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ARTICLE

Lifetime reproductive success of northern elephant seals (*Mirounga angustirostris*)

Burney Le Boeuf, Richard Condit, and Joanne Reiter

Abstract: Lifetime reproductive success of individuals in a natural population provides an estimate of Darwinian fitness. We calculated lifetime reproductive success in a colony of female northern elephant seals (*Mirounga angustirostris* (Gill, 1866)) by monitoring annual breeding throughout life of 7735 female weanlings marked individually at Año Nuevo, California, USA, from 1963 to 2005. Great variation in lifetime reproductive success was evident in three aspects of life history: (1) 75% of the females died before reaching breeding age and produced no pups; (2) nearly half of the survivors bred for only a few years before dying, and young females had low weaning success; (3) less than 1% of the females in the sample were exceptionally successful producing up to 20 pups in life. Many females that bred early, while still growing, had decreased lifespan, low weaning success, and lower lifetime reproductive success than females that postponed first breeding. Exceptional reproductive success was associated with giving birth annually, living long (up to age 23), and weaning large pups that were more likely to survive and breed. We conclude that there is strong selection for increased lifespan and multiparous supermoms that contribute significantly to pup production in the next generation.

Key words: northern elephant seals, *Mirounga angustirostris*, lifetime reproductive success, reproductive potential, long-term animal studies, age-specific survivorship, pup production, fecundity, weaning success, cost of breeding, multiparity, supermoms.

Résumé : Le succès de reproduction individuel sur la durée de vie dans une population naturelle fournit une estimation de l'aptitude darwinienne. Nous avons calculé le succès de reproduction sur la durée de vie dans une colonie d'éléphants de mer boréaux (*Mirounga angustirostris* (Gill, 1866)) femelles en surveillant la reproduction annuelle sur toute la durée de vie de 7735 femelles nouvellement sevrées marquées individuellement à Año Nuevo (Californie, États-Unis), de 1963 à 2005. Une grande variation du succès de reproduction sur la durée de vie est évidente dans trois aspects du cycle biologique, à savoir que (1) 75 % des femelles sont mortes avant d'atteindre l'âge de reproduction et avant de produire des chiots, (2) près de la moitié des survivantes ne se sont reproduites que quelques années avant de mourir, et les jeunes femelles présentaient un succès de sevrage faible, et (3) moins de 1 % des femelles dans l'échantillon ont connu un succès de reproduction exceptionnel, produisant jusqu'à 20 chiots durant leur vie. Bon nombre des femelles qui se sont reproduites tôt, avant la fin de leur croissance, ont eu une durée de vie plus courte, un succès de sevrage faible et un succès de reproduction sur la durée de vie inférieur à celui de femelles qui avaient repoussé leur première reproduction. Un succès de reproduction exceptionnel était associé à des parturitions annuelles, une longue vie (jusqu'à 23 ans) et le sevrage de chiots plus gros plus susceptibles de survivre et de se reproduire. Nous en concluons qu'il y a une forte sélection de super-mères multipares de longévité supérieure qui contribuent significativement à la production de chiots dans la génération subséquente. [Traduit par la Rédaction]

Mots-clés : éléphants de mer boréaux, *Mirounga angustirostris*, succès de reproduction sur la durée de vie, potentiel de reproduction, études sur les animaux de longue durée, survie en fonction de l'âge, production de chiots, fécondité, succès de sevrage, coût de la reproduction, multiparité, super-mères.

Introduction

Studies of lifetime reproductive success (LRS) that provide a complete representation of the lifetime reproduction of individuals are important because they approximate Darwinian individual fitness and can be viewed as the individual analogue of the net reproductive ratio of a population (Clutton-Brock 1988; Newton 1989; Brommer et al. 2002). Many important questions in ecology and evolutionary biology can only be answered with data on the life histories of recognizable known-age individuals collected throughout their lifetimes. LRS data are essential for understand-

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Data accessibility: The full data set of female breeding histories is available at a permanent, public archive of the University of California at Santa Cruz (https://dash.library.ucsc.edu/stash/dataset/doi:10.7291/D18084).

Authors' contributions: B.L. originated and directed the elephant seal tagging project for over 5 decades and drafted the manuscript. R.C. collected data, created the software for the database, updated it regularly, and was the Webmaster at manipulating it for queries of all kinds, and conducted the majority of the data analysis. J.R. was principally involved in collecting data in the field and putting data into the database. All authors contributed to conceptualization and reviewed, commented on, and approved the final manuscript. All authors declare no competing interests.

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ing the natural history of a species and these data provide valuable insights into how natural selection operates (Grafen 1988; Clutton-Brock and Sheldon 2010). Nevertheless, studies of LRS of mammals are rare because they require close monitoring of known individuals in their natural environments throughout their lives. This takes great effort and continuous observation over years and poses a special challenge when the lifespan of the animal under study may be as long as the research career of the human observer.

Our aim was to determine the LRS of female northern elephant seals (*Mirounga angustirostris* (Gill, 1866)) observed over the course of a long-term study spanning 50 years. We sought to determine the extent and causes of individual variation in a natural population. We addressed the different components of breeding success such as survival to breeding age, lifespan, fecundity, offspring survival, and the effect of age and size on breeding success. We measured the cost of breeding on subsequent survival and reproductive success by monitoring known-age, identifiable females, giving special attention to pup production, weaning success, and subsequent juvenile survival and reproductive success of the pups. We determined the onset of senescence. We estimated rates of dispersal, emigration, and intermittent breeding that influences measures of LRS. We sought to determine the effects of environment, phenotype, development, and genetic factors on breeding success. We addressed age at first reproduction and gaps in breeding because they are important life-history tactics that influence animal population growth and viability. Age at first reproduction reflects the cost of breeding and can act as a powerful filter for high-quality individuals (Pyle et al. 1997; Tavecchia et al. 2001; Gaillard and Yoccz 2003; Barbraud and Weimerskirch 2005; Desprez et al. 2014). We examined the effects of gaps in breeding records, due to failure to breed or failure to detect breeding females, on fecundity (Huber 1987; Huber et al. 1991; Sydeman and Nur 1994; Desprez et al. 2018).

Case histories of individuals, such as those in our database, provide details on the pattern of reproduction over a lifetime, show the reproductive potential of females, chronicle the consistency of breeding, yield information on the effects of age on survival and reproduction, and provide a basis for testing ideas about the costs of breeding. This permits testing several predictions of theoretical importance:

(1) Big mothers and experienced mothers are better mothers (Ralls 1976; Reiter et al. 1981; Sydeman et al. 1991);

(2) Large females wean large pups that are most apt to survive and breed (Reiter and Le Boeuf 1991; Crocker et al. 2001);

(3) Breeding early in life reduces survivorship and fecundity (Williams 1966; Stearns 1976; Reiter and Le Boeuf 1991; Sydeman et al. 1991; Sydeman and Nur 1994) because there is a cost to breeding (Bell 1980) especially while still growing;

(4) Female elephant seals, like many mammals (Hrdy 1999), give birth annually until they die (Le Boeuf et al. 1972; Reiter et al. 1981);

(5) Long lifespan of females is associated with greater reproductive output (Bercovitch and Berry 2017);

(6) Reproductive success decreases with age (Gadgil and Bossert 1970; Pianka and Parker 1975) because of senescence (Promislow 1991; Gaillard et al. 1994; Nussey et al. 2013; Jones et al. 2014); and

(7) Females bias the sex ratio of offspring, producing more females early in life and males later in life (Trivers and Willard 1973).

Background information

We summarize studies conducted over the last 5 decades whose results we employ in the present study and identify key publications that provide useful background information.

Natural history

Northern elephant seals breed on 15 island and mainland sites in Mexico and California (USA) (Le Boeuf et al. 2011). A female gives birth annually to a single pup in winter, nurses her pup for 4 weeks, copulates and is re-inseminated during the last few days of nursing, then weans and abandons her pup to go to sea on a foraging trip lasting approximately 2.5 months (Le Boeuf et al. 1972; Le Boeuf and Laws 1994). The egg is fertilized but does not implant to the uterine wall until 3 months later during the 1-month molting period on land. After molting, the female returns to sea again to forage for the entire 8-month-long gestation period.

Female elephant seals are extreme capital breeders that rely exclusively on stored reserves while nursing their pups (Crocker et al. 2001). Consequently, pup mass at birth or weaning reflects the success of maternal foraging during the 8 months prior to giving birth. Females feed primarily on mesopelagic squid, elasmobranchs, and myctophid fishes (Antonelis et al. 1987).

Long-term studies at Año Nuevo, California (Le Boeuf and Reiter 1988; Le Boeuf et al. 1972), and Southeast Farallon Island (Huber 1987; Sydeman et al 1991) show that most females give birth for the first time at age 4 (range = 2 to 6 years of age). Up to 90% of females in central California colonies breed on their natal colony and continue to breed there throughout their lives. The 5% to 10% that emigrate to breed elsewhere are primarily young females breeding for the first time or females breeding for the second time after failing to wean their first pups (Reiter et al. 1981).

Annual fecundity, as measured by the percentage of females present during the breeding season that give birth, is 97.5% (Le Boeuf and Reiter 1988; Crocker et al. 2006; Le Boeuf et al. 2011). A study of females bearing satellite tags, however, revealed that 9.9% of 172 females, tracked between 2004 and 2016, were not pregnant when sighted before or after the breeding season (Hückstädt et al. 2018). It is not clear whether these females had aborted or had failed to get pregnant; they were not observed during the breeding season. From these two sources, the annual fecundity is estimated to be between 87% and 97.5%. Another study reports that fecundity was reduced in a year when foraging was poor; fecundity during the 1999 breeding season was only 87% following a severe El Niño in which the mass gain of foraging females was the lowest recorded (Crocker et al. 2006).

Bias

Tag loss, failure to read tags, and emigration leads to overestimates of mortality and underestimates of LRS (Le Boeuf and Reiter 1988). Correction for tag loss was improved by retagging and double-tagging individuals and by using permanent brand marks. In the latter, 183 female weanlings were branded in 1985–1987 and tracked until 2012 (Condit et al. 2014). Annual survival probability averaged 86.3% per year at ages 5 to 16, then declined until age 21, demonstrating senescence in survival. There were strong age-related trends in the survival rate of females: 57% to age 1, 25% to age 4 (the modal age of primiparity), 9% to age 10, and 4% to age 17. The analysis of brands produced an estimated rate of non-detection of 40% per year, meaning we detected 60% of females that were alive in any 1 year.

Dispersal and emigration

Juvenile elephant seals of both sexes disperse widely during foraging trips, visiting non-natal colonies where some give birth as adults, i.e., emigrate (Le Boeuf et al. 1974; Reiter et al. 1981).

Females that gave birth on a non-natal colony, such as Southeast Farallon Island or Point Reyes, were considered immigrants, the majority of whom were young females breeding for the first time. As a general rule, most females did not immigrate; 87%–90% of females born at Año Nuevo were philopatric and gave birth there. Five of 37 females born and branded at Año Nuevo in 1985–1987 bred on the two nearby colonies to the north (Condit et al. 2014). The emigration rate for a sample of 105 females born and tagged at Año Nuevo in the years 1998 to 2000, which were observed breeding from 2001 to 2008, was 10% (B. Le Boeuf, R. Condit, and J. Reiter, unpublished data). These females bred at Point Reyes (7%), Piedras Blancas (2%), and Southeast Farallon Island (1%).

Some immigrants bred once at a new site then returned to breed at Año Nuevo for the rest of their lives. Our estimates of LRS among females at Año Nuevo are thus biased downward by 10%.

Demography

During this study, the northern elephant seal population continued to expand in numbers and range following near extinction in the last decade of the 20th century (Townsend 1912; Bartholomew and Hubbs 1960). In the 1890s, only a small remnant herd survived at Isla de Guadalupe, Mexico. The species lost genetic variability going through one or more population bottlenecks, which precludes conducting paternity studies (Bonnell and Selander 1974; Hoelzel et al. 1999, 2002).

As the population recovered, seals from Isla de Guadalupe settled new colonies in Mexico and southern California. Dispersal was to the north. The Año Nuevo colony was settled in 1961 (Radford et al. 1965) from immigrants from San Miguel and San Nicolas islands in southern California. The colony grew to 2500 pups born in the mid-1990s, owing in large part to immigrants. Numbers were stable from about 1990 to 2005 and then decreased slightly to 2100 pups born in 2010 (Le Boeuf et al 2011). Colony size remained at this level as of 2019. The total population in Mexico and the United States was in the range of 210 000 to 239 000 individuals in 2010 (Lowry et al. 2014). The population continues to grow at a mean annual rate of 3.8%.

Materials and methods

Over 5 decades (1963 to 2005), 7735 known-age females, marked with tags in the interdigital webbing of a hind flipper at weaning (Le Boeuf et al. 1972), were monitored throughout their lives at the Año Nuevo rookery every winter breeding season, as well as during the summer molting period. Weanlings tagged after 2005 are excluded in this study because some were still living. We attempted to determine whether and when an identifiable female gave birth, the sex of the pup, the location of parturition, and whether the pup was nursed and weaned successfully. Some pups of known females were weighed, measured, and tagged. We tagged individuals and marked them with a bleaching solution or a dye on the pelage to facilitate identification (Le Boeuf and Peterson 1969; Le Boeuf 1972). Weanlings were weighed from a tripod (Ortiz et al. 1978; Reiter et al. 1978). When tagged seals emigrated to nearby rookeries, we received reports about their behavior from colleagues observing at these sites (Le Boeuf et al. 1974; Huber 1987; Allen et al. 1989; Huber et al. 1991).

The effective sample size varied with questions addressed and available information. The main sample consisted of 2134 females of known age, known birthplace, and known reproductive history that gave birth at least once, and to 1294 females born at Año Nuevo. All subjects were born during the years 1963 to 2005 and bred during the years 1968 to 2018. Otherwise, the sample size varied with available information, e.g., the number of pups sexed or weighed. We specify the sample size used for each result presented.

We assume that a female produced a pup if she was (*i*) observed with a pup one or more times during the breeding season or (*ii*) simply observed on the rookery during the breeding season. The latter criterion produces the slightly higher estimate of pups produced. Both assumptions are reasonable because previous observations show that 97.5% of females observed on the Año Nuevo rookery during the breeding season give birth (Le Boeuf et al. 2011). Furthermore, we estimated weaning success for females observed on 5 or more days. Of this group of females, those seen more than 75% of the time with a single pup were assumed to have weaned the pup. The rest were assumed to have lost their pups. Examples of lifetime breeding records of females, from which all data were derived, are shown in Fig. 1. The entire database is available as an electronic supplement at https://dash.library.ucsc.edu/stash/dataset/doi:10.7291/D18084 and it is published online (Condit et al. 2018).

We corrected for tag loss and missed readings using a model based on the returns of 183 weanling females branded with permanent identification during the years 1985 to 1987 (Condit et al. 2014; see also Schwarz et al. 2012). The branding model used a Bayesian mark–recapture analysis to estimate annual survival and lifespan of females. We used the survival estimates from the branded cohorts to estimate a corrected LRS for females, mitigating the biases caused by tag loss, non-detection, and emigration.

We recorded annual immigration of our subjects to adjacent colonies. In receiving reports of our tagged animals from colleagues studying elephant seals at these colonies, we minimized loss of identity to emigration.

We estimated fecundity directly each breeding season for all identifiable females, which yielded annual fecundity rates and the pattern of fecundity in individuals. Counting a female as fecund meant that she had the ability to produce offspring, as reflected by being pregnant or having given birth. We recorded the absence of females during a breeding season or the failure to give birth after having given birth in the previous year.

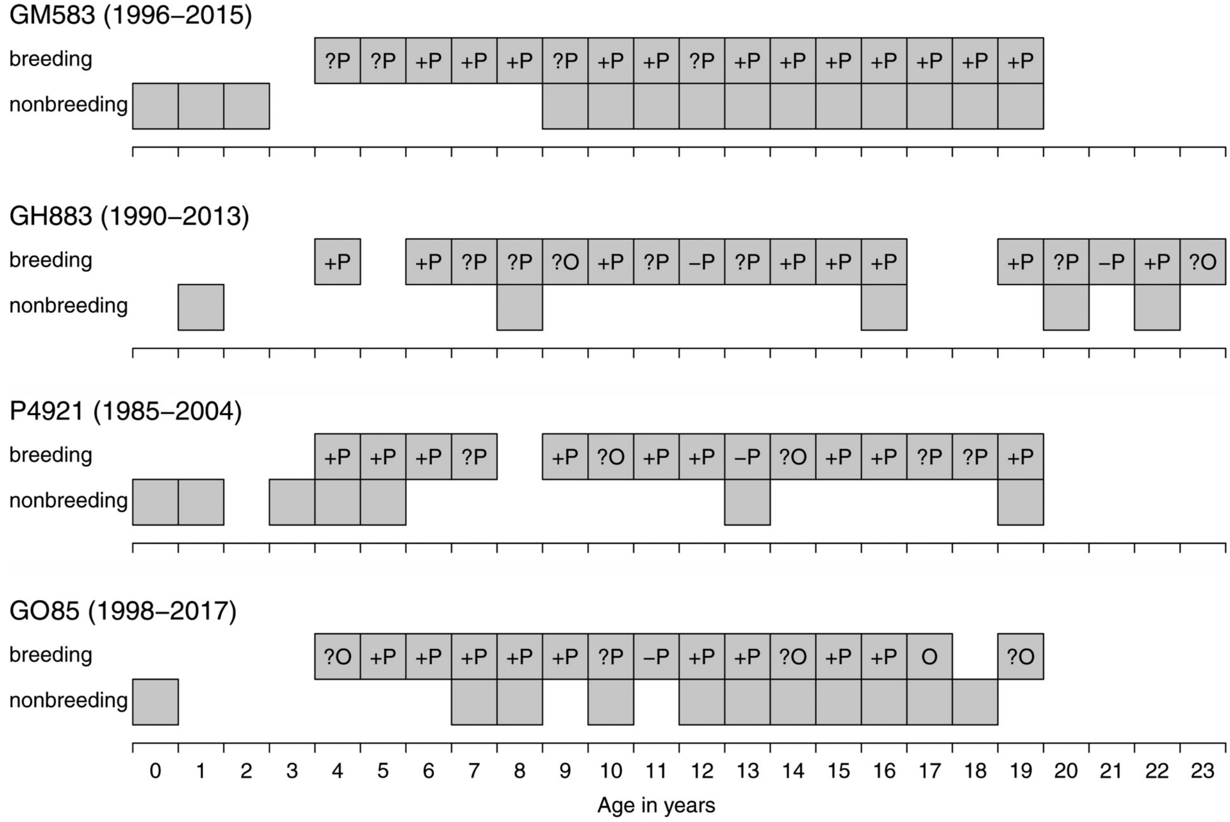
We recorded weaning success, mass of pups at weaning, and the sex ratio of pups as a function of the age of the mother. Pups were weighed and sexed within a week after weaning. We used the von Bertalanffy model of an asymptotic relationship between the dependent variable and the mother's age (Cailliet et al. 2006). The model has three parameters (Francis 1988). We used Akaike's information criterion (AIC) to compare the models and to determine which models were superior statistically (Hilborn and Mangel 1997). Weaning success and sex ratio are binomial variables, so the model was fitted using a binomial error, whereas a Gaussian error was employed for the weaning-mass model, the latter requiring an additional parameter for the standard deviation. Model parameters were estimated in a Bayesian framework using a Gibbs sampler (Condit et al. 2007), providing 95% credible intervals on all parameters and the dependent variables at every age. For a statistical test of the null hypothesis of no age-related change, two additional models were fitted to each data set: a linear increase with age and a constant model. The parameters of all models were fitted using an optimizing routine to find the likelihood of observing the data given the optimum parameters, i.e., the maximum likelihood.

We examined lifetime reproduction as a function of age of primiparity by comparing females that gave birth for the first time at age 3, 4, 5, or 6, and tracking their subsequent survival and reproductive success. A few females were observed giving birth for the first time at age 7 or older, but a high proportion of these are probably errors, either having given birth earlier but not observed or simply misread tags. They were not included in analyses of primiparity. Since adult survival is constant over many years (Condit et al. 2014), the lifespan and breeding success of females follow a geometric distribution, so parameter means and error bars were estimated using the beta-distribution, which is conjugate to the geometric, using the Gibbs sampler and Bayesian approach as for the other models.

We used logistic regression to estimate the probability that female pups returned to breed as a function of their mass at weaning. The model's two parameters were estimated using the same Gibbs sampler.

Statistical inference of all modeling results focused on a comparison of 95% credible intervals. This allowed any pair of parameter estimates to be assessed without recourse to p values (Amrhein et al. 2019). AIC assisted in inferences of asymptotic models with age.

Fig. 1. The breeding records of four female northern elephant seals (*Mirounga angustirostris*) in their lifetimes. Filled squares indicate presence during the breeding or nonbreeding season. P indicates that the female was observed with a pup and + indicates that she weaned it successfully or – indicates that she did not wean the pup. ?P indicates that the female was seen with a pup, but there were too few sightings to determine weaning success. O indicates that the female was observed often but never had a pup; ?O indicates that the female was never seen with a pup, but there were few sightings.



Animal care and ethics

All research at Año Nuevo and other northern elephant seal colonies were conducted under permits from the National Marine Fisheries Service and the California Department of Parks and Recreation, along with approval and authorization from the University of California at Santa Cruz Animal Care Committee.

Results

Fecundity

Annual fecundity, based on females of all ages, was estimated from previous studies as between 87% and 97.5% (Le Boeuf and Reiter 1988; Hückstädt et al. 2018). The overall mean proportion of gaps in the records of females of age 4 and older was 28.3% ± 1.2% (N = 5270 breeding seasons). If these gaps represent failure to breed, then the result would be lowered fecundity. We could not distinguish reliably, however, between failure to breed (a skip) and poor coverage (i.e., fecund females were present but not detected). Gaps in breeding records did not vary systematically with age; gaps were distributed uniformly across all female age groups. Gaps were not clearly and directly related to cyclical warming events such as El Niño years (https://ggweather.com/enso/oni.htm). There was an association in some years, allowing for time lags, but not in others. For example, peaks in gaps were associated with a strong El Niño in 1991–1992, with gaps lagging and peaking from 1993 to 1995; gaps were most frequent in 1998 to 2000 after a very strong El Niño in 1997–1998; and gaps were elevated in 2007–2009 following a weak El Niño in 2006–2007. Gaps were low, however, in very strong El Niño years such as 1982–1983 and 2015–2016, as well as in strong El Niño years such as 1987–1988.

Since the proportion of non-detected females has been observed as high as 40% (Condit et al. 2014), most gaps in breeding records were assumed to be due to non-detection of females with pups. Moreover, we add that the context for detecting tagged females changed over the course of the study period. Crowded conditions prevailed on Año Nuevo Island during the 1970s and 1980s, which precipitated females to begin breeding on the adjacent mainland in 1975, where breeding space was ample and remained so in 2019.

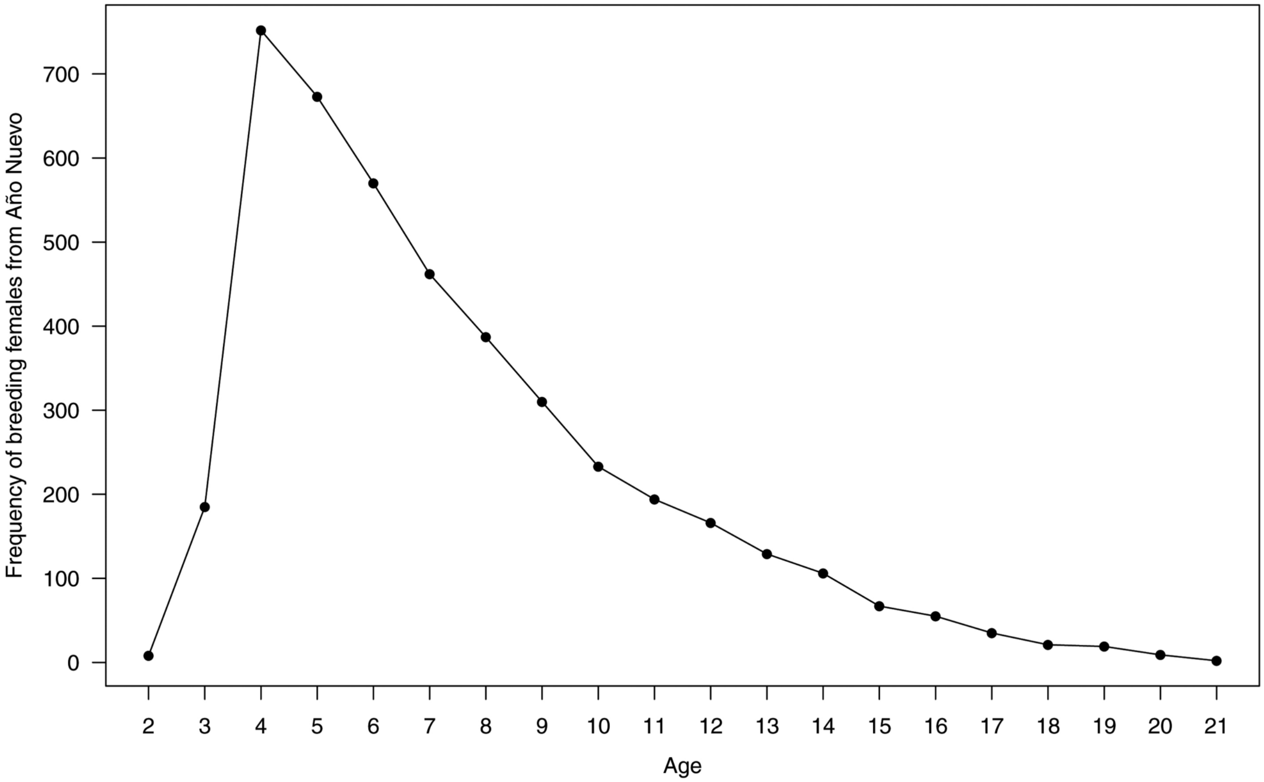
It is notable that gaps in breeding records were absent in some females with long lifespans, i.e., they did not skip breeding in any years. One female (GH583) bred for 16 consecutive years, from age 4 to age 19; 21 other females bred consecutively for 11 to 15 consecutive years without skipping a breeding season. Among 77 females that gave birth to 10 or more pups, 49% of them had no gaps in their breeding records and 31% exhibited only one gap in a lifetime of breeding. These results do not generalize to all females, but they show that consistent breeding over a lifetime occurs in some of females, indicative of elevated fecundity.

Intermittent breeding, to the extent that it occurs and can be distinguished, does not appear to reduce fecundity below the annual percentage estimates.

Emigration

Based on the studies described in the Introduction, we assume that 10% to 13.5% of females born at the Año Nuevo colony emigrate annually to other colonies, the majority to nearby colonies such as Point Reyes and Southeast Farallon Island. Widespread dispersal of juveniles is prominent prior to breeding.

Fig. 2. The age structure of the Año Nuevo northern elephant seal (*Mirounga angustirostris*) colony based on monitoring 1291 females tagged soon after birth at Año Nuevo in the years 1963 to 2005. Females whose age was known but were born elsewhere, or were tagged as yearlings, are omitted. The oldest female observed among those known cohorts was 21 years old; one female tagged as a 1-year-old in 1991 was observed in 2012 and 2013, lived to 23 years of age.



Age composition and pup production

The age structure of breeders in the colony during the study period ranged from 2 to 21 years old, with 4-year-old females being most numerous (Fig. 2). After age 4, the percentage of breeding females declined steadily with age. If we assume that 10% of breeding females emigrated, all points in this figure are underestimates by 10%, i.e., the shape of the age distribution is correct but elevated. Dispersal before breeding does not affect the shape of the age distribution curve.

Survivorship and breeding of young females

Figure 3 provides two estimates of the percentage of weanlings that survived to produce pups. The first shows that 83.3% of female weanlings produced no pups. This estimate does not distinguish between females that died, lost their tags, were present but not recorded, or emigrated from the colony and were not reported. The second estimate uses the branding model described in the Materials and methods, which compensates for both tag loss and emigration, making these errors insignificant. This procedure estimates that 75% of female weanlings produced no pups and 25% of the original sample survived to breed at least once (1934/7735).

Of the survivors that lived to breed, pup production of young females was low and mortality following breeding was elevated: 45.6% of the survivors (589) bred up to age 6 before they died. Of these, 61% (359) bred only once, 28.4% (167) bred twice, 9.3% (55) bred three times, and 1.4% (8) bred four times. Five 2-year-olds were observed during the breeding season, and two of them may have given birth, but all of them were never observed again. The percentage of females not seen again after giving birth for the first time was 8.2% (48) for age 3, 28% (165) for age 4, 14.8% (87) for age 5, and 9.2% (55) for age 6.

Pup production by long-lived, multiparous females

Multiparous females were responsible for the most pups produced. Six percent of the sample of 7735 females ($N = 468$ females), those that gave birth to 10 or more pups in their lives, were responsible for more than half (54.7%) of the total pup production of the sample (6 657 / 12 176). This stands out because they were outnumbered 3 to 1 by females that produced fewer than nine pups in life.

Figure 3 shows that the trend in pups produced declined steadily to one female that produced 17 pups in her lifetime. The latter (the longest-lived female observed) lived to age 23. Another female (GM583) produced pups in 16 consecutive years. Twelve females produced pups in 14 years, 15 females in 13 years, and 21 females in 12 years. The peak breeding years for the most successful females was from age 4 to about age 15, when 63% to 78% of each age cohort gave birth. Correcting LRS for tag loss and emigration leads to an estimate that a small fraction of females could produce 20 pups in a lifetime (Fig. 3).

The total number of pups produced by each parity group (number of births in life) in relation to the percentage of females surviving to breed is shown in Table 1. Survivorship of the mothers is based on the branding model described in the Materials and methods and illustrated by the open bars in Fig. 3. Parity group *n* refers to the number of females in a parity group that produced *n* pups in life. The table shows that multiparity of breeders is important in determining pup production in the next generation and the population.

The table makes several points:

(1) Total pup production of 326 females in parity group 1 (326 pups) is nearly identical to the total pup production of only 17 females from parity group 19 (324 pups);

Fig. 3. The lifetime production of northern elephant seal (*Mirounga angustirostris*) pups from direct observation of 7735 females in this study (solid bars) and corrected by the branding model for tag loss, overlooked females, and females that emigrated (open bars).

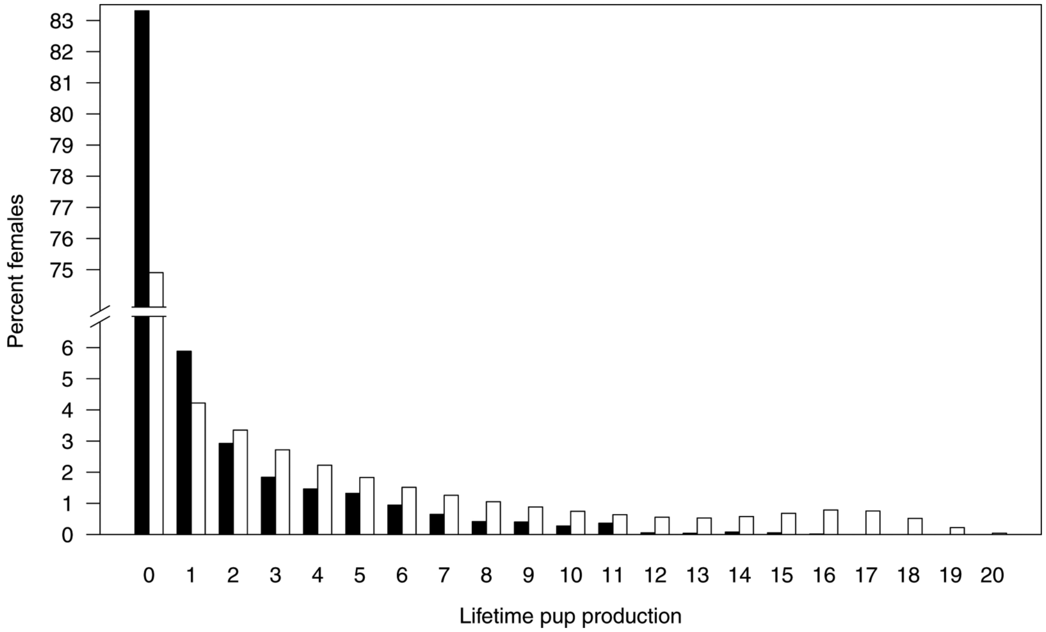


Table 1. Total northern elephant seal (*Mirounga angustirostris*) pups produced by each parity group of females based on a sample of 7735 weanlings.

Parity group: lifetime number of pups produced	Number of females in group	Group size: % females in sample	Total pups produced
0	5 794.01	74.91	0
1	326.40	4.22	326
2	259.21	3.35	518
3	210.20	2.72	631
4	172.00	2.22	688
5	141.53	1.83	708
6	117.03	1.51	702
7	97.30	1.26	681
8	81.33	1.05	651
9	68.32	0.88	615
10	57.70	0.75	577
11	49.19	0.64	541
12	43.06	0.56	517
13	40.97	0.53	533
14	44.59	0.58	624
15	52.62	0.68	789
16	60.82	0.79	973
17	58.21	0.75	990
18	40.04	0.52	721
19	17.04	0.22	324
20	3.40	0.04	68
Sum	7 735	100	12 176

Note: Survivorship is corrected for tag loss based on a study of branded northern elephant seals (Condit et al. 2014).

(2) There are peaks and valleys in total pups produced, but pup production is substantial in parity groups 2 to 18;

(3) Females from parity groups 16 and 17 produced the most total pups;

(4) Total pup production decreased substantially in the oldest females, i.e., 55% from parity group 18 to 19 and 79% from parity group 19 to 20;

(5) The largest pup production increase was 59% from parity group 1 to parity group 2; and

Table 2. Pup production of northern elephant seals (*Mirounga angustirostris*) by parity group.

Parity groups	Number of females	Pups produced	Mean pups per female
1 to 5	1 109	2 871	2.61
6 to 10	421	3 226	7.66
11 to 15	231	3 004	13
16 to 20	179	3 076	17.18
Sum	1 940	12 177	

(6) Total pup production divided by sample size was calculated as 12 176 / 7 735 = 1.57, i.e., less than 2 and indicative of a declining population.

Dividing the parity groups into four categories of five groups each (Table 2) reveals the following:

(1) Parity groups 1 to 5, although most numerous, produced the fewest pups;

(2) Parity groups 6 to 10 produced the most pups; and

(3) The mean number of pups produced per female was highest in parity groups 16 to 20.

Weaning success

Figure 4 shows that the weaning rate was lowest in 3-, 4-, and 5-year-old females; the few 2-year-olds that weaned no pups are not shown. The weaning rate increased from a low of 59% in primiparous 3-year-old females to an asymptote of approximately 89% in females between 8 and 13 years of age. Weaning success of the oldest females fell below the asymptote, especially among females of age 18 and older. As a post hoc test, credible intervals of weaning success in females age 14 and older (74%–86%) were below the asymptote (87%–91%).

Weaning success increased with age and experience of the mother as evidenced by the low first three or four breeding opportunities and increases thereafter (Fig. 4, Table 3). Weaning success in the first breeding year was lower than the second breeding opportunity for females of age 3, 4, or 5, following a similar trajectory with age in all groups (Table 3). Lifetime weaning suc-

Fig. 4. The proportion of northern elephant seal (*Mirounga angustirostris*) pups weaned as a function of the mother's age (N = 2384). The points are mean weaning success at each age and the curve is the optimum von Bertalanffy model. Vertical bars show 95% credible intervals from the model. The von Bertanlanffy model cannot accommodate a decline once an asymptote is reached, allowing for the succession of points below the curve in older females.

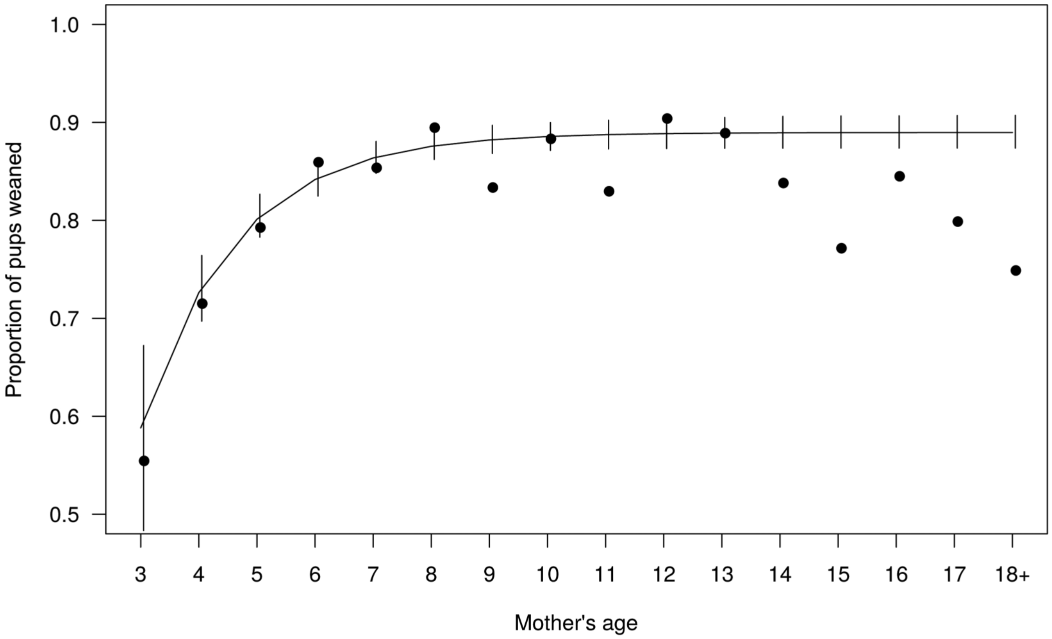


Table 3. Lifetime breeding experiences, lifespan, and weaning success as a function of age at primiparity in northern elephant seals (*Mirounga angustirostris*).

Age at primiparity (years)	N	Mean lifetime breeding appearances	Future expected lifespan (years)	Mean lifespan (years)	N	Weaning success at age				
						3	4	5	6+	Lifetime
3	184	3.80 (3.3, 4.4)	4.16 (3.4, 5.1)	7.16	313	0.60 (0.48, 0.71)	0.70 (0.54, 0.82)	0.82 (0.68, 0.90)	0.88 (0.83, 0.92)	0.79 (0.74, 0.83)
4	649	4.17 (3.9, 4.5)	4.55 (4.1, 5.1)	8.55	1537		0.72 (0.67, 0.76)	0.82 (0.77, 0.87)	0.87 (0.85, 0.89)	0.83 (0.81, 0.85)
5	210	3.00 (2.7, 3.4)	3.07 (2.6, 3.7)	8.07	313			0.72 (0.63, 0.81)	0.87 (0.82, 0.91)	0.83 (0.78, 0.87)
6	104	2.93 (2.5, 3.5)	3.12 (2.4, 4.1)	9.12	116				0.89 (0.82, 0.93)	0.89 (0.82, 0.93)
Sum	1147				2279					

Note: Values in parentheses are the 95% confidence intervals.

cess was similar in all primiparity groups, slightly lower in P3s but with overlapping credible intervals. The lifespan of P3s was shorter than that of P4s, and despite starting a year earlier, P3 females had slightly fewer lifetime breeding attempts than P4 females (Table 3).

Known-age females that produced 10 or more pups in their lifetimes (N = 58) weaned pups successfully right from the start, having a 90% weaning success rate even as primiparous 3- and 4-year-olds.

Weaning mass, lifespan, and reproductive success

Weaning mass of pups was positively correlated with the mother's age (Fig. 5). Weaning mass increased from 96 kg for 3-year-old females up to an asymptote of 138 kg for females between 8 and 17 years of age. Weaning mass of pups from mothers that were age 18 or older declined, and a post hoc test shows credible intervals of 100–132 kg (N = 11 females), well below the asymptote of 136–140 kg.

Pup weaning mass was associated with increased lifespan and lifetime reproductive success (Table 4). The lifespan of the heaviest weanlings was more than double that of the lightest weanlings, the probability of breeding increased three-fold, and breeding appearances doubled. For example, the 105 females that were 150+ kg at weaning had, on average, 1.086 breeding season appearances each, and 36% of that group were observed breeding.

Pup weaning mass was associated positively with reproductive success as evidenced by the probability of subsequent breeding as an adult (Fig. 6).

Senescence

The prime reproductive years of most elephant seal females lasted from age 3 to about age 14, i.e., 12 years, then declined in older females (Fig. 4). Signs of senescence were evident at 15 to 18 years of age as reflected by increased failure to wean pups and decreased weaning mass of pups (Figs. 4 and 5).

Nevertheless, it is notable that the majority of females that lived to age 18 or older continued to breed until they died. Ninety-one percent of the oldest females (29/32 = 90.6%) bred one to four times after reaching age 18, and a 22-year-old female weaned her pup. This female returned for the next breeding season at age 23. She was observed only once late in the season with no pup near her and may have failed to get pregnant in her final year.

Sex ratio

The sex ratio of pups born to 2630 known-age females was biased to females early in life and males later in life. The sex ratio

Fig. 5. Northern elephant seal (*Mirounga angustirostris*) pup mass at weaning as a function of the mother's age ($N = 1120$). The points are individual pup masses at weaning and the curve is the optimum von Bertalanffy model.

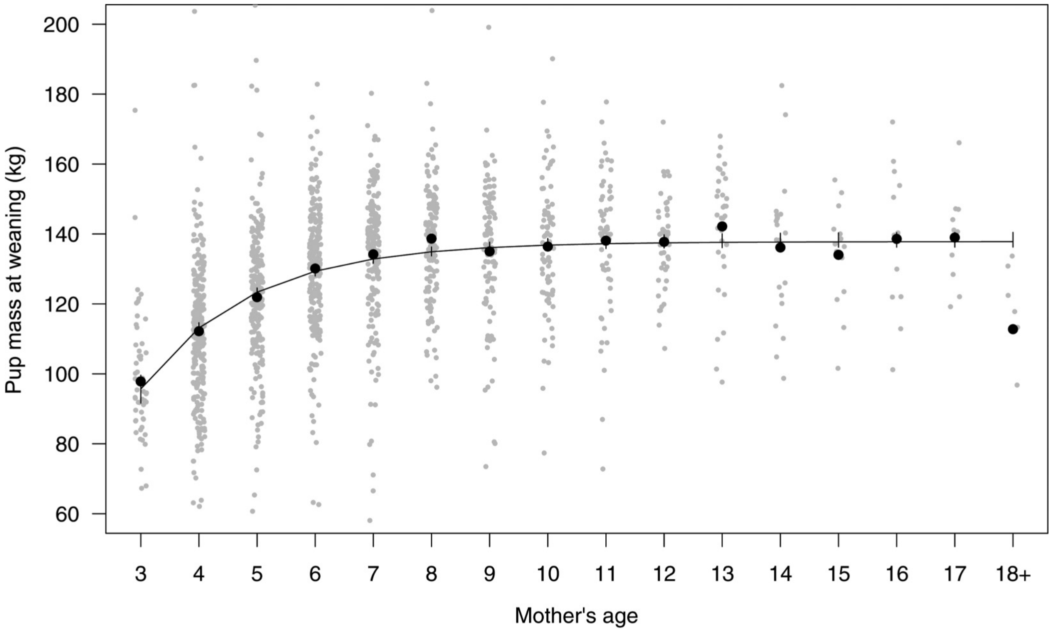


Table 4. Lifespan, probability of future breeding, and breeding appearances as a function of mass at weaning in northern elephant seals (*Mirounga angustirostris*).

Mass at weaning			Future survival and breeding		
Mean (kg)	Range (kg)	Sample size (*N*)	Mean lifespan (years)	Probability of breeding (%)	Mean observed breeding appearances
79.37	<90	75	1.08	12	0.53
95.88	90–100	81	1.67	23	0.83
105.57	100–110	127	1.60	23	0.71
115.10	110–120	180	1.49	17	0.74
125.05	120–130	208	1.25	16	0.40
135.26	130–140	221	2.03	24	0.99
144.04	140–150	183	1.80	25	0.72
159.99	150+	105	2.86	36	1.09
Sum		1180			

increased from 48.9% males for 3-year-old females to 55%–60% for females of age 10 or more. The increase was marginally significant, with the linear model having an AIC of 0.3 higher than the constant model; the asymptotic model did not improve the fit (AIC of 1.8 was lower than the linear model).

Daughters of successful females

Some females that produced 10 or more pups in their lifetimes produced daughters with similar high lifetime reproductive success (for details see Appendix A (Fig. A1) and Appendix B). At age 4, G7932 gave birth to GF24, who bred 10 times just like her mother and often at the same breeding locations and at similar times. The daughter outlived the mother by 3 years. GK861 bred 10 times as did her daughter (GO535). Both mother and daughter bred in the same location and overlapped in time for several years. We saw no sign of the mothers recognizing their daughters or helping or protecting them in any way.

Discussion

This study shows that great variation in LRS is characteristic of female northern elephant seals. Three aspects of female life history give a sense of the range of variation in LRS and its causes that are critical for drawing conclusions about population effects, adaptations, and contributions to natural and sexual selection. The three aspects are as follows:

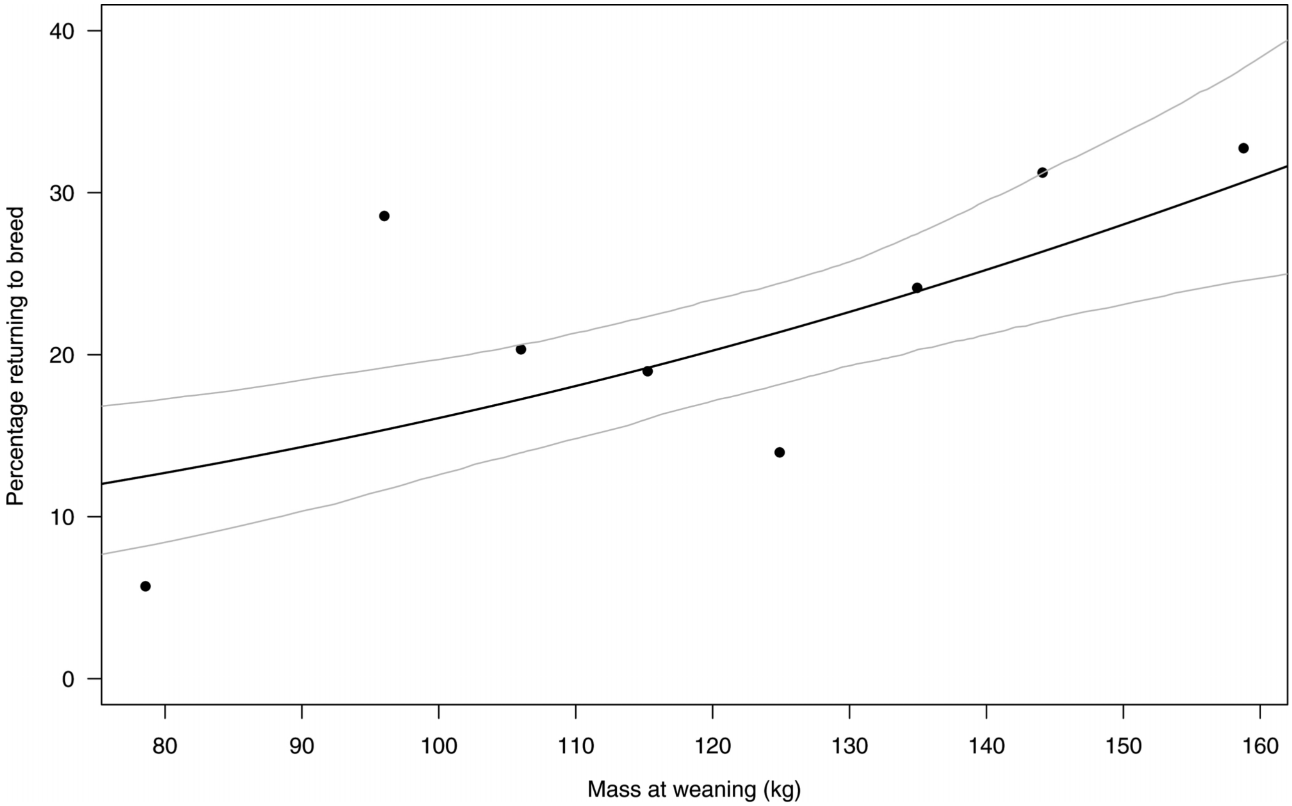
(1) High mortality prior to breeding;
(2) Low reproductive output of most young breeders; and
(3) Exceptional reproductive success of long-lived females.

Pre-breeding mortality

Northern elephant seals exhibit the most common survivorship curve of mammals in nature characterized by a steep decline in survivorship early in life (Wilson and Bossert 1971). Mortality on the rookery prior to weaning varies from 8% up to 70% of pups born, the rate varying with weather and context (Le Boeuf and Briggs 1977; Le Boeuf and Reiter 1991). In the present study, three out of four females weaned died before reaching breeding age and produced no pups. Evidently, the time at sea is a significant hurdle, especially the first foraging trip to sea. Mortality at sea for 8362 weanlings from Año Nuevo during the years 1971 to 1988 averaged 63% to year 1 (R = 50%–80%), 74% to year 2 (R = 65%–90%), 81% to year 3 (R = 71%–92%), and 84% to year 4 (R = 73%–95%) (Le Boeuf et al. 1994).

High mortality during the first foraging trip to sea is not surprising. The 4-week-old pup is weaned and abandoned forever by

Fig. 6. The probability that a northern elephant seal (*Mirounga angustirostris*) pup returns to breed at the rookery increases as a function of its mass at weaning ($N = 555$). The points show the percentage returning in 10 kg categories of weaning mass. The solid black curve is the fitted logistic regression and the dashed gray curves are 95% credible intervals. The estimated slope parameter is 0.014.



its mother when she goes to sea to forage. Weighing, on average, 132 kg, 59% of which is blubber, the weanling fasts while spending about 2.5 months learning to swim and dive in the shallows of the rookery before going to sea for its maiden foraging trip. At departure, it has lost 25% to 30% of its weaning mass (Reiter et al. 1978). The weanling is naïve and knows not what to eat, where to find its prey or how to catch it, and what predators to avoid. Surviving foraging trips at sea during the first 3 years of life poses many dangers and is the first and greatest barrier to reproducing. High mortality at sea during these early years may be due mainly to predation and insufficient foraging. White sharks (*Carcharodon carcharias* (Linnaeus, 1758)) and killer whales (*Orcinus orca* (Linnaeus, 1758)) take an unknown quantity of them (Le Boeuf et al. 1982; Klimley et al. 2001). Finding, catching, and consuming sufficient prey may be difficult. Yearlings gain no mass at sea during the first two foraging trips, at the end of which, they are 15–16 months old; the lean muscle to fat ratio increases and they are about 10 cm longer but weigh no more than when they departed the rookery on their maiden foraging trip at 3.5 months of age (P. Morris, personal communication). Nevertheless, the diving pattern and migratory routes of young seals approach that of adults even on the first trip to sea (R. Beltran, personal communication). By age 2, the deep diving pattern is similar to that of adult females (Le Boeuf 1994).

Low reproductive output of young females

Among females that survive to breed, those that are 3 to 6 years of age are most numerous. This suggests that they would have a significant impact on the population because there are four times more of them than females that are 12 years of age or older. Quantity of females, however, is not directly associated with greater pup production. Most young females breed only once before they die; the rest may breed 2 to 4 times before they die. Reiter and Le Boeuf (1991) reported that 31% to 40% of 98 females primiparous at ages 3, 4, and 5 at Año Nuevo from the 1973 to 1976 cohorts were not observed the year following production of their first pup, but they were later confirmed to be alive. Evidently, recovery from the effort of first reproduction is difficult and costly. Part of the problem is that young females start reproducing while still growing and do not reach full growth until age 7. Females, who are primiparous at age 3 or 4, exhibit a slightly lowered lifespan and a low rate of weaning pups, and they produce smaller weanlings that are less likely to survive and breed. The cost of first reproduction has also been documented for southern elephant seals (*Mirounga leonina* (Linnaeus, 1758)) (Desprez et al. 2014). The negatives associated with breeding early offset the dominance in numbers of young females, which in turn lowers their genetic contribution to the next generation.

Exceptional reproductive success of long-lived females

The reproductive success of some females is close to their maximum reproductive potential. Multiparity and long life is a key element in their success. Although relatively few in number, females that gave birth to 10 or more pups in their lifetimes — although outnumbered 3 to 1 by females that produced fewer than 9 pups in life — were responsible for more than half of the total pup production of all females in the sample. Only a fraction of females weaned achieved this lofty status, but they exert a significant influence on the population and future generations.

What enabled these “supermoms” to achieve outstanding lifetime reproductive success? The simple answer is that they bred at every opportunity and lived long. They weaned a high rate of pups produced, even in their earliest breeding attempts, i.e., they gambled and won, unlike other females. On the rookery, mature females expressed size-related dominance over younger, smaller females that enabled them to best protect their pups, and locate in the safest areas near the alpha bull, while keeping younger females on the periphery of harems where high surf and mating attempts of peripheral males disturbed nursing and often led to mother–pup separation and pup mortality (Le Boeuf et al. 1972; Le Boeuf and Panken 1977; Reiter et al. 1981).

To explain the great variation in LRS among females, we must look to the at-sea component of their life history. The conclusion from 5 decades of observing elephant seals during the breeding season and the molt on land is that mortality on land is rare; therefore, virtually all deaths of juveniles and adult elephant seals of both sexes occur at sea. The exception is that nursing pups and some weanlings die on the rookery (Le Boeuf and Briggs 1977; Rose et al. 1991). A few breeding females are killed inadvertently by males during attempted mating (Le Boeuf and Mesnick 1991) and a few adult males die during the breeding season from wounds incurred in fights.

Therefore, it is during the two annual foraging sojourns at sea, where an adult female spends 10 of the 12 months of the year, that we must look for causes of the great variation in LRS of females. Finding sufficient food and avoiding predators would seem to be the major obstacles to survival.

We have scant information on how well females avoid predators, ship strikes, or being caught in drift nets or ghost nets, or marine debris (Le Boeuf et al. 1982, 2000; Klimley et al. 2001; Le Boeuf 2004; White et al. 2019). We know from mass gain at sea that some females are more adept at foraging than others (Crocker et al. 2006).

One might gain insight into where, when, and how death occurs at sea by examining the numerous adult female migration tracks that have been recorded with a variety of diving instruments by University of California at Santa Cruz researchers over the last 30 years, e.g., Le Boeuf et al. 2000; Robinson et al. 2012. These records, obtained originally for determining diving behavior, foraging patterns, and migration routes and using a variety of recording instruments attached to the seals, may contain information that suggests the cause of death at sea. Identifying records where data collection stopped abruptly along the migratory route is a key variable to examine. What caused the "stop"? Does the location of the seal and its diving pattern prior to the stop give clues to whether the seal was preyed on, caught in a net, struck by a ship, or whether the stop was simply due to battery or instrument failure?

Moreover, instrument packages carried by pinnipeds or fishes are getting increasingly sophisticated and some of them are being designed to optimize information that might give a cue to cause of death (e.g., Fletcher et al. 1996; Horning and Mellish 2012, 2014; Horning et al. 2017).

It is not clear whether long-lived females are more adept at foraging than other females, but this question warrants study. Some adult females have difficulty finding food during severe El Niño events, as evidenced by increased foraging duration, reduced residence time in prey patches and increased travel time between patches, and a marked decrease in mass gain rate, as well as reduced fecundity (Crocker et al. 2001, 2006; Le Boeuf and Crocker 2005). This may arise because the aggregation sites for prey are disrupted or the seal cannot locate prey (Robinson et al. 2012). El Niño events impact the foraging behavior of females and the weaning mass of their pups (Le Boeuf and Crocker 2005; Crocker et al. 2006). Robinson et al. (2012) recorded wide interindividual variation in mass gain during the post-breeding migration. Females gained more mass per day during the post-molt migration than the post-breeding migration, natality rates across years averaged 84%, with a high of 96% and a low of 68%, and energy gain during the post-molt migration did not predict mortality but predicted pregnancy. We expect that the large body size of older females may help maintain high rates of natality and weaning success in years with reduced prey availability. The data suggest that foraging success affects fecundity, consistent breeding, and the size of pups weaned. Foraging success and weanling size have implications for the growth and dynamics of the population (Clausius et al. 2017). It is not clear if mortality is affected directly by the inability of seals to gain sufficient nourishment.

Although intermittent breeding has been documented in both northern and southern elephant seals (Huber 1987; Huber et al. 1991; Sydeman and Nur 1994; Desprez et al. 2018; Hückstädt et al. 2018), the present study does not elucidate the prevalence and influence on fecundity. Gaps in breeding records of long-lived females suggest that females were overlooked in crowded harems. Moreover, we directed minimal effort to tag reading in the months immediately before or after the breeding season, a time when some non-pregnant females have been observed.

We showed that pup production of the Año Nuevo colony, owing to internal recruitment alone, was insufficient to explain the growth of the colony over the study period. That is, growth and fluctuations in pup production were determined primarily by the influx of young immigrant females from southern colonies, a general pattern observed since the colony originated (Le Boeuf and Reiter 1988; Reiter and Le Boeuf 1991; Le Boeuf et al. 1994, 2011).

How does the LRS of female northern elephant seals compare with males? A study of the LRS of males born on Año Nuevo Island during the mid-1960s (Le Boeuf and Reiter 1988) showed that only 8 males (5.8% of the sample) of 138 males bred at least once in life. Only six of these males (4.4%) were estimated to have sired 17 or more pups in their lifetimes and the most successful male was estimated to have sired 121 pups. It is noteworthy that about the same percentage of both sexes bred at least once in life, and females in this study with the highest LRS were as successful in reproducing as all but the most successful alpha males. To be sure, the reproductive potential of males is substantially greater than that of females; one exceptional male dominated mating for 4 consecutive years and may have inseminated over 200 females (Le Boeuf and Peterson 1969; Le Boeuf 1974). Nevertheless, there is substantial overlap between the sexes. Some females achieve high LRS by breeding virtually every year of their lives; males put the majority of their reproductive effort into having one or a few highly productive years. In both sexes, most individuals never mate because they die before reaching breeding age, and only a few that survive and live long achieve exceptional LRS. Since females can only produce one pup annually, breeding earlier than males and living long is selected. Females breed until they die, as this study shows, whereas males stop breeding a year or two before they die (Le Boeuf and Reiter 1988). Females outlive males by about 9 years.

The data presented here supports several predictions stated earlier. Our data confirm that big mother elephant seals are better mothers. Big mothers wean heavier pups that are more likely to survive and breed. Moreover, weaning mass is positively correlated with the mother's foraging success during the period at sea prior to giving birth (Reiter and Le Boeuf 1991; Crocker et al. 2001). In contrast, primiparous females, who have attained only 75% of their mature mass at age 3, are poor mothers and have a low rate of weaning pups. Female, aged 2 to 5, do not achieve full growth until about age 6 or 7 (Deutsch et al. 1994). The weaning rate of pups increases with the age, size, and experience of mothers to advanced age. The longest-lived females produce the most pups. The lifespan and LRS of females that breed early in life, such as age 3 or 4, have reduced lifespan and LRS, indicative of a cost to breeding. The exception is that long-lived females were successful breeding early. Most females give birth until they die. Reproductive success increases with age up to about age 15, when signs of senescence begin to appear in the form of a decline in weaning rate and weaning mass of pups. The oldest females, however, continued to produce pups until they die. We observed a modest bias in sex ratio to a higher production of females early in life and males later in life.

We show that some supermoms produced super daughters, but no more than would be expected by chance. The sample size is small and it is not clear that a genetic predisposition is operative.

Comparison of female elephant seal LRS with other animals is most appropriate for other phocid seals such as the hooded seal (*Cystophora cristata* (Erxleben, 1777)), the bearded seal (*Erignathus barbatus* (Erxleben, 1777)), the harp seal (*Pagophilus groenlandicus* (Erxleben, 1777)), and the gray seal (*Halichoerus grypus* (Fabricius, 1791)). All females of these species produce a single pup annually and wean their pups quickly. Nursing is brief and intensive. The milk is rich (23%–65% fat) and pups gain mass fast. Pups are weaned with a thick blubber layer, and at weaning, they are left to fend for themselves. The mother abandons the pup and returns to forage at sea for resources required for her post-partum recovery and for producing the next pup. Delayed implantation enables these females to give birth at about the same time every year (Stirling 1969; Bowen et al. 1985; Riedman 1990; Iverson et al. 1995). But because of the inhospitable habitat in which the majority of these seals live, such as moving ice and ice floes, it is difficult to track individuals and monitor the reproductive success of individuals from year to year and throughout their lives. Exceptions to this generalization are the southern elephant seals and Weddell seals (*Leptonychotes weddellii* (Lesson, 1826)).

The behavior and biology of southern elephant seals is similar in many ways to northern elephant seals as revealed by numerous long-term studies at various colonies in the southern hemisphere (e.g., McMahon et al. 2000; McConnell et al. 2002; Hindell et al. 2016). Although the population of the northern elephant seal is increasing, populations at several colonies in the Antarctic are declining (e.g., Hindell 1991). Foraging success of females appears to have a greater effect on population status in the southern seals than in the northern seals. In a Weddell seal colony, where individuals have been monitored for 30 consecutive years, "robust" females produce twice as many pups as "frail" females in normal and perturbed years (Chambert et al. 2013).

Among terrestrial species, polygynous red deer (*Cervus elaphus* Linnaeus, 1758) and elephant seals are comparable in many respects; the data for both are derived from long-term data sets (Clutton-Brock et al. 1982; http://rumdeer.biology.ed.ac.uk/kilmory-hall-fame). Males have higher variance in breeding success than females; some males sire dozens of offspring, but most males sire no offspring at all. Hinds, like elephant seals, produce a single calf most years of their life after age 3 or 4. The lifespan of hinds is similar to that of elephant seals. Some hinds produce as many as 14 sons and daughters, but observations of the next generation reveal that it is the mothers that produce lots of offspring which survive and reproduce that are the most successful. In hinds, senescence begins at age 9 and hinds that produce offspring early in life exhibit faster rates of senescence.

Comparison with other mammals is complicated by variables such as the duration of nursing in many primates, including humans, that reduces total pregnancies, long temporal spacing between offspring, infanticide in African lions (*Panthera leo* (Linnaeus, 1758)) and Indian langurs (genus *Semnopithecus* Desmarest, 1822) that reduces a female's number of offspring produced, and annual variation in available forage that reduces reproduction in ruminants (Hrdy 1977, 1979, 1999; Clutton-Brock et al. 1982; Pusey and Packer 1994). Moreover, elephant seals are capital breeders, not income breeders (Jönsson 1997), that simplifies and maximizes the transfer of energy to offspring. Nevertheless, there are exceptional female breeders in each of these species.

Several long-term studies of birds reveal that year and food availability are the most important determinants of the variance in individual reproductive success, much more so than in seals (McCleery and Perrins 1988; Smith 1988). Many birds die between fertilization and first breeding due to bad weather and losses during migration (Bryant 1988; Newton 1988). Since many House Martins (*Delichon urbicum* (Linnaeus, 1758)) breed for only one or two seasons, one unsuccessful year has a strong influence on LRS. Like seals, older birds with breeding experience are more reproductively successful in any year; "better" birds also start breeding at a younger age (Harvey et al. 1988). A general pattern for seals, other mammals, birds, and insects is that lifespan has an important influence on LRS (e.g., Fincke 1982; Partridge and Farquhar 1983; Clutton-Brock et al. 1988; Ollason and Dunnet 1988). Like in seals, there are indications of senescence in several long-lived bird species (Newton 1988). Large size is positively correlated with reproductive success in anurans (Howard 1988).

In conclusion, LRS is highly variable in female northern elephant seals. Much of the cause of variation in LRS is due to high mortality at sea while foraging. Successful foraging during gestation has a strong influence on the breeding success of pups. The majority of pups born do not survive to breed. Most survivors produce only one or a few pups before they die and the youngest breeders have a poor record of weaning pups. Some supermoms achieve exceptionally high LRS, producing up to 20 pups in a lifetime, near the maximum lifetime reproductive potential. High LRS is associated with living long, breeding annually, and weaning pups successfully even during initial breeding attempts. These exceptional, long-lived, multiparous females, although relatively few in number compared with young breeders, produce numerous offspring that have a significant impact on population dynamics and future generations. Reproductive success in female elephant seals is associated with living long and being pregnant or nursing throughout adult life until death.

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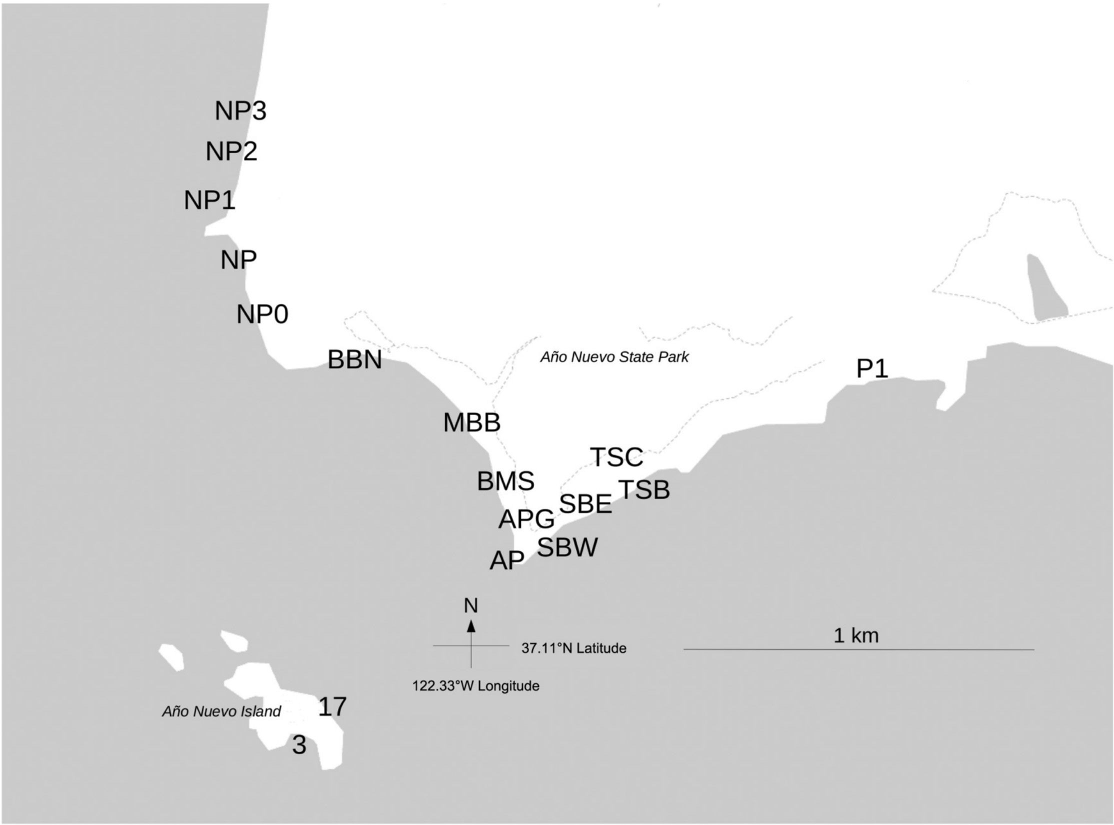
Appendix A

Fig. A1. The main breeding locations of northern elephant seals (*Mirounga angustirotris*) on Año Nuevo island (numbers) and the mainland (letters) in central California, USA.



Appendix B

Selected female profiles are listed below. For abbreviations of breeding locations see Fig. A1 in Appendix A.

GG959

GG959 had a long and well-documented history, although her age and birthplace were unknown. She was tagged in 1991 as a breeding adult. Thereafter, she was seen often, including 15 breeding seasons over 19 years between 1991 and 2009. In every one of her 12 years of breeding, she was seen with a pup. Eleven of her pups were weaned, but in 1997, she gave birth to a pup on 30 January that died the next day. In the 3 other years, she was seen with a pup late in the breeding season and most likely weaned it. Her pup's sex was recorded in 11 different years; she produced six males and five females. In all 15 breeding attempts, she pupped at the south point area, favoring the central bight area, using MBB three times, BMNN twice, BMN twice, BMC twice, and BMS twice. Only in 1 year (2005) did she use the same harem as the prior year (BMC). She was seen only during the molt period in 5 years, and 3 of those years were on the island (2006–2008); she molted at BMC in 1990 and MBB in May 2009, the last time that she was observed.

R4841

R4841 is an example of a relatively short-lived supermom. She was born on San Nicolas Island in 1985 and migrated to Año Nuevo as a yearling. She was observed on both the mainland and the island in spring and the fall of 1986–1987. She gave birth at age 3 and produced pups in 10 consecutive years until age 12. She was seen once more in the molt season at age 13. During the 10 consecutive breeding years, observations of her reproductive behavior were detailed. The observations included at least 16 different days each breeding season over a span of at least 20 days. Thus, we are certain that she weaned her pup in 9 of 10 years. In 1991, at age 6, she gave birth on 22 January, was with the pup regularly through 31 January, but then they became separated. The pup was marked and later weighed, and at 63 kg was categorized as an orphan. There were five other seasons in which her pup was weighed; it was usually large, with a maximum mass of 199 kg in 1994. The sex of her pup was noted in 8 of 10 years, which included six females and two males. Her breeding location was known in 10 straight years, indicating a shift northward as she aged, from southern beaches (TS, APG, SBW, AP) at ages 3–6, to BMS at age 7, and then to NP or BBN at ages 8–12. She never used the same breeding location in consecutive years.

GR426

GR426 was an unusual supermom with a penchant for adopting orphans. She was born in 1999 at North Point and was still living in May 2018 at age 19. She was observed breeding on 13 occasions, and every year she was with a pup. In 6 of her 13 breeding attempts, she was associated with two or more pups. Two of those breeding attempts were especially striking. At age 6, she carried a satellite receiver and consequently was watched closely. She arrived on 15 January and gave birth around 20 January at TS. Her pup was marked. On 1 February and again on 3 February, she was observed with five different pups. From this time to 12 February, she was seen with just her own marked pup or with three pups. She repeated this behavior at age 13 at APG, where she was seen with 2–3 pups on 7 different days, and with 6 pups on 4 February! None of these supernumerary pups were her own. There were only four breeding seasons in which GR426 was consistently associated with just one pup, at ages 4, 7, 15, and 18.

GG732

GG732 holds the distinction of the longest consecutive breeding run of 17 years, from 1990 to 2006. Her age was not known, as she was tagged as a breeding adult in 1990. She also carried an easily visible injury; her right eye was injured between 2002 and 2003 and this blinded eye was noted during the last four breeding season of her life, 2003–2006.

G1214

G1214 was a supermom born in 1972 at Año Nuevo Island, before there was a mainland colony associated with the rookery. She was seen at ages 1 and 2 on the island, but not observed at age 3. She bred on the island from 1976 to 1980. At age 9, she emigrated across the channel to the mainland and finished her life breeding there for 10 breeding seasons spanning 1981 to 1991. She did not breed in 1982. She was observed frequently, which included at least 10 sightings per breeding season spanning at least 23 days each year. She was often seen with orphans her first 3 years and lost her own pup in those years. In 1979 and 1980, she was with a pup regularly for 2 weeks but ended up with orphans. Her success reversed after moving to the mainland, where she always pupped near AP and was successful every year except 1990, when she lost her pup after 5 days and it became an orphan. Her arrival dates and weaning dates were consistent. Even including years when she lost a pup, she was last seen in the interval, 15–26 February, and in the 9 years she weaned her pup, her mean departure was 20 February (SD = 2.6 days). Even after moving to the mainland to breed, she continued to molt on the island, being observed there in 1983 and from 1985 to 1988 She was seen on both the island and the mainland during three molts.

G1214 provides an example of a detailed parturition record spanning 16 years during which she was observed for 15 breeding seasons. It is notable that she was accompanied by orphaned pups during the first 4 years of breeding.

- 1976, Area 17: Observed 13 January to 18 February with orphans.
- 1977, Area 17: Observed 5 to 28 February with orphans or weanlings.
- 1978, Area 17: Observed 29 January to 25 February, seldom with a pup and sometimes with an orphan.
- 1979, Area 17: Observed 22 January to 24 February; she was with a pup up to 10 February, then was sighted many times with orphans or weanlings.
- 1980, Area 17: Observed 21 January to 15 February; she was with a pup until 7 February, then without a pup in her last three sightings.
- 1981, BBS/AP: Observed 25 January to 22 February, always with a pup.
- 1983, AP: Observed 28 January to 20 February, always with a pup. She was observed copulating and departing.
- 1984, AP/SB: 18 January to 16 February, sparse sightings but regularly with a pup.
- 1985, AP/SB: Observed many times with a pup from 17 January to 17 February. Her male pup weighed 168 kg at weaning.
- 1986, AP: Observed with a pup from 26 January to 22 February. Her male pup weighed 156 kg at weaning.
- 1987, SBE: Observed regularly with a pup from 19 January to 19 February. Her male pup weighed 136 kg at weaning.
- 1988, SBE: Observed regularly with a pup from 23 January to 22 February. Her male pup weighed 161 kg at weaning.
- 1989, BMS: Observed regularly with a pup from 21 January to 24 February. Her female pup weighed 141 kg at weaning.
- 1990, APBN: Observed many times from 21 January to 26 February. She gave birth and lost her pup who became an orphan. The orphaned male weighed 50 kg.
- 1991, SBE: Observed regularly with a pup from 20 January to 21 February.

G7932

G7932 stands out as one of two supermoms that produced a daughter that became a supermom. She was born in 1983 and then was observed breeding on the mainland 10 times from age 4 to age 16. Her first birth at age 4 produced GF 24**,** who went on to become a supermom, producing 10 or more pups, like her mother. The daughter also had 10 breeding observations, from age 4 to age 15, all on the mainland. Mother and daughter were observed breeding in the same season in 1991, 1992, 1993, 1995, and 1997 (daughter was missed in 1994 and 1999; the mother was missed in 1996 and 1998). In 1991, they both raised pups at the north end of the North Point, although the mother bred about 150 m farther north than the daughter. They had similar birthing patterns; the daughter weaned her pup on 31 January and mother weaned her pup on 2 February. In 1992, both females moved south, the mother all the way to TS and the daughter to BBN. They continued to maintain similar birthing patterns. In 1993 and 1995, the daughter moved back to NP, while the mother stayed south at TS or AP. In 1997, both were at TS with pups, although each was seen only once. G7932 was last seen in 1999 and her daughter (GF24) was last seen in 2002.

GK861

The other supermom that produced a daughter that became a supermom was GK861, who gave birth to GO535. GK861 was not known-age, but she bred 10 times. She was observed during 11 breeding seasons from 1995 to 2005. Her daughter (GO535**)** was born in 1998, when the mother was at least 6 years old; the pup weighed only 111 kg at weaning. Both mother and daughter were at the same breeding location (APG) in 2002 at about the same time. The daughter was 4 years old that year and was seen numerous times over 4 weeks, always without a pup. Perhaps she was not pregnant. In 2003, at age 5, she had a pup but lost it. She and her mother were both seen that year and again in 2005. The mother was never seen again and was assumed dead. The daughter was seen 11 times through 2014.

Besides the two successful daughters mentioned above, no other female offspring of G7932 or GK861 were ever observed breeding.