal distribution with mean, μ (measurement in days), with standard deviation, σ , and that all females haul out for the same length of time, *S*. If N_{Fi} denotes the haul out population size in a given beach and $n_i(t)$ the number of females counted at time *t* (day) at beach *i*, then:

$$n_i(t) = N_{ii}\left(\emptyset\left(\frac{t-\mu_i}{\sigma_i}\right) - \emptyset\left(\frac{t-S-\mu_i}{\sigma_i}\right) \right)$$

where, μ_i is the average date of arrival at beach *i*, σ_i is the standard deviation, and ϕ is the cumulative distribution function of the standard normal density. The total number of females in the study area (*N*_{*r*7}) is as follows:

$$N_{FT} = \sum_{i=1}^{14} N_{Fi}$$

The variance of N_{FT} is the sum of the squared standard errors. As the values for the terms μ_i and σ_i pertain to a specific beach, one must estimate the values of μ and σ for all of the beaches using the N_{FT} weighted by solving for the least sum of the squares of the residual variations between the model and the observed data. The proportion of females at the peak of the season with respect to the total number of females is estimated as $2\phi((S / \sigma) - 1 \text{ (Rothery & McCann, 1987).})$

Since not all of the marked females remained on the island, it was necessary to subtract the number of females that stopped being seen within a few days of their arrival (F_o) from the total number that had been marked (F_M). The birth rate was thus estimated as the following:

$$B_r = \frac{F_p}{F_M - F_o} *100\%$$

where, B_n denotes birth rate and F_p is the number of marked females with pups (whether or not the pups survived until weaned).

Since neither of the two samplings embraced the entire breeding season, in both years there were pups that had not yet been weaned at the end of the field studies. To calculate the preweaning pup mortality, I ignored the pups that were still suckling, so that the death rate prior to weaning (q_x) was estimated as the following:

$$q_{x} = \frac{(n_{x} - n_{y}) - n_{x+1}}{n_{x} - n_{y}} * 100\%$$

where, n_x is the total number of marked pups, n_y is the number of unweaned marked pups, and n_{x+1} is the number of living, weaned marked pups. The sex ratio of the weaned pups was estimated as the number of marked female pups divided by the number of marked male pups (male:female).

Comparisons of the birth and mortality rates between seasons were made using the method of the comparison of m proportions and that of the sex ratios by the simple comparative trial (Fleiss, 1981). Comparisons of the intervals between arrival and parturition, and parturition and copulation; the length of stay on the island; and the duration of breastfeeding were made using the Student *t*-test (Zar, 1999).

Results

The breeding season began in early December in both years. Although no records are available for the first two weeks of the month for either survey, by applying the model of Rothery & McCann (1987) and performing the corresponding projections (Figures 2a & 2b), the first females must have arrived at the beginning of December and the last must have departed at the beginning of March, so that the length of the entire season would have been at least 100 days. The distribution through time of the females followed a very regular pattern, well-described by the model ($r^2 = 0.96$ in 2001-2002 and $r^2 = 0.95$ in 2002-2003) (Figures 2a & 2b). The average date of arrival did not vary between seasons; the peak of the season occurred on January 19th in both years; and the proportion of females during the peak was similar (0.79 in 2001-2002 and 0.82 in 2002-2003). The average length of the stay on land per female was also not different between years (t = 0.06, d.f. = 469, p = 0.95) (Table 1). The number of females that arrived in 2002-2003 ($N_{FT} = 545$, interval = 500-590) was greater than estimated for 2001-2002 $(N_{FT} = 413, \text{ interval} = 382-443).$

The number of harems that formed on the 14 beaches differed between years—7 in 2001-2002 and 9 in 2002-2003—but the average harem sizes were similar (35.4 ± 6.6 and 37.7 ± 18.3 , respectively; t = -0.61, d.f. = 10, p = 0.55). The range in size of the harems was 9 to 134 in 2001-2002 and 18 to 144 in 2002-2003. Because of the large spread, the harems situated at the extremes were not included when calculating the average harem size. In both years, the number of adult males

Table 1. Parameters of the breeding biology of northern elephant seal females at San Benito del Oeste, México; SD = standard deviation; n =sample size; CI = 95% confidence interval; and Day 1 represents December 1.

		2001-2002			2002-2003			
	Mean	SD	n	CI	Mean	SD	n	CI
Day of arrival	35	12.6	245	± 3.1	36	11.5	308	± 2.4
	(January 4)				(January 5)			
Arrival-parturition								
interval (in days)	6.1	2.8	195	± 0.4	6.2	2.7	273	± 0.3
Length of stay								
(in days)	31.0	5.0	190	± 0.7	31.2	4.6	281	± 0.5
Day of parturition	42.1	10.7	201	± 1.4	41.9	9.3	276	± 1.1
•	(January 11)				(January 11)			
Duration of								
lactation (in days)	26.6	2.8	158	± 0.4	27.1	2.6	223	± 0.3
Day of copulation	59.7	11.1	84	± 2.8	61.0	10.9	45	± 3.2
•	(January 30)				(January 30)			
Parturition-								
copulation interval								
(in days)	23.1	3.7	54	± 1.0	24.2	2.9	37	± 0.9
Copulation-								
departure interval								
(in days)	3.3	2.7	81	± 0.6	3.4	2.6	44	± 0.8
Day of departure	63.6	10.6	289	± 1.2	65.3	9.6	393	± 0.9
	(February 2)				(February 3)			



Figure 2. Temporal distribution of northern elephant seal females and pups at San Benito del Oeste: (A) females, 2001-2002 breeding season; (B) females, 2002-2003 breeding season; (C) pups, 2001-2002 breeding season, and (D) pups, 2002-2003 breeding season.

increased from the start of the sampling (middle December) until January 14th, after which they remained constant until the end of the six weeks of observation. The number of males was similar during the second half of both sampling periods, but during the first half of the 2001-2002 season, they were significantly fewer males (t = -3.08, d.f. = 118, p = 0.003).

The proportion of females that stopped being recorded in the study area (and that were also not seen during weekly trips around the entire perimeter of the island) was not different between years ($\chi^2 = 0.353$, d.f. =1). In 2001-2002, 9.7% of the 350 marked females abandoned the island, while

in 2002-2003, the proportion was 10.9%. This did not affect the birth rate estimates between years, which were not significantly different ($\chi^2 = 1.304$, d.f. = 1) (Table 2).

The mean date of parturition was the same for both seasons (Table 1) as was the maximum number of unweaned pups (January 24th) (Figures 2c & 2d). The average length of time between arrival and parturition (Table 1) was also not different (t = -0.63, d.f. = 466, p = 0.53). Although the birth rates were similar, the number of pups produced was greater in 2002-2003 because the number of females was greater (see Figures 2a & 2b). The lengths of lactation also were not

 Table 2. Natality, preweaning pup mortality rates, and sexual ratio of weaning pups at San Benito del Oeste, México

	2001-2002	2002-2003
Natality (Br)	92.50%	90.00%
Mortality (qx)	7.80%	8.70%
Sexual ratio (males:females)	1:0.83	1:0.91

different between years (t = -1.87, d.f. = 379, p =(0.06) (Table 1), even according to the sex of the pups (males: 26.8 ± 2.6 days, females: 26.9 ± 2.5 days) (t = 0.344, d.f. = 188, p = 0.73). In 2001-2002, of the 263 pups marked, 18 had not weaned by the end of the study, while the next year these represented 24 of the 310 that were marked. The estimated preweaning pup mortality (Table 2) was not different between years ($\chi^2 = 0.184$, d.f. = 1). The first case of weaning observed in 2001-2002 was on 27 December the first season and on 30 December the following season, so these pups should have been born at the beginning of this month. The sex ratio in both years (Table 2) did not diverge from the expected 1:1 (z = 1.126 in 2001-2002 and z = 0.514 in 2002-2003), so there were no differences between years ($\chi^2 = 0.041$, d.f. = 1).

The first acts of copulation were recorded on 2 January and 3 January in 2001-2002 and 2002-2003, respectively. Since some of the females had already abandoned the island before the beginning of January, the first mating of both seasons probably occurred at the end of December. Neither the average date of copulation (t = -0.60, d.f. = 127, p = 0.55) nor the interval between parturition and copulation (Table 1) were significantly different between years (t = -1.50, d.f. = 89, p = 0.14). The average dates of departure (Table 1), however, were different between seasons (t = -2.13, d.f. = 680, p = 0.03).

Discussion

A key aspect of understanding the biology and ecology of polygynous species is to know the number of reproducing females. As the limiting sex, they indicate the size, condition, and trend of the colonies (Trivers, 1972). Due to the annual cycle of the northern elephant seal, the various sex and age classes are never encountered together at any one time of the year. Therefore, the usual method of estimating the size of a colony is by means of an approximation of the total number of females during the breeding season and the evaluation of pup production (Boveng et al., 1988; McCann, 1985). The beaches of northeastern Isla San Benito del Oeste were the most heavily populated of the island. In both seasons, more than 50% of the females congregated there (García-Aguilar & Morales-Bojorquez, 2003), so the present study can be considered representative of the dynamics of the entire island colony.

The number of females that arrived in the study area in 2002-2003 was greater than in 2001-2002 (about 130 more females, an increment of 31%). This does not necessarily indicate that the colony was growing, since this increase could have been due to a different distribution of the females among the San Benito Islands. This displacement hypothesis is supported by the observed mobility of the females. Based on the daily records of their locations, it was possible to note that the females never stayed at the beach on which they had first arrived. During both seasons, furthermore, females that had been marked on San Benito del Oeste were recorded on San Benito del Centro, so that interchanges between islands cannot be ruled out. San Benito del Centro is the most densely populated by elephant seals of all the Islas San Benito (Hernández-Camacho & Aurioles-Gamboa, 2000; Stewart et al., 1994) and it is separated from San Benito del Oeste by less than 1 km. It is thus possible that the increase recorded on San Benito del Oeste could have been caused by the displacement of young and marginal females from San Benito del Centro looking for less densely occupied beaches to successfully produce pups, as was reported previously by Reiter et al. (1981).

The average size of the harems was similar between seasons, but because of the increase in females in 2002-2003, the number of harems increased, establishing themselves on beaches that had previously been unpopulated. Most of the harems were small (average about 40 females) compared to other colonies, where harems as large as 350 females could be observed (Le Boeuf, 1978). The size of the harems is related to the topography of San Benito del Oeste. Most of the beaches are small and are separated from each other by rock formations, which impede the gathering of a large number of animals. Although there is certainly a better dispersion of females, the potential of polygyny is reduced due to the higher energy costs males expend to monopolize the females (Emlen & Oring, 1977). The lower density also helps females reduce the probability of losing their pups, which is reflected in lower mortalities compared to large harems with their high degree of disturbance (Campagna et al., 1993; Le Bouef & Briggs, 1977).

The total number of males arriving at the island was similar in both seasons, but their numbers were lower during the first half of the 2001-2002 season compared to the first half of 2002-2003. The greater number of females and the formation of harems in marginal areas may explain this behavior of the males. Le Boeuf (unpublished data) related the size of the harems to the presence of marginal males, these being low in numbers for harems of less than 50 females. An earlier, short-term study, however, noted that the presence of marginal males was not related to the size of the harems but, rather, to the aggressiveness and dominance of the alpha male (García-Aguilar & Aurioles-Gamboa, 2001). With females on marginal beaches, under the custody of less dominant males, the probability of success of marginal males should increase, so that they appeared more frequently from the beginning of the season.

The birth rates and preweaning pup mortality were the same during both seasons (90% and 8%, respectively), indicating that the conditions at the colony did not vary significantly, and the sex ratio was not different from the expected 1:1. The birth rate was slightly higher than that at Año Nuevo Island (85%) (Le Boeuf et al., 1972), with the difference being that the preweaning pup mortality was considerably lower. Año Nuevo's preweaning pup mortality had been estimated at 24% (Le Boeuf et al., 1994). The mortality difference could be the result of a combination of factors. Le Boeuf et al. (1972) pointed out that winter storms were one of the main causes of death for the pups. These are infrequent at San Benito. As mentioned earlier, another important factor is harem size, which, being smaller at San Benito, reduces the probability of the separation, injury, and death of the newborn (Bester & Lenglart, 1982).

The results for the reproductive biology of the northern elephant seal at this Mexican colony at the southern limit of its distribution agree in various aspects with those previously reported by other authors for the Año Nuevo Island colony in central California (e.g., arrival-parturition interval, duration of lactation, length of stay on land, and interval between parturition and mating) (Le Boeuf & Panken, 1977; Le Boeuf & Reiter, 1988). Some important differences were found, however. Reiter et al. (1981) reported the arrival of the first females at the breeding beaches around the middle of December, while at San Benito the first arrivals were at the beginning of December (some might have arrived at the end of November). The peak of the season at San Benito was on 19 January compared to 26 January to 2 February, a difference of between 7 and 13 days (Le Boeuf, pers. comm.). The initiation of births is another notable difference. Le Boeuf et al. (1972) mentioned that the first births occurred about 23 December, while at San Benito, given that the first weaning took place on 27 December in 2001-2002 and 30 December in 2002-2003, the first births must have taken place at the beginning

of the month. Similarly, the peak in births (about 47%) occurred in the first two weeks of January at San Benito compared to the second two weeks at Año Nuevo (50%). Despite the difference in the start of birthing, this phase appears to end at the beginning of February at both locations, and the cubs, therefore, would have been weaned about the 10th of March.

These differences may be due to the respective latitudes of the two colonies. Various pinniped studies have analyzed the relationship between latitude and the start and duration of the breeding season (e.g., Boyd, 1991; Campagna et al., 1993; Galimberti & Sanvito, 2001; Pitcher et al., 2001). Even similar studies are needed to obtain precise information about the colonies at San Benito del Centro, San Benito del Oeste, and Cedros Islands, but because of their closeness and the interchange of animals between islands, the present study provides a broad view of the dynamics of the northern elephant seal breeding season at lower latitudes.

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