Lifetime survival rates and senescence in northern elephant seals

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ABSTRACT

The aim of this study was to extend 40 yr of prior demographic work on northern elephant seals (*Mirounga angustirostris*) at Año Nuevo, California, by including the oldest animals. We used a Bayesian mark-recapture analysis to estimate lifelong survival and lifespan of a cohort of 372 weaned pups branded in 1985–1987 and resighted until 2008. Annual survival probability of females averaged 86.3%/yr at ages 5–16, then declined until age 21, the age of the oldest female. Male survival was lower, averaging 67.7%/yr from age 1 to age 15, the age of the oldest male. Northern elephant seal females in the expanding population at Año Nuevo live longer than southern elephant seal females (*M. leonina*) at colonies whose populations are declining. This comparison suggests that high survival of females is a key factor in population growth.

Key words: demography, lifetime survival, vital rates, elephant seal, *Mirounga angustirostris*, pinniped, life history.

The population of northern elephant seals (*Mirounga angustirostris*) has been increasing in number and expanding in range since near extinction over a century ago (Townsend 1885, Bartholomew and Hubbs 1960, Stewart *et al*. 1994, Lowry 2002). The demographics of this growth phase have been documented at the Año Nuevo colony in central California over the last four decades, addressing variation in male survival and mating success, primiparity in females, pup mortality, and juvenile survivorship (Le Boeuf 1974; Reiter *et al*. 1978, 1981; Le Boeuf and Reiter 1988; Reiter and Le Boeuf 1991; Clinton and Le Boeuf 1993; Le Boeuf *et al*. 1994). Most of this research focused on young animals and prime-age adults. The aim of this paper is to extend earlier work by documenting survival rates of the oldest animals, testing for mortality-related senescence, and comparing the lifespan of males and females. This yields a full life table for adult northern elephant seals of both sexes, necessary for understanding population growth of this long-lived mammal (Pistorius *et al*. 1999, Eberhardt 2002).

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Our previous demographic studies were based on numbered plastic tags affixed to the interdigital webbing of the hind flippers. These worked well for studies of juveniles and young adults. With time, however, tags wore smooth or broke, necessitating retagging (Le Boeuf and Reiter 1988, Clinton and Le Boeuf 1993). Thus, survival estimates in older animals may be unreliable, even when tag loss is modeled (Pistorius *et al*. 2000, McMahon and White 2009). Branding offers a more permanent alternative for marking, and in southern elephant seals (*Mirounga leonina*) permitted identification of individuals throughout life without deleterious effects (Hindell 1991, McMahon *et al*. 2006, Schwarz *et al*. 2012). We thus undertook a branding study of northern elephant seals at Año Nuevo in 1985 aimed at studying survival rates of seals throughout their lifespan.

MATERIALS AND METHODS

The Colony

All branding was done during 1985–1987 at the elephant seal colony in Año Nuevo State Park (37.113°N, 122.329°W), 31 km north of Santa Cruz, California. The colony was established as a breeding site in 1961 (Radford 1965) but expanded rapidly and had 1,500–1,700 pups born during the branding years and as many as 2,500 after 1995 (Le Boeuf and Panken 1977, Le Boeuf *et al*. 2011).

Branding

Weanlings, 8–14 wk of age, were captured on the Año Nuevo mainland in March–May during their postweaning fast. They were restrained in cone-shaped canvas bags opened at both ends (Ortiz *et al*. 1978, Reiter *et al*. 1978, Crocker *et al*. 2006, Hassrick *et al*. 2007). Brands fashioned out of welded steel rods, each a single digit 15 cm high, slightly concave, and ringed by a guard to hold the brand evenly against the animal, were heated until dark red (600–650°C) with a propane torch, or in a propane oven. The brands were applied to the flank for 3–4 s. Each animal was given a 1–3 digit number, always on the left side in 1985 and 1987 and the right side in 1986. The entire procedure took 5–8 min. Subjects were released immediately after branding, and within 5 min engaged in normal behavior, including sleeping, swimming, and socializing. The brand site blistered and opened within a few days, then dried and began healing within two weeks; none became infected. Similar methods have been used for hot-branding in southern elephant seals, and long-term studies showed no deleterious effects and few brands lost (van den Hoff *et al*. 2004).

After branding 78 animals in 1985, we redesigned the brands, adding the guard ring to ensure uniform application, resulting in digits that were easier to read. The new brands were applied to 294 animals in 1986 and 1987 (Table 1). As a check for failure or illegibility, two plastic Rototags (Dalton USA Inc., Fort Atkinson, WI) were attached to the hind flippers of 239 of the branded animals (Le Boeuf *et al*. 1972).

Resighting

Searches for marked seals were done at the Año Nuevo colony from 1986 to 2012 on 95% of all days during the January–February breeding season, and >100 individual seals with brands or tags (including those without brands) were identified every

Table 1. Number of weanling elephant seals branded by year at Año Nuevo.

	Female	Male
1985	36	42
1986	74	79
1987	73	68
Total	183	189

year (median 261 animals, minimum of 108 in 1999, maximum of 505 in 1986). In 1986–1989, additional searches were done during March–June, a juvenile haul-out period, covering 85% of all days. Hair dye was applied to the fur of identified individuals when possible to facilitate subsequent observations within the year (Le Boeuf and Peterson 1969). Observations were also made at the two colonies nearest Año Nuevo (Fig. 1): Southeast Farallon Island (37.698°N, 123.005°W; Huber *et al.* 1991) was searched every day in winter and spring haul-outs, and Point Reyes (37.995°N, 123.009°W; Allen *et al.* 1989) was searched an average of 12 d/mo during January and February. At the next closest breeding colony, 150 km south of Año Nuevo at Point Piedras Blancas, pups were first born in 1992 and no brands have been seen.[2] A few reports of branded animals elsewhere along the coast were sent by other observers and are included in analyses (Fig. 1).

We consider all sightings of females age three or older between mid-December and early March at a breeding colony as breeding events, whether a pup was seen with the female or not. The vast majority of females (>97%) on colonies during that period have pups (Le Boeuf *et al.* 2011). We refer to males seen during the winter at age five and above as breeding, since they are sexually mature at that age, though they are not physically mature until age 8–10.

Modeling Survival

Annual survival—We used the Cormack-Jolly-Seber mark-recapture method to estimate annual survival rate as a function of age (Cormack 1964, Jolly 1965, Seber 1965, Cameron and Siniff 2004, Hastings *et al.* 2011). The method allows a different survival estimate for every age, but we sought parametric models describing smooth shifts in survival with age. There are two advantages to a parametric model: first, hypotheses about maturity and senescence are about consistent changes with age, and second, parametric models add power. The model we chose was piecewise linear regression (McGee and Carleton 1970), describing linear change in three separate age categories. Because the divisions between age categories are estimated along with the regression coefficients, there are no *a priori* assumptions about when survival increases or decreases (Sibly *et al.* 1997), and regression parameters provide explicit statistical tests for age-related shifts. We tested several other models allowing increases and decreases with age: piecewise regression with two or four categories, piecewise logistic regression, and the Siler model, and all produced broadly similar results (Appendix S1, S2). We include two alternative models in the main presentation: the model with survival differing at every age, for graphical comparison with the piecewise regression results, and a model with constant survival across age ranges identified by piecewise

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Figure 1. Locations where branded northern elephant seals were observed, including the tagging location at Año Nuevo, where most were resighted. Three other elephant seal breeding colonies are labeled. Branded animals bred at two, Pt. Reyes and SE. Farallon I., but not at San Miguel I., where only one juvenile was observed. The other sighting locations are not breeding colonies. Two sightings are not on the map because precise locations were never provided, one in Oregon and one in Central California. The latter was the animal that eventually died at a rescue center. Latitude is indicated to the right.

regression (5–16 yr in females, 1–15 yr in males) intended to produce the best-supported estimates for future modeling studies. All models were run separately for males and females.

The piecewise regression model starts with two ages, β_1 and β_2, with $\beta_1 < \beta_2$, to serve as break points defining three age categories. There is a regression slope α_i relating survival to age within each category i and a single intercept, $\pi = S(m)$, the survival rate at age $x = m$, where m is an arbitrary age, usually the midpoint of the age range (we used $m = 10$ yr in females, $m = 8$ in males). A single intercept suffices due to the constraint that fitted lines join at break points. The equation defining annual survival rate $S(x)$ from age $x - 1$ to age x differs in the three segments:

$$S(x) = \begin{cases} S(\beta_1) + a_1(x - \beta_1) & x = \beta_1 \\ S(\beta_1) + a_2(x - \beta_1) & \beta_1 = x = \beta_2 \\ S(\beta_2) + a_3(x - \beta_2) & \beta_2 = x \end{cases} \tag{1}$$

where $S(\beta_1)$ and $S(\beta_2)$ are survival rates at the breaks points. The formula for $S(\beta_2)$ depends on where β_1 and β_2 lie relative to the fixed point m:

$$S(\beta_2) = \Pi + \alpha_1(\beta_1 - m) + \alpha_2(\beta_2 - \beta_1) \quad \text{(if } m \leq \beta_1)$$

$$S(\beta_2) = \Pi + \alpha_2(\beta_2 - m) \quad\quad\quad\quad\quad \text{(if } \beta_1 \leq m \leq \beta_2)$$

$$S(\beta_2) = \Pi + \alpha_3(\beta_2 - m) \quad\quad\quad\quad\quad \text{(if } \beta_2 \leq m),$$

while $S(\beta_1) = S(\beta_2) + \alpha_2(\beta_1 - \beta_2)$ regardless of the locations of β_1 and β_2. The six parameters, β_1, β_2, α_1, α_2, α_3, and π, were estimated simultaneously. We included constraints on the break points, $2 < \beta_1 < \beta_2 - 1 < Max$, where Max is the maximum age (15 in males, 21 in females). Since linear models can predict rates >1 or <0, constraints on the regression parameters were added to hold $S(x)$ in (0, 1) for all x. These constraints were incorporated in the model as prior probabilities on parameters.

Cohort differences and temporal variation—We initially fitted survival models to the 1985, 1986, and 1987 cohorts separately, but results were statistically noisy, with cohort- and age-related variation in survival within estimated credible intervals (see the section on Uncertainty), especially at ages >4 yr (Appendix S3). Since the main focus was older animals, we pooled the cohorts, producing an estimate of their average survival versus age function.

Since the three cohorts were born over a fairly short time interval, we need to address how age-related variation is confounded with year-related variation. For a single cohort, they are completed confounded: animals born in 1986, for example, could suffer poor survival at age 17 due to aging or due to conditions changing after the year 2003. Combining cohorts averages over short-term impacts, such as El Niño (Crocker *et al.* 2006), but not impacts that last >3 yr. With enough cohorts from a wide enough time interval, it is possible to estimate age and year effects separately, but with only three cohorts, statistical power is limited. Instead, we compared the survival-age model with an alternative model relating survival to calendar year: Equation 1 is unchanged, but x represents year instead of age. Success of the two models was measured by deviance, calculated from the likelihood function: deviance $Dev = -2P$, where P is the log-likelihood (*i.e.,* log of the probability) of all observations given the model's predictions (Appendix S3).

Survivorship—Survivorship $L(x)$ is the cumulative survival from weaning to age x, so $L(x) = \Pi_{i<x} S(i)$, where $S(i)$ is the survival rate from age $i - 1$ to age i. There is no separate model for survivorship, rather $L(x)$ was calculated for any model from the estimated survival function $S(x)$.

Detection—The detection probability $\delta(x)$, defined as the probability that a living animal is observed at age x, must be estimated in the mark-recapture model. We assumed $\delta(x)$ differed at ages $x = 1, 2, 3,$ and 4 but was constant at $x \geq 5$, based on the observation that adults come ashore regularly to breed, while juvenile haul-outs are less predictable. $\delta(x)$ is the mean detection probability of all animals at age x; individuals may vary without impacting survival estimates (Carothers 1979, Kendall 2001). Any annual or age-related variation in detection causing a systematic shift through time, however, could affect age-related survival estimates. We thus considered a hierarchical model in which $\delta(a)$ differed across ages, but was constrained by an over-arching logit-normal distribution (Gelman and Hill 2007); this allows age-related variation while still benefitting from support across ages (Clark *et al.* 2005). Survival estimates from this model were indistinguishable from the model with

constant $\delta(a)$, and there was no age-related trend in detection probability. Few animals were seen at the Point Reyes and Farallon colonies, especially after adulthood, so we ignored variation in detection probability among locations.

Parameter estimation—Survival and detection parameters were estimated in a Bayesian framework using Markov chains and a Gibbs sampler with the Metropolis update algorithm (Metropolis *et al.* 1953, Poole 2002, Williams *et al.* 2002, Condit *et al.* 2007, Mackey *et al.* 2008). The Bayesian method produces credible intervals for every parameter, and for every statistic derived from the parameters, based on posterior distributions described by the Markov chains, plus it simplifies the likelihood formulation by incorporating a latent parameter, Dj, for the age at which animal j dies (Clark *et al.* 2005; Appendix S2). Constraints on parameters served as prior probability distributions: the probability of any parameter combination was set to zero if it predicted survival rate outside the interval (0,1) at any age. We compared prior probabilities of survival rates to fitted posterior distributions to show that priors had negligible impact on results (Appendix S4).

Single Markov chains of 10,000 steps were completed for all the models tested (Appendix S1). For the piecewise regression model with three segments, we carried out four additional chains of 22,000 steps, each with different starting values for the parameters, in order to test for convergence. Parameter estimates, survival rates, and credible intervals based on the four runs were indistinguishable, and Gelman and Rubin's (1992) scale reduction factor was <1.01, so the four chains were merged for a total of 80,000 estimates (discarding the first 2,000 of each as burn-in). There was autocorrelation in parameter chains, particularly for β_1 (the first age division), so the final samples of 80,000 were thinned to 2,000 randomly drawn sets of parameters. The thinned chains describe the model's estimate of each parameter's posterior distribution. Every parameter combination was also used to calculate age-specific survival (Eq. 1) and thence survivorship, yielding posterior distributions of all $S(x)$ and $L(x)$. The mean of each posterior distribution was taken as the best estimate for every statistic, including survival and detection rates.

Uncertainty of parameter estimates and survival—The central 95 percentiles of the posterior distributions served as credible intervals for each model parameter, survival, and survivorship at every age. We state that differences are "statistically significant" when credible intervals did not overlap a null hypothesis, for example, when intervals for slope parameters did not overlap zero.

An additional source of uncertainty resulted from misread or failed brands. We documented misread brands by matching observed sex, brand position (left *vs.* right flank), and tag number to original records, and by examining repeated sightings. For example, the female with brand number 247 was seen many times from 1991 onward, while the brand 297 appeared in 1997 and 2000; the two numbers were never recorded in the same year. Since the real brand 297 was applied to a male, we assigned the 1997 and 2000 sightings to Brand-247. Five of the 61 animals seen as adults, however, could not be identified with certainty, all cases where the digits 5/6/8 or 4/9 were confounded. To propagate this uncertainty into error in survival estimates, we repeated the female models after altering the identity of 1–2 individuals, meaning the resight matrices had one more or one less female at breeding age. Adult survival barely changed under these alterations, but juvenile survival was increased or decreased by 0.01/yr (for example, from 0.54 to 0.55/yr). This leads to a 20% increase in variance of the juvenile survival estimates, relative to the variance estimated by the Bayesian model, and only slightly inflates credible intervals. It is approximate in that

we do not know exact probabilities associated with misidentifications, but we conclude misidentification had a small impact on survival estimates.

Failure of brands would add more error, but because some branded animals were also tagged, failure would be detected. Indeed, in one of the 38 adults both tagged and branded, the brand apparently failed: the male branded with number 205 was identified by tags on numerous occasions at ages 5, 6, and 7 with no brand noted. Failure of one out of 38 is similar to the rate reported for southern elephant seals (McMahon *et al*. 2006) and too low to affect estimates of juvenile survival appreciably. Brand failure prior to adulthood would not affect estimates of adult survival.

Results

Resightings

Of the 372 branded animals, 52% (193) were seen at least once as yearlings or older (Table 2). Males were resighted slightly more often than females, 55% (104 animals) to 49% (89 animals). Sixty-one were observed to reach maturity, including 37 females that were observed breeding on at least one occasion and 24 males seen at age 5 or above (Table 2).

Table 2. Number of branded elephant seals seen at each age, and the number whose last sighting was at the same age. Age turned on 1 December, *i.e.,* animals reached age 1 in December of their first year, age 2 the next December, *etc*. The number of sightings at age 0 is the number branded; the number with maximum age 0 is the number never seen after November of their branding year.

	Sightings		Maximum Age	
Age	Female	Male	Female	Male
0	183	189	94	85
1	71	84	25	34
2	44	55	16	22
3	27	33	7	17
4	28	14	4	7
5	23	17	6	8
6	24	11	5	5
7	20	10	5	5
8	15	5	3	2
9	11	4	3	2
10	9	1	1	0
11	11	1	2	0
12	6	2	3	0
13	5	1	0	1
14	3	1	0	0
15	5	1	0	1
16	7	0	2	0
17	5	0	2	0
18	3	0	0	0
19	4	0	4	0
20	0	0	0	0
21	1	0	1	0

Most sightings were at Año Nuevo, but 40 branded animals were observed else-where, including 20 males and 20 females (Fig. 1). Most were juveniles, including 17 females and 18 males, and most were at the colonies at Southeast Farallon (26 juveniles) and Point Reyes (3 juveniles). The few seen elsewhere included one juvenile female at San Miguel Island and five juvenile males in northern California, Oregon, and British Columbia (Fig. 1). Several foreign sightings were within the animal's first year, includ-ing one in Oregon seven weeks after branding. Nineteen of the 35 dispersing juveniles were later seen at Año Nuevo, but none were seen at two different foreign locations.

Nine branded animals were observed at maturity at a foreign colony: two females breeding at the Farallones, five females breeding at Point Reyes, plus two males at ages 6–8 at Point Reyes. Four of those had been seen as juveniles at the same colony, while one of the females and both males were resighted first as juveniles at Año Nuevo prior to emigrating to breed. Two females bred at two locations: Brand-208 had a pup at age 3 at Southeast Farallon then returned to Año Nuevo and pupped every year at ages 4 through 9; Brand-82 had a pup at Point Reyes at age 3 then back at Año Nuevo at ages 7 and 11.

One yearling died after being taken to a treatment center near Año Nuevo. An additional sighting relevant to mortality was a 19 yr old female observed at Año Nuevo with one of her hind flippers entirely missing, the wound still fresh. She departed the colony but was not seen again.

Longevity

The longest-lived female, Brand-222, was observed beyond her 21st birthday, on 8 March 2008 at Point Reyes; she was not seen with a pup that year, but she was in other years, all at Point Reyes. Four other females were seen at age 19, all with pups at Año Nuevo. The oldest male, Brand-152, reached age 15 at Año Nuevo in 2001. One other male was observed until age 13 (Table 2).

Age-specific Survival

There were strong age-related trends in survival rate of females. Just 57% survived to age 1, but annual survival rose quickly thereafter, reaching 83%/yr at age 5 and 88%/yr at age 16, before declining abruptly in the oldest females (Fig. 2, Table 3). The increase to age five and the decrease beyond age 16 were both statistically signifi-cant, but the slight change from age 5 to 16 was not (based on the slope parameters from piecewise regression). In a model in which annual survival was held constant from age 5 to 16, the mean rate for females was 86.3%/yr, with credible limits 82%–90%.

In contrast, males showed little age-related variation in survival. The first year rate was 66%, and it rose only slightly in older seals and remained between 66% and 72%/yr until age 14 (Fig. 2, Table 3). The small fluctuations with age were not sta-tistically significant, based on the slope parameters from piecewise regression. From a model of constant annual survival at all ages, the mean rate for males was 67.7%/yr, with credible limits 63%–72%. Male survival was significantly lower than female survival at ages >3, but did not differ in younger animals (Table 3).

Survivorship

Survivorship of females from weaning was estimated at 31% to age 3 and 25% to age 4 (Fig. 3, Table 3). Thus, 46 of the 183 branded females reached age 4, the
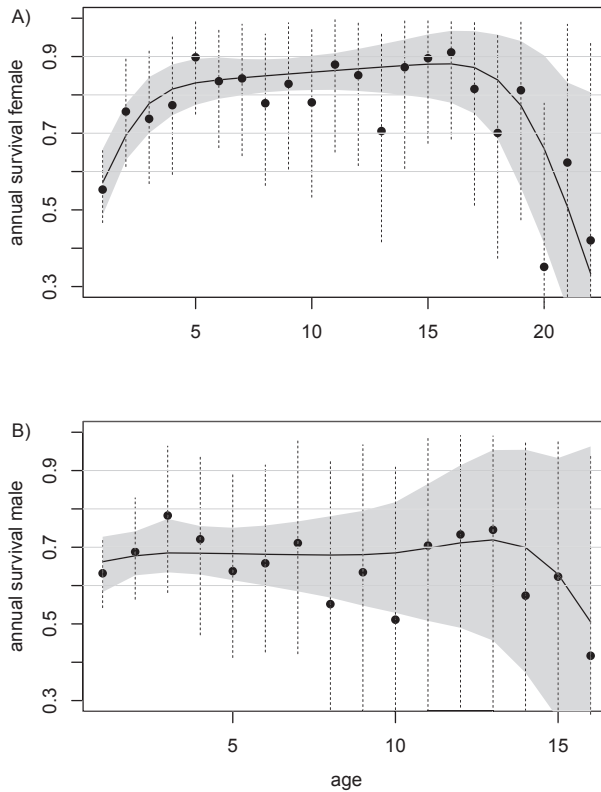
Figure 2. Annual survival rates of branded (A) female and (B) male northern elephant seals from Año Nuevo. Survival rate at x is the probability that an animal alive at age $x - 1$ was still alive at age x. The black curve shows the the piecewise regression model with three age categories, with 95% credible intervals shaded in gray. Individual points are the rates estimated at every separate age, with credible intervals indicated by vertical bars. Horizontal lines at rates of 0.6, 0.7, 0.8, and 0.9 are included as guides.

modal age of primiparity. Since we observed 37 females breeding, we missed several that were alive at breeding age but died before being seen again. Estimated survivorship to age 10 was 9% (or 16 females), and to age 17 just 4% (seven females).

In males, estimated survivorship from weaning was 31% to age 3 and 14% to age 5 (Fig. 3, Table 3), *i.e.*, 27 animals reached age 5, the time when most males attain puberty. Only 5% (eight males) survived to age 8, the beginning of physical maturity. We observed six animals at age 8 or older, and thus missed two.

Detection

Estimated annual detection probability was similar in males and females and varied little with age (Table 4). Only the low rate in 4 yr old males differed significantly from other rates.
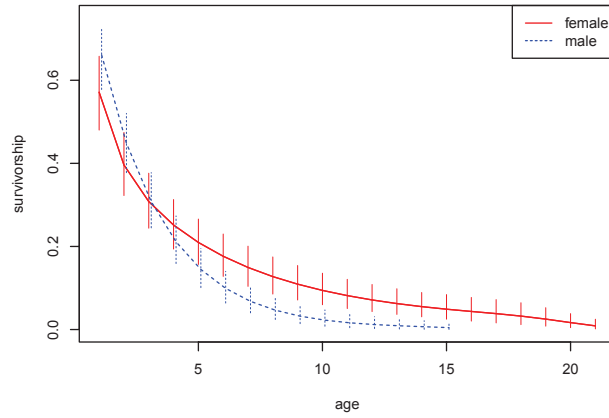
Figure 3. Postweaning survivorship of branded male and female northern elephant seals from Año Nuevo based on the piecewise regression models (see Fig. 2). Survivorship at x is the cumulative survival from weaning to age x, and thus does not include pup mortality. Vertical bars are 95% credible intervals.

Table 3. Age-specific survival and survivorship probabilities starting at weaning in branded elephant seals, estimated by mark-recapture; 95% credible intervals are given in parentheses. Survival at age x is the probability of surviving from $x - 1$ to x, based on the piecewise regression survival models with three age categories; age 0 means weaning. Survivorship is the cumulative survival from weaning until x. Credible intervals are the central 95 percentiles of Bayesian posterior distributions.

	Annual survival		Survivorship	
Age	Female	Male	Female	Male
1	0.573 (0.49,0.66)	0.661 (0.58,0.73)	0.570 (0.48,0.66)	0.663 (0.59,0.73)
2	0.693 (0.63,0.77)	0.676 (0.62,0.74)	0.395 (0.32,0.47)	0.449 (0.38,0.52)
3	0.777 (0.70,0.85)	0.683 (0.63,0.77)	0.307 (0.24,0.38)	0.307 (0.24,0.38)
4	0.816 (0.75,0.88)	0.683 (0.63,0.75)	0.250 (0.19,0.31)	0.210 (0.16,0.27)
5	0.833 (0.77,0.89)	0.682 (0.62,0.75)	0.209 (0.16,0.27)	0.144 (0.10,0.20)
6	0.840 (0.79,0.90)	0.681 (0.61,0.75)	0.175 (0.13,0.23)	0.098 (0.06,0.14)
7	0.846 (0.80,0.89)	0.680 (0.59,0.76)	0.149 (0.10,0.20)	0.067 (0.04,0.10)
8	0.851 (0.81,0.89)	0.679 (0.57,0.78)	0.126 (0.09,0.17)	0.046 (0.02,0.08)
9	0.855 (0.81,0.90)	0.681 (0.55,0.80)	0.108 (0.07,0.15)	0.032 (0.01,0.06)
10	0.860 (0.81,0.90)	0.685 (0.53,0.82)	0.093 (0.06,0.13)	0.022 (0.01,0.04)
11	0.864 (0.81,0.91)	0.698 (0.50,0.86)	0.081 (0.05,0.12)	0.016 (0.00,0.04)
12	0.869 (0.81,0.92)	0.711 (0.48,0.91)	0.070 (0.04,0.10)	0.012 (0.00,0.03)
13	0.873 (0.80,0.93)	0.717 (0.45,0.95)	0.062 (0.04,0.10)	0.009 (0.00,0.03)
14	0.877 (0.80,0.95)	0.698 (0.39,0.96)	0.054 (0.03,0.09)	0.007 (0.00,0.02)
15	0.880 (0.79,0.96)	0.633 (0.28,0.93)	0.048 (0.02,0.08)	0.004 (0.00,0.02)
16	0.880 (0.78,0.97)		0.043 (0.02,0.08)	
17	0.870 (0.75,0.97)		0.038 (0.02,0.07)	
18	0.839 (0.68,0.96)		0.032 (0.01,0.06)	
19	0.774 (0.56,0.94)		0.025 (0.01,0.05)	
20	0.659 (0.42,0.90)		0.017 (0.00,0.04)	
21	0.507 (0.25,0.83)		0.009 (0.00,0.03)	

Table 4. Detection probability, or the probability that an animal still alive at age x was observed between ages $x - 1$ and x, estimated by mark-recapture. The probability was estimated separately at each age up to 4, and pooled for all older animals.

Age	Female	Male
1	0.69	0.68
2	0.60	0.65
3	0.48	0.55
4	0.61	0.35
≥ 5	0.60	0.63

Survival as a Function of Calendar Year

The piecewise regression model with three segments for females had a higher deviance when year was the predictor rather than age (Appendix S2), meaning age was a better predictor of observation histories. The improved fit of the age model was due to older animals: late declines in survival were better aligned by age than by year (Fig. S3.1). Moreover, the decline in annual survival rate after 2004 in the year model was not statistically significant, though in the age model, decline after age 17 was. In males, however, the year model produced a better fit to data than the age model (Fig. S3.2).

Nevertheless, the survival-year model added information, because it revealed fluctuations in young animals not evident in the age model (Appendix S3). Survival was high in 1986, low in 1987, then increased until 1989 before settling on a long plateau (Fig. S3.3). The 1986–1986 variation was a cohort effect: first-year survival was high for the 1985 cohort relative to the 1986 and 1987 cohorts in both males and females. The cohort difference, however, did not persist in older animals (Fig. S3.1, Fig. S3.2). The age model produced an intermediate estimate for first-year survival, averaging the three cohorts.

DISCUSSION

Annual survival of adult females was high from age 5 to 16, averaging 86%/yr, but then declined abruptly. This is a higher rate and a longer duration of prime survival than we expected and the first evidence for senescence in survival rates of northern elephant seals. Our earlier work did not detect the decline in female survival because there were no data on females older than 15 yr (Le Boeuf and Reiter 1988, Reiter and Le Boeuf 1991). Schwarz *et al.* (2012) found limited power in estimating survival beyond age 15 due to the small number of animals retaining tags.

Average male survival was <72%/yr at all ages and lower than female survival after age 3, as reported in earlier studies (Clinton and Le Boeuf 1993). Neither our current analysis nor the earlier work detected senescence in male survival, but high mortality throughout life meant few males were still living at age 12 when senescence would be most likely. On the other hand, our earlier study did detect declining competitive ability in males past age 12 (Clinton and Le Boeuf 1993).

Juvenile survivorship in the current study was 31% from weaning to age 3 and similar in the two sexes, a rate close to the average reported across several previous cohorts (Le Boeuf and Reiter 1988, Le Boeuf *et al.* 1994). This average masked

variation, however, and low survival in 1986–1987 may have been due to poor foraging conditions associated with an El Niño event (Trenberth and Stepaniak 2001, Crocker *et al*. 2006). Our earlier study of juvenile survival also described substantial year-to-year fluctuations (Le Boeuf *et al*. 1994). These rates of survivorship, though, began at weaning and omit pup mortality, and 10% of pups in the Año Nuevo mainland colony died before weaning in 1985–1987 (Le Boeuf *et al*. 2011). In population modeling, the relevant rate of juvenile survivorship (from birth) was thus 28%, not 31%.

Dispersal of branded animals to nearby colonies—"prospecting" for alternative breeding sites—also confirms earlier observations (Le Boeuf *et al*. 1974, 2011). Seven of the 37 females observed to breed did indeed choose an alternative, but two of those subsequently returned home.

Since our sample consisted of only three cohorts born over three years, we should be circumspect about generalizing. The number of branded adults was small, and our results on survival in mature females hinges on the 15 animals observed at age 10 or older. Moreover, declining survival in old females might be attributed to poor conditions that all three cohorts experienced after 2002, rather than senescence. We found, however, that a model based on age outperformed a model based on calendar year, and there is no evidence that feeding conditions were better in the 1990s than after 2000. In fact, the switch in the Pacific Decadal Oscillation around 1998 apparently favored elephant seal foraging (Le Boeuf and Crocker 2005), as females tracked at sea gained more weight in 2004–2005 than in 1995–1997 (Simmons *et al*. 2010). In contrast, there is ample precedent for attributing declining survival in mammals to aging (Nussey *et al*. 2008, Turbill and Ruf 2010).

The southern elephant seal offers an illuminating comparison of lifetime survival because many of its populations are declining while the northern elephant seal's is expanding (McMahon *et al*. 2005*a*). Differences in survival rates between the species might thus indicate factors regulating population growth (Le Boeuf *et al*. 1994; McMahon *et al*. 2003; Pistorius *et al*. 2008, 2011). For example, juvenile survival at Año Nuevo is low relative to the southern species, suggesting that the Año Nuevo colony is not sustained by internal recruitment but by immigration (Le Boeuf *et al*. 1994).

Contrary to the pattern in juveniles, we found higher adult female survival in the northern species, averaging 86%/yr compared to 81%/yr or lower at both Marion and Macquarie colonies (Hindell 1991, McMahon *et al*. 2003, Pistorius *et al*. 2008), two southern elephant seal colonies where populations have declined, and 84% at Peninsula Valdes, the only expanding population of the southern species (Pistorius *et al*. 2004, Ferrari *et al*. 2012). Moreover, survival in the branded cohorts of Año Nuevo females remained high until age 16, whereas a life table based on branded animals at Macquarie Island showed steadily declining survival in southern elephant seal females after age 11 (Hindell 1991). High survival through age 15, however, was observed in the southern species at Marion Island (Pistorius and Bester 2002*a*, Pistorius *et al*. 2011).

Our results to date thus lead us to hypothesize that high survival of adult females has been a key factor in the recovery of northern elephant seals from the population nadir in 1890. It follows that reduction in female survival will be important in curbing population growth. In southern elephant seals, Pistorius *et al*. (2004) attributed differences in population trends at different colonies to variation in adult survival, but juvenile survival, fecundity, and age at primiparity have also been implicated as key density-dependent factors (Pistorius *et al*. 2001; Pistorius and Bester 2002*b*;

McMahon *et al.* 2003, 2005*a*, *b*; de Little *et al.* 2007). In the northern elephant seal, we have likewise found substantial variation in juvenile survivorship and annual fecundity (Huber *et al.* 1991, Reiter and Le Boeuf 1991, Le Boeuf *et al.* 1994, Crocker *et al.* 2006), suggesting ample opportunity for either to affect population growth. Except for pup mortality, however, density-dependent variation in survival and fecundity has not been demonstrated (Le Boeuf *et al.* 2011).

On the other hand, when compared to other large mammals, elephant seals are short-lived. Adult females of most large herbivores have survival rates >90%/yr (Gaillard *et al.* 1998), as do many pinnipeds (Cameron and Siniff 2004, Hastings *et al.* 2011). In gray seals (*Halichoerus grypus*), 95% of adult females survive annually (Harrison *et al.* 2006) and a 42 yr old has been observed (Bowen *et al.* 2006). Elephant seals must have higher fecundity than gray seals in order to sustain population growth with their relatively short lifespan. At least one pinniped, though, is similar to elephant seals: in monk seals (*Monachus schauinslandi*), survival declined starting at age 17 (Baker and Thompson 2007).

Our next steps are to study fluctuations in vital rates over time by studying other cohorts, then to build models of the Año Nuevo colony and the entire population of northern elephant seals based on complete life tables. Given our current estimate of a 21 yr life span and 86% annual survival of adult females, we will explore variation in juvenile survival to find a rate that would support the rapid worldwide recovery in the 20th century. We can also use the observed life table at Año Nuevo to quantify the immigration rate needed to account for local population growth. Other pinniped species offer excellent precedents for this sort of modeling (Cameron and Siniff 2004, Harrison *et al.* 2006). With the northern elephant seal, we will soon have the bonus of observing the cessation of population growth, allowing us to document vital rates across the transition to stability and test hypotheses about environmental and demographic factors important in regulating the population.

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Supporting Information

The following supporting information is available for this article online: http://onlinelibrary.wiley.com/doi/10.1111/mms.12025/suppinfo.

Appendix S1. Definitions and formulae for the models presented in the main text and alternative models tested.

Appendix S2. Results from alternative models compared to results from models presented in the main text.

Appendix S3. Models relating annual survival rate to year instead of age, and differences among cohorts in survival rates.

Appendix S4. Prior and posterior distributions of survival rates.