

Effects of environmental variability and breeding experience on northern elephant seal demography

DEREK E. LEE*

PRBO Conservation Science, Marine Ecology Division, 3820 Cypress Drive #11, Petaluma, CA 94954, USA
Present address: Dartmouth College, Department of Biological Sciences, 103 Gilman Life Sciences Laboratory, Hanover, NH 03755, USA

* Correspondent: derek.e.lee@dartmouth.edu

Demographic rates of animals (i.e., survival and breeding success) generally increase with experience early in life, but temporal variation in the effect of experience on demography is not well understood. The demographic difference between inexperienced versus experienced breeders can be accentuated during poor environmental conditions when food is scarce, or the difference can remain constant regardless of environmental fluctuation. I tested the hypothesis that environmental variation accentuates the difference between inexperienced and experienced breeders using 20 years of capture–mark–recapture data for northern elephant seals (*Mirounga angustirostris*) from the Farallon Islands, California. I estimated year-specific survival probabilities, breeding propensity (the probability that an individual will breed in year x), and breeding success of primiparous (inexperienced) and multiparous (experienced) females. Primiparous breeders did not suffer more than experienced breeders during years of environmental stress. The selection hypothesis (a decrease in heterogeneity in individual quality within cohorts over time, based on selection pressure) could explain the experience-related improvement in survival and breeding success. Lower variances in survival of multiparous breeders suggest that primiparous adults constitute a more heterogeneous portion of the population, and the 1st breeding event might act as a selective process leading to a more homogeneous pool of multiparous breeders.

Key words: climate, El Niño, El Niño–Southern Oscillation (ENSO), mammal, *Mirounga angustirostris*, Phocidae, reproductive success, survival

© 2011 American Society of Mammalogists
DOI: 10.1644/10-MAMM-A-042.1

Understanding how temporal environmental variability influences demographic rates such as survival and breeding success is central to interpreting variation in life-history strategies (Emlen 1984; Pianka 1988; Stearns 1992; Williams 1966) and change in animal populations (Caswell 2001; Croxall and Rothery 1991; Ratcliffe et al. 1998). Mounting evidence indicates that temporal environmental variability and recent climatic changes (Intergovernmental Panel on Climate Change 2007) impact population dynamics (Walther et al. 2002). For example, temporal variation impacts survival or breeding success in >30 species of large mammals (Gaillard et al. 2000).

Life-history theory predicts that individuals have a limited amount of energy that can be allocated to survival and breeding, leading to a theoretical trade-off between them (Roff 1992; Stearns 1992). Because breeding performance is known to increase with age and experience (prior to senescence), breeding costs should be highest in younger individuals (Forslund and Pärt 1995; Newton 1998). In mammalian and

avian populations several studies have found evidence that 1st-time breeders are poor performers, with a lower probability of breeding successfully (Forslund and Pärt 1995; Lee et al. 2007; Newton 1998), a lower probability of breeding the following year (Reiter and LeBoeuf 1991; Weimerskirch 1992), and a lower probability of survival after 1st breeding (Chastel et al. 1995; Clutton-Brock et al. 1996; Pistorius et al. 2008; Promislow 1991; Reiter and LeBoeuf 1991) compared with older, more experienced individuals. Such differences can be explained by 3 nonexclusive hypotheses (Curio 1983; Forslund and Pärt 1995; Sæther 1990; Weimerskirch 1992). The 1st is constraint; breeding and survival abilities improve as animals age and gain experience (Greig et al. 1983). Primiparous animals might be unable to defend space and protect offspring or forage as successfully, or both, as



multiparous animals. This hypothesis predicts lower mean reproductive success, breeding propensity (the probability that an individual will breed in year x), and survival of primiparous seals versus multiparous seals with no difference in variance. The 2nd hypothesis is restraint, the optimization of breeding effort or ability with survival (Williams 1966). Primiparous animals might allocate their reproductive effort in a manner that does not impact lifetime reproduction. This hypothesis predicts lower mean reproductive success and breeding propensity of primiparous versus multiparous seals, but equal survival. The 3rd hypothesis is selection, where natural selection eliminates poor performers from the multiparous class, resulting in a temporal decrease in heterogeneity among individuals as lower-quality animals die off (Cam and Monnat 2000; Curio 1983; Forslund and Pärt 1995). This hypothesis predicts lower mean and higher variance in reproductive success, breeding propensity, and survival of primiparous versus multiparous seals.

How temporal environmental fluctuations affect the demographic parameters of inexperienced and experienced breeders is a critical issue. If inexperienced animals are more susceptible than experienced breeders, any sustained change in mortality of 1st-time breeders could affect populations. However, the long-term demographic response of individuals to a variable environment relative to breeding experience is poorly documented. The difference in breeding success, breeding propensity, and survival probability of younger versus experienced breeders can be accentuated during extreme environmental conditions such as when resources are scarce (Bunce et al. 2005; Nevoux et al. 2007). Alternatively, younger breeders can be affected by climatic fluctuations in the same manner as experienced breeders (Nevoux et al. 2008). Thus, the distinction between younger, less experienced animals and older, more experienced animals is fundamental to explaining population dynamics in variable ecosystems.

The aim of this study is to compare the demographic response of primiparous (inexperienced) and multiparous (experienced) individuals of a long-lived marine mammal species to climatic variation on the foraging grounds by simultaneously analyzing adult survival, breeding propensity, and breeding success. I studied the northern elephant seal (*Mirounga angustirostris*) population of the South Farallon Islands, California. Previous studies have demonstrated the impacts of age and experience on northern elephant seal breeding success (Huber 1987; Reiter and Le Boeuf 1991; Sydeman et al. 1991), and climatic variation has been shown to affect foraging success (Le Boeuf and Crocker 2005) and pup sex ratio (Lee and Sydeman 2009), but annual variation in the demographic differences between primiparous and multiparous seals has not been addressed.

I began by estimating year-specific breeding propensity, breeding success, and survival probability of primiparous and multiparous individuals using 20 years of capture–mark–recapture data. Based on previous findings for birds (Barbraud and Weimerskirch 2005; Bunce et al. 2005; Laaksonen et al.

2002; Nevoux et al. 2007) and mammals (Coulson et al. 2001; Gaillard et al. 1993, 1998, 2000; Sydeman et al. 1991), I expected that multiparous breeders would have higher survival and breeding success than inexperienced breeders. To examine the potential experience-based response of breeders to temporal climatic variation I tested for significant correlations between the 3 demographic parameters and fluctuations in ocean climate and prey abundance on the foraging grounds (Gaillard et al. 2000; Nevoux et al. 2007, 2008). I predicted that warm-water years and years of lower hake abundance would result in lower demographic rates of all breeding females, and that the difference between primiparous and multiparous seals would either remain constant during temporal environmental fluctuations or increase during years of more extreme warm water or decreased hake abundance.

MATERIALS AND METHODS

Study area and data collection.—Northern elephant seals are large (adult females ~300 kg), capital-breeding, marine mammals that breed during January and February each year at rookeries along the Pacific coasts of Mexico and California with very high natal and breeding-site fidelity. PRBO Conservation Science (PRBO; formerly Point Reyes Bird Observatory) has studied the population biology of northern elephant seals on the South Farallon Islands, part of the Farallon National Wildlife Refuge, 45 km west of San Francisco, California (37°42'N, 123°00'W), since the breeding colony was reestablished in 1972. Exploitation of these seals in the 1800s extirpated the Farallon population. Recolonization of these islands began in 1959 when immatures 1st hauled out to molt, and the 1st pup was born in 1972. This study encompassed the years 1975 through 1994, when sample size in both experience classes was adequate. Since 1972 nearly all weaned pups and several immature animals were flipper-tagged every year (Dalton Supplies Ltd., Henley-on-Thames, United Kingdom). PRBO biologists identified returning females by flipper tags, distinguishing marks such as scars, or by dye marks placed on animals during postbreeding molt. After recording tag numbers, PRBO biologists used hair dye (Clairol, Stamford, Connecticut) to mark females temporarily so they could observe animals from a distance. Pups usually were marked with dye 1 or 2 days after birth. PRBO biologists checked mothers and pups daily, weather permitting, to determine parturition and breeding success. All work was carried out according to guidelines of the American Society of Mammalogists (Gannon et al. 2007), under Marine Mammal Permit 373-1868-00.

At 4 weeks old a pup has tripled its birth weight and is weaned when the mother returns to sea in February for a 2-month postpartum bout of foraging to recover the one-third of her body mass lost during nursing. Females disperse widely to forage in the northeastern Pacific twice per year, from 38° to 60°N and from the coast to 188°E, feeding at depths of 300–600 m with occasional dives to 1,500 m (Le Boeuf et al. 2000). Between their postpartum and gestation foraging bouts,

females haul out to molt. After continuous foraging during the 8-month gestation period (mid-April to mid-December), females return to rookeries to give birth and nurse their pups (Deutsch et al. 1994; Le Boeuf et al. 1972). Females begin breeding at age 3–6 (median = 4—Huber 1987). Females that begin breeding at age 3 (23% of primiparous females) have lower subsequent pupping rates and weaning success than females that begin breeding at age 4 or 5 (77% of primiparous females—Huber 1987).

During El Niño events warm-water intrusion northward up the west coast of North America to British Columbia and Southeast Alaska shifts the usual female northern elephant seal foraging area northward and farther away from California rookeries (Fulton and LeBrasseur 1985) and disrupts the formation and propagation of mesoscale eddies that promote or aggregate prey (Okkonen et al. 2001). Under warm-water conditions adult female elephant seals spend more time foraging, gain less mass than usual, and begin breeding later (Crocker et al. 2006; Huber et al. 1991; Le Boeuf et al. 2000; Le Boeuf and Reiter 1991; Simmons et al. 2007). Thus, warm-water years apparently result in low prey availability (Crocker et al. 2006; Le Boeuf and Crocker 2005; Simmons et al. 2007). Northern elephant seal diet is mostly r-selected pelagic squid species and K-selected Pacific hake (*Merluccius productus*, also known as Pacific whiting—Antonelis et al. 1994). Although the ecologies of pelagic squid species in the northern elephant seal diet are not well studied, based on previous findings that warm water on foraging grounds resulted in longer foraging trips and less mass gain, I predicted that warm-water years signify lower squid abundance or availability (Le Boeuf and Crocker 2005; Simmons et al. 2007), resulting in reduced demographic rates of breeding female elephant seals. The most important fish prey for northern elephant seals is Pacific hake, the most abundant groundfish off the North American west coast (Methot and Dorn 1995). Pacific hake life history is characterized by low recruitment punctuated by occasional very strong year classes, and the role of ocean climate in hake ecology is complex (Ressler et al. 2007). Hake is the only prey species of the northern elephant seal with reliable abundance metrics throughout the study period, so I used Pacific hake annual stock assessments of total and spawning biomass as a direct index of annual variation in the fish component of northern elephant seal diet (Helsler et al. 2008).

Environmental covariates.—I used 2 climate indices (Southern Oscillation Index [SOI] and Northern Oscillation Index [NOI]) and annual stock assessments of hake biomass as covariates of ocean climate and food availability. The El Niño–Southern Oscillation (ENSO) cycle, a fluctuation between unusually warm (El Niño) and cold (La Niña) conditions in the eastern tropical Pacific, is the predominant year-to-year climate variation on Earth (McPhaden et al. 2006). El Niño and La Niña develop in association with phase shifts in the Southern Oscillation, an atmospheric pressure gradient comparing the strength of the Tahitian High pressure system and Darwin, Australia Low pressure system. There-

fore, ENSO events often are examined relative to the SOI (Trenberth 1984). The SOI is the difference in sea-level pressure between Darwin, Australia, and Tahiti, French Polynesia (Trenberth 1984), and indicates the primary signal of the ENSO phenomenon. Positive SOI values indicate strong Pacific trade winds (La Niña), and negative values indicate the reversal of Pacific trade winds (El Niño).

Another indicator of atmospheric pressure gradients is the NOI, which, like the SOI, compares the differences in large-scale pressure, and thereby winds (Schwing et al. 2002). The NOI compares the North Pacific High against the Darwin Low, and like the SOI is related to El Niño and La Niña events. Positive values of the NOI indicate productive, La Niña periods in ocean productivity, with strong upwelling-associated winds along the west coast of North America. NOI is a counterpart of SOI that relates variability in the atmospheric forcing of climate in northern midlatitude hemisphere regions and represents a wide range of local and remote climate signals. ENSO is unique among climate phenomena in its strength, predictability, and global influence, projecting beyond the tropical Pacific through oceanographic and atmospheric teleconnections that affect patterns of weather and ocean productivity variability worldwide (McPhaden et al. 2006). The possible teleconnections to higher latitudes influences the North Pacific High and other pressure cells of the North Pacific. The NOI measures changes in pressure gradients that influence winds and primary productivity in the Northeast Pacific (Schwing et al. 2002). SOI and NOI are highly correlated (Fig. 1a) but indicate specific climate signals. Each index provides information pertaining to the timing and mechanism of the effect on prey and consequent effects on seal demography.

Pacific hake biomass is estimated using models that incorporate total fishery catches, fishery age or size compositions, or both, and data from nonfishery samples and acoustic surveys (Helsler et al. 2008). The 2008 assessment used the Stock Synthesis modeling framework (SS2 version 2.0) written by Dr. Richard Methot (Northwest Fisheries Science Center) in AD Model Builder (Helsler et al. 2008). I converted raw annual spawning and total (age 3+) hake biomass estimates (1974–2008) to standardized anomalies by subtracting the mean from each annual estimate and dividing by the *SD*.

Estimation of demographic parameters.—I analyzed capture–recapture data to model and estimate annual values of apparent local survival (ϕ), breeding propensity (BP), and breeding success (BS). Apparent local survival (ϕ) is the probability that an animal survives from year x to year $x + 1$. Apparent survival cannot discriminate between mortality and permanent emigration. BP is the probability that an animal bred in year x , given that it survived. BS is the probability of successfully weaning a pup in year x . All seals began their encounter histories with their 1st breeding attempt, so for primiparous seals BS is breeding success during the 1st attempt, ϕ is survival between their 1st and 2nd breeding attempts, and BP is the probability of breeding in the year

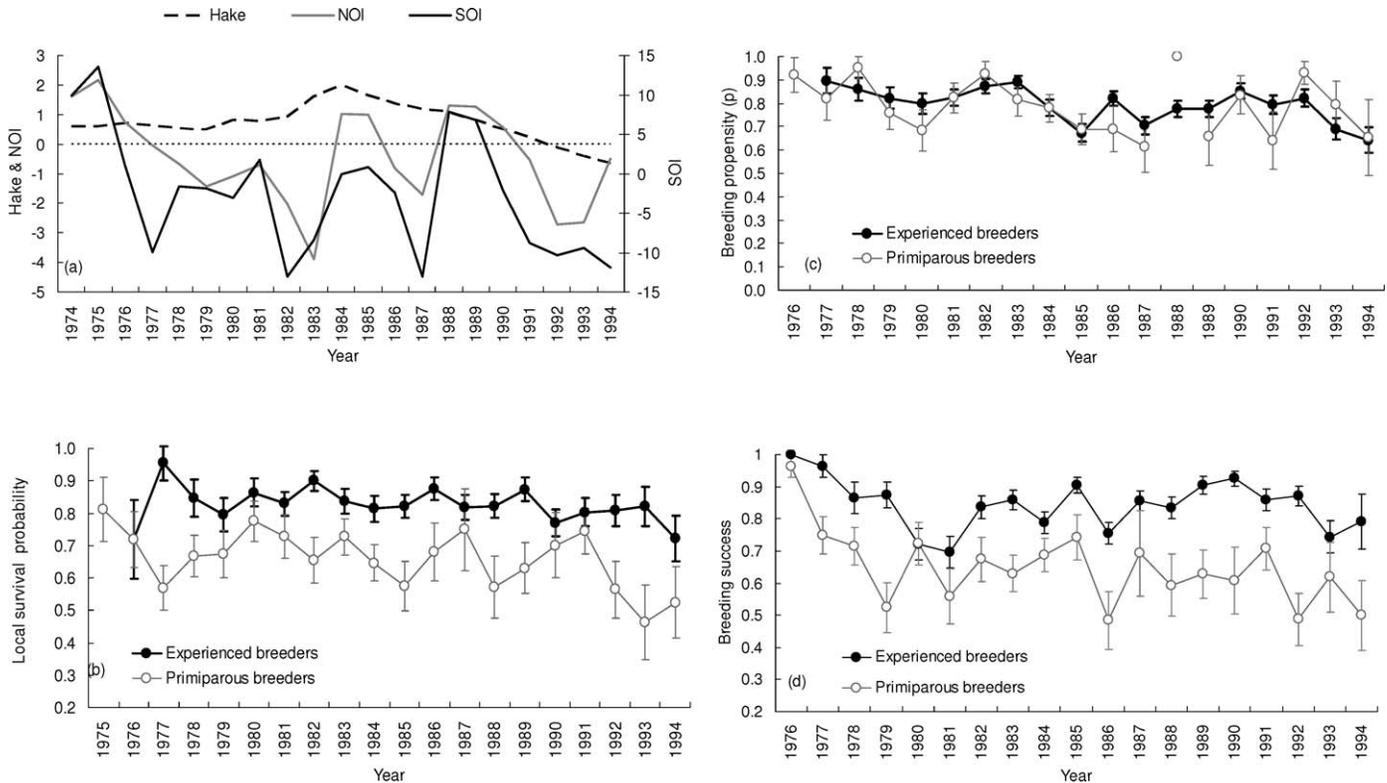


FIG. 1.—Annual variation in environmental covariates and demographic parameters of northern elephant seals according to experience at the South Farallon Islands, California. a) Annual variation in Pacific hake spawning biomass (Hake), Southern Oscillation Index (SOI), and Northern Oscillation Index (NOI). b) Annual variation in local survival probability for experienced and primiparous breeders (year x to $x+1$). c) Annual variation in breeding propensity (p ; $1 - \text{probability of skipping breeding}$) for experienced and primiparous breeders. d) Annual variation in the probability of breeding success for experienced and primiparous breeders.

immediately after their 1st attempt. Thus, the probability of skipping breeding in the breeding season immediately following their 1st attempt = $1 - \text{BP}$.

Accurate estimates of survival are best obtained from analysis of capture–recapture data with models that estimate survival and recapture probabilities separately (Lebreton et al. 1992; Mayfield 1975). The recapture probability of species with high breeding-site fidelity, such as northern elephant seals, incorporates the conditional probability that an individual will breed in a particular year given that it has survived to that year (Clobert et al. 1994; Lebreton et al. 1990). Thus, capture–recapture data can be used to infer breeding propensity. Accurate data on breeding success also are best obtained from a marked, known-age population where animals are monitored frequently during the breeding season (Mayfield 1975), as is the case at South Farallon Islands.

Breeding and resight histories of marked female elephant seals were available for 860 individuals between 1975 and 1994. Number of tagged cows each year averaged 162 (range = 36–264). I did not incorporate age of individuals because of difficulty obtaining tagging records for females breeding at South Farallon Islands that were born and tagged at Channel Island rookeries. Also, restricting my sample to only known-age individuals would have significantly reduced sample sizes. Thus, I defined experience as the number of breeding events observed for each individual. Previous work on this species

(Huber 1987; Reiter and LeBoeuf 1991; Sydeman et al. 1991) and preliminary analysis of these data on the definition of breeding experience confirmed that differentiating 1st-time breeders (hereafter called primiparous) from individuals with at least 1 breeding attempt (hereafter called multiparous) effectively differentiates between young and experienced adults in terms of survival, breeding propensity, and breeding success. I presumed that the 1st breeding event was detected correctly, based on the high natal site fidelity of the species, frequent surveys of the rookeries by field workers, and high recapture probability of breeders (see “Results”).

I modeled and estimated annual probabilities using the general methods described by Lebreton et al. (1992) and Burnham and Anderson (2002). I modeled and estimated ϕ and BP using program MARK 5.1 (White and Burnham 1999) “recaptures only” model structure. BS was defined as successfully weaning a pup after >20 days of nursing. Because the breeding data included repeated measurements of individuals, I modeled and estimated BS using generalized linear mixed model with binomial error structure and logit link function where female identity was a random factor. I analyzed BS using STATA 10.0 (StataCorp LP 2007).

My process was to assess goodness of fit for my data using a global model that included year- and experience-related variation, then find the best model of temporal variation for ϕ , BP, and BS of the 2 experience classes, and, finally,

examine covariate models of climate and prey indices to determine whether primiparous breeders suffered more in years of environmental stress. Goodness of fit for ϕ and BP was evaluated using estimates of the variance inflation factor \hat{c} , a measure of overdispersion. I used the median- \hat{c} approach (Cooch and White 2005). Following Lebreton et al. (1992), I considered values of $\hat{c} < 3$ as indicative that model structure provided an adequate fit to the data. Goodness of fit for BS was analyzed using a Pearson goodness of fit (χ^2) test (StataCorp LP 2007).

I used the logit link function and 2nd part variance estimation throughout the MARK analyses. I determined model parsimony using the quasi Akaike information criterion corrected for small sample size (qAIC_c). I used qAIC_c weights as a measure of the strength of evidence for a given model. Δ qAIC_c is the difference between the qAIC_c for a model and the qAIC_c for the current minimum qAIC_c model. For the minimum qAIC_c model, the most-parsimonious model in the set, the Δ qAIC_c = 0. Means of parameters between experience classes were compared using paired (by year), 1-tailed *t*-tests. Variances were compared using *F*-statistics.

Model sets.—I defined the global model during goodness of fit testing as (ϕ (*experience * year*)BP(*experience * year*)) and (BS(*experience * year*)). This global model is a multiplicative interaction of annual variation and 2 experience categories, meaning primiparous and multiparous seals each have a unique value for ϕ , BP, and BS every year. The a priori model set for analyses of temporal variation included ϕ , BP, and BS parameters modeled separately for primiparous and multiparous seals: as constants (*constant*), and as fully time-dependent (Lebreton et al. 1992), with year treated as a categorical variable (*year*). I also included an additive model with annual variation where the 2 experience classes vary in parallel, the difference between them remaining constant (*experience + year*).

To examine whether inexperienced animals are more susceptible than experienced breeders to environmental fluctuations, I ranked a set of models where parameters were linear functions of environmental covariates. If primiparous and multiparous breeders have significantly different means, experience will be a significant effect, and each experience class will have a unique intercept coefficient. If the difference between experience classes is the same in all years, the slope coefficient will not differ by experience, and the 2 covariate functions should be parallel. If primiparous breeders are affected more severely by climate variation, climate covariate slope coefficients for the 2 experience classes will have the same sign, but the slope coefficient for primiparous breeders will be significantly steeper. In essence, if primiparous breeders are impacted more severely by bad climate years, the multiplicative interaction model (*experience * covariate*) should be ranked higher than the model with additive interaction of experience and environmental covariate (*experience + covariate*). Alternatively, if the model with additive interaction of experience and environmental covariate ranks higher than the model with multiplicative interaction of

TABLE 1.—Mean (*SD*) of demographic parameters (probabilities of survival, breeding propensity, and breeding success) for primiparous and multiparous breeding northern elephant seals at the South Farallon Islands, California, 1976–1994. Statistics generated from year-specific estimates of parameters for both experience classes. *t*-statistics and *P*-values from paired *t*-tests.

	Survival	Breeding propensity	Breeding success
Primiparous	0.659 (0.091)	0.788 (0.199)	0.647 (0.116)
Multiparous	0.826 (0.056)	0.794 (0.075)	0.845 (0.08)
<i>t</i> -statistic (<i>d.f.</i>)	7.42 (18)	0.54 (17)	8.42 (18)
<i>P</i> -value	<0.001	0.30	<0.001

experience and environmental covariate, primiparous breeders are not more susceptible than multiparous breeders to environmental fluctuations.

Because breeding and animal resight efforts were concentrated in January and February each year, I used the environmental index values of the year preceding the breeding effort as covariates for breeding parameters (BP and BS). I used the index value of the current year as the covariate of survival between breeding seasons (ϕ).

RESULTS

From 1975 to 1994, 860 individual females that were tagged as weaned pups or immatures returned to breed at least once at South Farallon Islands. Effective sample size for capture–mark–recapture analysis was 2,847. The capture–recapture data provided a very good fit to the global model. Global model deviance ranked 76 of 100 simulated deviances (estimated $\hat{c} = 1.187$, *SE* = 0.0079); the variance inflation factor applied was $\hat{c} = 1.187$. The breeding success global model also fit the data well (number of observations = 1,923; Pearson $\chi^2_{19} = 43.37$, *P* = 0.11). Estimates of year-specific survival, breeding propensity, and breeding success for both experience classes revealed large temporal variation in all 3 parameters (Figs. 1b–d), with significant differences between experience classes in survival and breeding success but not in breeding propensity (Table 1). Mean survival probability for primiparous seals was 16.7% lower than for multiparous seals (Table 1). Variance in survival probability for primiparous breeders was significantly higher than multiparous breeders ($F_{18,19} = 2.67$, *P* = 0.042). Mean breeding success was 19.8% lower for primiparous seals versus multiparous seals (Table 1). Variance in breeding success for primiparous breeders was not significantly higher than for multiparous breeders ($F_{19,19} = 2.08$, *P* = 0.130). Mean breeding propensity was similar between experience classes (Table 1). Variance in breeding propensity was higher for primiparous seals, but the difference was marginally nonsignificant ($F_{17,18} = 2.53$, *P* = 0.062).

The most-parsimonious model of survival was a constant that differed according to breeding experience (Table 2). Survival of primiparous breeders in the year following their 1st breeding attempt was significantly lower than survival of experienced seals (*primiparous* $\beta = -0.885$, *SE* = 0.110).

TABLE 2.—Table of model selection results for survival, breeding propensity, and breeding success of northern elephant seals at the South Farallon Islands, California, 1976–1994. *exp* = 2 experience classes, *year* = annual variation, ϕ = survival, *BP* = breeding propensity. $qAIC_c$ = quasi Akaike information criterion corrected for small sample size, $\Delta qAIC_c$ = difference between the $qAIC_c$ for a model and the $qAIC_c$ for the current minimum $qAIC_c$ model. Bold models are the highest-ranked for each parameter.

	$qAIC_c$	$\Delta qAIC_c$	$qAIC_c$ weights	No. parameters	$qDeviance$
Survival ($\phi(x)$ BP(year))					
exp	4,415.88	0	0.33	22	1,228.48
exp + NOI	4,416.61	0.73	0.23	23	1,227.18
exp + hake	4,417.73	1.85	0.13	23	1,228.30
exp + SOI	4,417.91	2.03	0.12	23	1,228.48
exp * NOI	4,418.55	2.68	0.09	24	1,227.09
exp * hake	4,419.72	3.84	0.05	24	1,228.26
exp * SOI	4,419.88	4.00	0.05	24	1,228.42
exp + year	4,439.38	23.50	0	40	1,215.17
exp * year	4,463.19	47.31	0	58	1,201.69
constant	4,470.14	54.27	0	20	1,286.81
year	4,496.56	80.69	0	39	1,274.41
Breeding propensity ($\phi(\text{exp})$ BP(x))					
year	4,415.88	0	0.70	22	1,228.48
exp + year	4,417.79	1.91	0.27	23	1,228.36
constant	4,425.42	9.54	0.01	3	1,276.37
hake	4,425.69	9.81	0.01	4	1,274.63
exp	4,426.67	10.80	0	4	1,275.62
exp + hake	4,427.04	11.16	0	5	1,273.98
NOI	4,427.29	11.41	0	4	1,276.23
SOI	4,427.34	11.46	0	4	1,276.28
exp * hake	4,428.42	12.55	0	6	1,273.35
exp + NOI	4,428.53	12.65	0	5	1,275.47
exp + SOI	4,428.60	12.72	0	5	1,275.54
exp * NOI	4,430.43	14.56	0	6	1,275.37
exp * SOI	4,430.47	14.59	0	6	1,275.40
exp * year	4,433.10	17.22	0	42	1,204.77
Breeding success					
exp * year	227.80	0.00	1.00	38	150.85
exp * NOI	245.42	17.62	0	4	237.41
exp + NOI	245.44	17.64	0	3	239.44
exp + year	248.27	20.47	0	34	179.51
exp + SOI	249.25	21.45	0	3	243.24
exp * SOI	251.25	23.45	0	4	243.23
exp	258.86	31.06	0	2	254.86
exp + hake	260.85	33.05	0	3	254.84
exp * hake	262.11	34.31	0	4	254.10
year	326.53	98.73	0	19	288.29
constant	356.89	129.09	0	1	354.88

The top-ranked model of breeding propensity was annual variation ($BP(\text{year})$), with no experience effect (Table 2). *Experience* was included in the 2nd-ranked model of breeding propensity but was not an important effect; effect size was negligible, with 0.005 lower mean annual breeding propensity for primiparous breeders when mean BP was 0.794 ($SD = 0.075$) for multiparous breeders. Breeding success was best modeled as ($BS(\text{experience} * \text{year})$) with considerable weight of evidence for this being the best model of the set (Table 2). This interaction model indicates that breeding success of multiparous and primiparous seals varied independently by

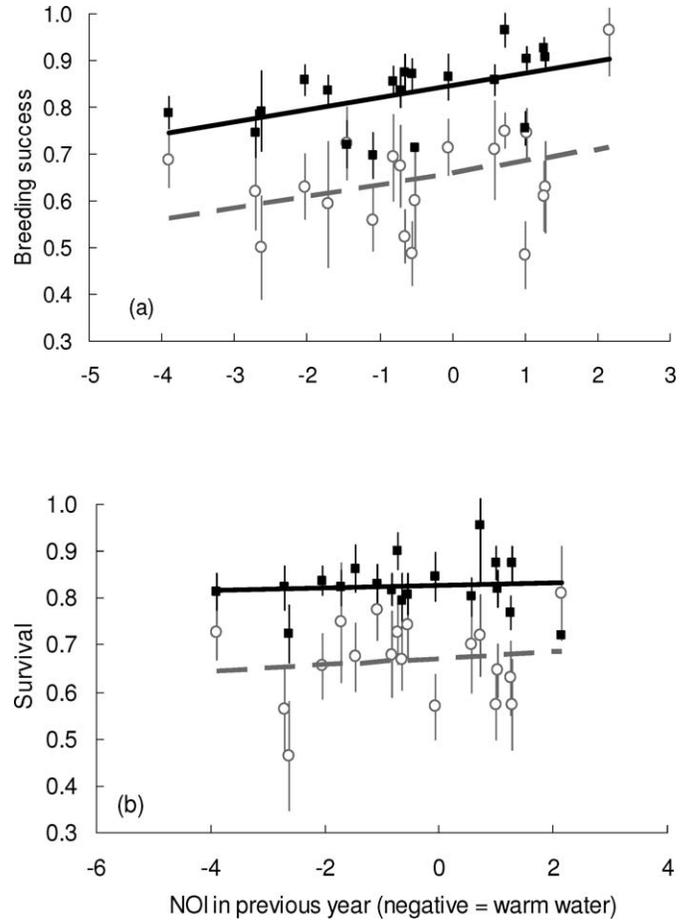


FIG. 2.—Relationships between environmental climate indices and demographic parameters of primiparous (○) and multiparous (■) northern elephant seals at the South Farallon Islands, California, 1975–1994. Darker trend lines are for multiparous females, lighter dashed trend lines are for primiparous females. a) Relationship between Northern Oscillation Index (NOI) during pregnancy and breeding success. b) Relationship between NOI during pregnancy and survival.

year. Mean difference in BS between primiparous seals and multiparous seals was 0.207 ± 0.022 (SE).

Climate results.—I found no significant environmental covariates of annual variation in northern elephant seal demographic parameters (Table 2). Additive models of covariates were consistently ranked equal to, or better than, interaction models, indicating that primiparous breeders did not suffer disproportionately from adverse environmental fluctuations (Table 2). Additive models indicate that the difference in demographic parameters between experience classes does not change as the severity of annual conditions increases (Fig. 2).

DISCUSSION

This study simultaneously quantifies annual variation in survival, breeding propensity, and breeding success according to breeding experience for female northern elephant seals. Similar to previous studies (Forslund and Pärt 1995; Newton

1998), year-specific estimates of survival had a lower mean (constraint, restraint, and selection hypotheses) and higher variance (selection hypothesis) for primiparous breeders relative to multiparous seals. I found that primiparous seals responded to climatic variation similarly to experienced breeders and were not more susceptible to climate extremes than multiparous seals. The difference in demographic parameters between primiparous and multiparous seals did not increase according to the extremity of the climatic variation. These results expand and elaborate on previous work related to experience effects in the northern elephant seal (Huber 1987; Reiter and LeBoeuf 1991; Sydeman et al. 1991) and other species (Barbraud and Weimerskirch 2005; Cam and Monnat 2000; Coulson 1966; Gaillard et al. 1998, 2000; Nevoux et al. 2007; Pinaud and Weimerskirch 2002; Pistorius et al. 2008; Sadleir 1969).

The demographic response of a population to its environment depends on its life-history traits, the manner in which individuals trade off the allocation of resources between breeding and survival (Erikstad et al. 1998; Stearns 1992). In long-lived animals the survival of adults in general, and experienced individuals in particular, should be highly buffered against external forces, at the expense of breeding success (Gaillard et al. 2000; Pfister 2005). Survival of both experience classes of female northern elephant seals was best described by a constant, but the best models of breeding success and breeding propensity included annual variation indicating that survival might be buffered relative to breeding effort and success.

The constraint hypothesis suggests that primiparous seals are less able than multiparous seals to defend space and protect their pups in the colony, or to forage successfully postpartum. This hypothesis predicts lower mean reproductive success, breeding propensity, and survival of primiparous seals compared to multiparous seals, but equal variance between primiparous and multiparous seals, which I did not find. The restraint hypothesis predicts lower mean reproductive success and breeding propensity of primiparous than multiparous seals, but equal survival. I found unequal survival between experience classes.

The selection hypothesis (Forslund and Pärt 1995) could explain the experience-related improvement in survival and breeding success. This hypothesis predicts lower mean and higher variance in reproductive success, breeding propensity, and survival of primiparous versus multiparous seals. Lower variance in survival of multiparous breeders suggests that primiparous adults constitute a more heterogeneous portion of the population, and the 1st breeding event can act as a selective process leading to a more homogeneous pool of multiparous breeders (Barbraud and Weimerskirch 2005; Cam and Monnat 2000; Nevoux et al. 2007). Because breeding demands a large energetic investment from individuals, it could act as a filter on the heterogeneous pool of primiparous females, leading to a progressive decrease in the proportion of lower-quality individuals among cohorts (Barbraud and Weimerskirch 2005; Cam and Monnat 2000; Curio 1983;

Forslund and Pärt 1995). Although inexperienced individuals of high quality might be able to perform as well as experienced breeders, poor-quality individuals are more susceptible to adverse conditions, contributing to the lower average performance of primiparous breeders (Lescroel et al. 2009). Sydeman et al. (1991) found evidence for the constraint or restraint hypotheses, or both, in their analysis of northern elephant seal lifetime breeding success. Our combined results add to understanding of life-history trade-offs in this long-lived marine mammal.

I found no biologically significant difference in breeding propensity between experience classes. This result should be considered in light of the reality that breeding propensity can be estimated only for those seals that survived to breed again following their 1st attempt, and survival was much lower and more variable for primiparous than experienced seals. First-time breeders are younger, relatively smaller seals, and thus the reduction in body mass following successful weaning of a pup could be expected to take a greater toll than for larger, experienced seals. As a result, 1st-time breeders might be less likely to regain their own body mass and additionally store enough energy to produce a pup again in the following year. Cases of inexperienced individuals requiring a longer recovery time following a breeding season have been documented in numerous species (Ollason and Dunnet 1988; Viallefont et al. 1995; Weimerskirch 1990; Wooller and Coulson 1977), including Weddell seals (*Leptonychotes weddellii*—Hadley et al. 2007). In the present study primiparous breeders had lower survival rather than breeding propensity, suggesting that natality adversely affects survival of younger northern elephant seals rather than their propensity to breed the following year.

This study quantified the relationship between North Pacific climate oscillations and demographic parameters of northern elephant seals that had been related anecdotally based on the extreme El Niño of 1982–1983 (Huber et al. 1991; Le Boeuf and Reiter 1991). Recently, Le Boeuf and Crocker (2005) found that foraging success of breeding females (measured as mass gain) was correlated negatively with ocean temperature on the foraging grounds. However, I found no significant relationship between ENSO signals indexed by the SOI or NOI and northern elephant seal demography. Differences in temperature and foraging success detected on the foraging grounds might be influenced more by upwelling and downwelling in mesoscale eddies than by basin-scale climate.

Recurrent large-scale oceanographic events and low-frequency ocean climate regime shifts (Steele 1998) can result in new vital rates and changes in population structure for northern elephant seals and other top marine predators. Changes in the growth and behavior of predator populations are thought to reflect broadscale environmental changes occurring over long periods (Croxall et al. 2002; Hindell et al. 2003). Thus, if population responses are sensitive to environmental shifts and manifest in vital rates (e.g., survival, breeding propensity, and breeding success) over relatively short time periods, marine predators could be useful indicator

species for ecosystem changes over broad geographical regions (Hindell et al. 2003). This is particularly relevant for wide-ranging species such as elephant seals that procure their food across entire ocean basins (Bradshaw et al. 2004), whose principal squid prey are not well studied and whose principal fish prey species supports a substantial fishery, and that exert a wide ecological influence as both predator and prey (Ressler et al. 2007). However, no clear demographic signal of ocean climate variation was apparent in these data. Although breeding success was best modeled with an interaction model, no pattern of primiparous breeders suffering significantly greater than multiparous breeders in bad years was apparent. This model seems to indicate that primiparous breeding success is simply more variable than multiparous breeding success.

Stronger relationships between demographic rates of northern elephant seals and environmental conditions might exist but will require more study to determine the relevant resolution for annual environmental covariates. Moreover, vital rates of these seals might not be linked to a single climate variable, and instead might respond to some combination of factors (De Little et al. 2007). An alternative explanation is that individual heterogeneity in primiparous animals has a larger effect than climate on annual variation in vital rates. More detailed exploration of sophisticated climate and prey indexes could address such questions.

ACKNOWLEDGMENTS

I thank the United States Fish and Wildlife Service—San Francisco Bay National Wildlife Refuge and managers of the Farallon National Wildlife Refuge for facilitating our research on the island. I thank B. J. Le Boeuf, who initiated the tagging program in California and provided original tagging information throughout the duration of this study. D. G. Ainley initiated the study on the Farallones (with B. J. Le Boeuf). I gratefully thank B. Johnson and the skippers of the Farallon Patrol of PRBO, the United States Coast Guard, and United States Fish and Wildlife Service for providing logistical support. I am also grateful to the many interns that collected northern elephant seal data under supervision of the PRBO Farallon biologists. Financial support for this project was provided by PRBO/Friends of the Farallones and the United States Fish and Wildlife Service. I thank Clairol Laboratories for donating hair bleach and dye. C. Abraham, G. Ballard, M. Bond, J. Jahncke, L. Crespín, and anonymous referees offered constructive comments on the manuscript. This is PRBO contribution 1755.

LITERATURE CITED

- ANTONELIS, G. A., M. S. LOWRY, C. H. FISCUS, B. S. STEWART, AND R. L. DELONG. 1994. Diet of the northern elephant seal. Pp. 211–223 in *Elephant seals: population ecology, behavior, and physiology* (B. J. Le Boeuf and R. M. Laws, eds.). University of California Press, Berkeley.
- BARBRAUD, C., AND H. WEIMERSKIRCH. 2005. Environmental conditions and breeding experience affect costs of reproduction in blue petrels. *Ecology* 86:682–692.
- BRADSHAW, C. J. A., J. HIGGINS, K. J. MICHAEL, S. J. WOTHERSPOON, AND M. A. HINDELL. 2004. At-sea distribution of female southern elephant seals relative to variation in ocean surface properties. *ICES Journal of Marine Science* 61:1014–1027.
- BUNCE, A., S. J. WARD, AND F. I. NORMAN. 2005. Are age-related variations in breeding performance greatest when food availability is limited? *Journal of Zoology (London)* 266:163–169.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York.
- CAM, E., AND J.-Y. MONNAT. 2000. Apparent inferiority of first-time breeders in the kittiwake: the role of heterogeneity among age class. *Journal of Animal Ecology* 69:380–394.
- CASWELL, H. 2001. *Matrix population models: construction, analysis and interpretation*. 2nd ed. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.
- CHASTEL, O., H. WEIMERSKIRCH, AND P. JOUVENTIN. 1995. Body condition and seabird reproductive performance: a study of three petrel species. *Ecology* 76:2240–2246.
- CLOBERT, J., J.-D. LEBRETON, D. ALLAINE, AND J. M. GAILLARD. 1994. The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrate populations: II. Longitudinal models. *Biometrics* 50:375–387.
- CLUTTON-BROCK, T. H., I. R. STEVENSON, P. MARROW, A. D. MACCOLL, A. I. HOUSTON, AND J. M. MCNAMARA. 1996. Population fluctuations, reproductive costs and life-history tactics in female Soay sheep. *Journal of Animal Ecology* 65:675–689.
- COOCH, E., AND G. WHITE. 2005. Using MARK—a gentle introduction. 4th ed. <http://www.phidot.org/software/mark/docs/book/>. Accessed 27 September 2010.
- COULSON, J. C. 1966. The influence of the pair bond and age on the breeding biology of the kittiwake gull, *Rissa tridactyla*. *Journal of Animal Ecology* 35:269–279.
- COULSON, T., ET AL. 2001. Age, sex, density, winter, weather, and population crashes in Soay sheep. *Science* 292:1528–1531.
- CROCKER, D. E., D. P. COSTA, B. J. LE BOEUF, P. M. WEBB, AND D. S. HOUSER. 2006. Impact of El Niño on the foraging behavior of female northern elephant seals. *Marine Ecology Progress Series* 309:1–10.
- CROXALL, J. P., AND P. ROTHERY. 1991. Population regulation of seabirds: implications of their demography for conservation. Pp. 272–296 in *Bird population studies: their relevance to conservation and management* (C. M. Perrins, J.-D. Lebreton, and G. J. M. Hiron, eds.). Oxford University Press, Oxford, United Kingdom.
- CROXALL, J. P., P. N. TRATHAN, AND E. J. MURRAY. 2002. Environmental change and Antarctic seabird populations. *Science* 297:1510–1514.
- CURIO, E. 1983. Why do young birds reproduce less well? *Ibis* 125:400–404.
- DE LITTLE, S. C., C. J. A. BRADSHAW, C. R. McMAHON, AND M. A. HINDELL. 2007. Complex interplay between intrinsic and extrinsic drivers of long-term survival trends in southern elephant seals. <http://www.biomedcentral.com/1472-6785/7/3>. Accessed 27 September 2010.
- DEUTSCH, C. J., D. E. CROCKER, D. P. COSTA, AND B. J. LE BOEUF. 1994. Sex and age-related variation in reproductive effort of northern elephant seals. Pp. 169–210 in *Elephant seals: population ecology, behavior and physiology* (B. J. Le Boeuf and R. M. Laws, eds.). University of California Press, Berkeley.
- EMLÉN, J. M. 1984. *Population biology: the coevolution of population dynamics and behavior*. Macmillan, New York.
- ERIKSTAD, K. E., P. FAUCHALD, T. TVERRA, AND H. STEEN. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology* 79:1781–1788.
- FORSLUND, P., AND T. PÄRT. 1995. Age and reproduction in birds—hypotheses and tests. *Trends in Evolution & Ecology* 10:374–378.

- FULTON, J. D., AND R. J. LEBRASSEUR. 1985. Interannual shifting of the subarctic boundary and some of the biotic effects on juvenile salmonids. Pp. 237–252 in *El Niño north* (W. S. Wooster and D. L. Fluharty, eds.). Washington Sea Grant Program, University of Washington, Seattle.
- GAILLARD, J.-M., D. DELORME, J.-M. BOUTIN, G. VAN LAERE, B. BOISAUBERT, AND R. PRADEL. 1993. Roe deer survival patterns: a comparative analysis of contrasting populations. *Journal of Animal Ecology* 62:778–791.
- GAILLARD, J.-M., M. FESTA-BIANCHET, AND N. G. YOCOZ. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution* 13:58–63.
- GAILLARD, J.-M., M. FESTA-BIANCHET, N. G. YOCOZ, A. LOISON, AND C. TOÏGO. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31:367–393.
- GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809–823.
- GREIG, S. A., J. C. COULSON, AND P. MONAGHAN. 1983. Age-related differences in foraging success in the herring gull (*Larus argentatus*). *Animal Behaviour* 31:1237–1243.
- HADLEY, G. L., J. J. ROTELLA, AND R. A. GARROTT. 2007. Influence of maternal characteristics and oceanographic conditions on survival and recruitment probabilities of Weddell seals. *Oikos* 116:601–613.
- HELSEY, T. E., I. J. STEWART, AND O. S. HAMEL. 2008. Stock assessment of Pacific hake, *Merluccius productus*, (a.k.a. whiting) in U.S. and Canadian waters in 2008. Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, Washington.
- HINDELL, M. A., C. J. A. BRADSHAW, R. G. HARCOURT, AND C. GUINET. 2003. Ecosystem monitoring: are seals a potential tool for monitoring change in marine systems? Pp. 330–343 in *Marine mammals fisheries, tourism and management issues* (N. J. Gales, M. A. Hindell, and R. Kirkwood, eds.). CSIRO Publishing, Melbourne, Australia.
- HUBER, H. R. 1987. Natality and weaning success in relation to age of first reproduction in northern elephant seals. *Canadian Journal of Zoology* 65:1311–1316.
- HUBER, H. R., C. BECKHAM, AND J. NISBET. 1991. Effects of the 1982–83 El Niño on northern elephant seals on the South Farallon Islands, California. Pp. 219–233 in *Pinnipeds and El Niño: responses to environmental stress* (F. Trillmich and K. A. Ono, eds.). Springer-Verlag, Berlin, Germany.
- INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE. 2007. Climate change 2007: synthesis report. Contribution of working groups I, II and III to the fourth assessment report of the intergovernmental panel on climate change (R. K. Pachauri and A. Reisinger, eds.). Intergovernmental Panel on Climate Change, Geneva, Switzerland.
- LAAKSONEN, T., E. KORPIMÄKI, AND H. HAKKARAINEN. 2002. Interactive effects of parental age and environmental variation on the breeding performance of Tengmalm's owls. *Journal of Animal Ecology* 71:23–31.
- LE BOEUF, B. J., AND D. E. CROCKER. 2005. Ocean climate and seal condition. <http://www.biomedcentral.com/1741-7007/3/9>. Accessed 27 September 2010.
- LE BOEUF, B. J., D. E. CROCKER, D. P. COSTA, S. B. BLACKWELL, P. M. WEBB, AND D. S. HOUSER. 2000. Foraging ecology of northern elephant seals. *Ecological Monographs* 70:353–382.
- LE BOEUF, B. J., AND J. REITER. 1991. Biological effects associated with El Niño Southern Oscillation, 1982–83, on northern elephant seals breeding at Año Nuevo, California. Pp. 206–218 in *Pinnipeds and El Niño: responses to environmental stress* (F. Trillmich and K. A. Ono, eds.). Springer-Verlag, Berlin, Germany.
- LE BOEUF, B. J., R. J. WHITING, AND R. F. GANTT. 1972. Perinatal behavior of northern elephant seal females and their young. *Behaviour* 43:121–156.
- LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- LEBRETON, J.-D., G. HEMERY, J. CLOBERT, AND H. COQUILLART. 1990. The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrate populations. I. Transversal models. *Biometrics Journal* 46:609–622.
- LEE, D. E., N. NUR, AND W. J. SYDEMAN. 2007. Climate and demography of the planktivorous Cassin's auklet *Ptychoramphus aleuticus* off northern California: implications for population change. *Journal of Animal Ecology* 76:337–347.
- LEE, D. E., AND W. J. SYDEMAN. 2009. North Pacific climate mediates offspring sex ratio in northern elephant seals. *Journal of Mammalogy* 90:1–8.
- LESCROEL, A., K. M. DUGGER, G. BALLARD, AND D. G. AINLEY. 2009. Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. *Journal of Animal Ecology* 78:798–806.
- MAYFIELD, H. F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456–466.
- MCPHADEN, M. J., S. E. ZEBIAK, AND M. H. GLANTZ. 2006. ENSO as an integrating concept in earth science. *Science* 314:1740–1745.
- METHOT, R. D., AND M. W. DORN. 1995. Biology and fisheries of North Pacific hake (*M. productus*). Pp. 389–414 in *Hake: biology, fisheries and markets* (J. Alheit and T. J. Pitcher, eds.). Chapman & Hall, London, United Kingdom.
- NEVOUX, M., J.-C. BARBRAUD, AND C. BARBRAUD. 2008. Breeding experience and demographic response to environmental variability in the white stork. *Condor* 110:55–62.
- NEVOUX, M., H. WEIMERSKIRCH, AND C. BARBRAUD. 2007. Environmental variation and experience-related differences in the demography of the long-lived black-browed albatross. *Journal of Animal Ecology* 76:159–167.
- NEWTON, I. 1998. Population limitation in birds. Academic Press, San Diego, California.
- OKKONEN, S. R., G. A. JACOBS, E. J. METZGER, H. E. HURLBURT, AND J. F. SHRIVER. 2001. Mesoscale variability in the boundary currents of the Alaska Gyre. *Continental Shelf Research* 21:1219–1236.
- OLLASON, J. C., AND G. M. DUNNET. 1988. Variation in breeding success in fulmars. Pp. 263–278 in *Reproductive success* (T. H. Clutton-Brock, ed.). University of Chicago Press, Chicago, Illinois.
- PFISTER, C. 2005. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences* 95:213–218.
- PIANKA, E. R. 1988. Evolutionary ecology. Harper Collins, New York.
- PINAUD, D., AND H. WEIMERSKIRCH. 2002. Ultimate and proximate factors affecting the breeding performance of a marine top-predator. *Oikos* 99:141–150.
- PISTORIUS, P. A., M. N. BESTER, G. J. G. HOFMEYR, S. P. KIRKMAN, AND F. E. TAYLOR. 2008. Seasonal survival and the relative cost of first reproduction in adult female southern elephant seals. *Journal of Mammalogy* 89:567–574.

- PROMISLOW, D. E. L. 1991. Senescence in natural populations of mammals: a comparative study. *Evolution* 45:1869–1887.
- RATCLIFFE, N., R. W. FURNESS, K. C. HAMER, AND B. SHORROCKS. 1998. The interactive effects of age and food supply on the breeding ecology of great skuas. *Journal of Animal Ecology* 67:853–862.
- REITER, J., AND B. J. LE BOEUF. 1991. Life history consequences of variation in age at primiparity in northern elephant seals. *Behavioral Ecology and Sociobiology* 28:153–160.
- RESSLER, P. H., J. A. HOLMES, G. W. FLEISCHER, R. E. THOMAS, AND K. C. COOKE. 2007. Pacific hake, *Merluccius productus*, autecology: a timely review. *Marine Fisheries Review* 69:1–24.
- ROFF, D. A. 1992. The evolution of life histories—theory and analysis. Chapman & Hall, New York.
- SADLEIR, R.M.F.S. 1969. The ecology of reproduction in wild and domestic mammals. Methuen, London, United Kingdom.
- SÆTHER, B.-E. 1990. Age-specific variation in reproductive performance of birds. *Current Ornithology* 7:251–283.
- SCHWING, F. B., T. MURPHREE, AND P. M. GREEN. 2002. The Northern Oscillation Index (NOI): a new climate index for the northeast Pacific. *Progress in Oceanography* 53:115–139.
- SIMMONS, S. E., D. E. CROCKER, R. M. KUDELA, AND D. P. COSTA. 2007. Linking foraging behaviour of the northern elephant seal with oceanography and bathymetry at mesoscales. *Marine Ecology Progress Series* 346:265–275.
- STATA CORP LP. 2007. STATA statistical software: release 10.0. Stata Corporation, College Station, Texas.
- STEARNS, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, United Kingdom.
- STEELE, J. H. 1998. Regime shifts in marine ecosystems. *Ecological Applications* 8:S33–S36.
- SYDEMAN, W. J., H. R. HUBER, S. D. EMSLIE, C. A. RIBIC, AND N. NUR. 1991. Age-specific weaning success of northern elephant seals in relation to previous breeding experience. *Ecology* 72:2204–2217.
- TRENBERTH, K. E. 1984. Signal versus noise in the Southern Oscillation. *Monthly Weather Bulletin* 112:326–332.
- VIALLEFONT, A., F. COOKE, AND J.-D. LEBRETON. 1995. Age specific costs of first-time breeding. *Auk* 112:67–76.
- WALTHER, G.-R., ET AL. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- WEIMERSKIRCH, H. 1990. The influence of age and experience on breeding performance of the Antarctic fulmar, *Fulmarus glacialis*. *Journal of Animal Ecology* 59:867–875.
- WEIMERSKIRCH, H. 1992. Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the wandering albatross. *Oikos* 64:464–473.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- WILLIAMS, G. C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, New Jersey.
- WOOLLER, R. D., AND J. C. COULSON. 1977. Factors affecting the age of first breeding of the kittiwake *Rissa tridactyla*. *Ibis* 119:339–349.

Submitted 2 February 2010. Accepted 3 December 2010.

Associate Editor was Jane M. Waterman.

Copyright of Journal of Mammalogy is the property of Allen Press Publishing Services Inc. and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.