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NORTH PACIFIC CLIMATE MEDIATES OFFSPRING SEX RATIO IN NORTHERN ELEPHANT SEALS

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Determinants of sex ratios in animal populations have been of general interest to ecologists for decades. We tested the hypothesis that offspring sex ratio in a population of northern elephant seals (*Mirounga angustirostris*) was related to large-scale environmental indices reflecting ocean climate and productivity that affected the condition of reproductive females over 31 years (1976–2006). More males were produced during years of weaker pressure differences and warmer sea surface temperature anomalies in the northeastern Pacific, conditions that reduce or disperse prey resources for gestating females in the North Pacific Ocean. For this species, sexually distinct forage resources exist, so competition for food resources occurs predominately within sex. These results are consistent with the resource competition model for facultative adjustments of offspring sex ratio. Anthropogenic global warming is predicted to warm the North Pacific. This could result in altered basin-scale ocean productivity, increased nutritional stress, and an overabundance of males that may adversely affect this and other similarly regulated mammalian populations.

Key words: climate change, elephant seal, Farallon Islands, *Mirounga*, Northern Oscillation Index, Pacific Decadal Oscillation, Phocidae, sex ratio

Evolutionary theory predicts that parents should invest in offspring in ways that enhance their own lifetime reproductive success (Fisher 1930). Darwin (1871) thought that natural selection controls sex ratio of animals. Selection theoretically should result in an equal offspring sex ratio (probability of a son = 0.5), but vertebrates often deviate from this ideal (Clutton-Brock and Iason 1986; Darwin 1871). Hypotheses concerning adaptive (or facultative) parental adjustment of offspring sex ratio in mammals focus on differences in the expected future reproductive success of the 2 sexes.

The 2 major hypotheses explaining offspring sex-ratio adjustment in mammals are the Trivers–Willard (TW) model (Trivers and Willard 1973) and the resource competition (RC) model (Clark 1978; Silk 1983). Trivers and Willard (1973) postulated that when parental investment affects offspring reproductive success, mothers who can afford to invest heavily (i.e., mothers in good condition) should invest more in the sex with greater variance in reproductive success. In polygynous, sexually dimorphic species, females in good condition could produce larger male offspring that would have a disproportionately higher mating success, therefore the TW model predicts that the sex ratio of offspring should be male-biased during years of abundant food resources (Trivers and Willard 1973). Mothers in poor condition would gain more reproductively from producing daughters than sons because the survival and reproductive success of daughters is usually less affected by low levels of preweaning investment (Clutton-Brock et al. 1988). The RC model (Clark 1978), a generalization of the local mate competition model of Hamilton (1967), proposes that competition for resources between mothers and philopatric offspring imposes a cost of producing offspring of the philopatric sex. This hypothesis predicts that females should bias offspring sex ratio toward the dispersing sex to avoid ecological competition with their offspring. The majority of mammals show female philopatry, whereas males disperse. Therefore, the RC model predicts that if resources are limiting, females should produce a male-biased sex ratio (Dittus 1998; Johnson 1988).

Evidence for environmentally mediated offspring sex-ratio adjustment is equivocal; studies have reported mammalian offspring sex ratios that are male-biased, female-biased, or unbiased in relation to maternal condition (see reviews in Cameron 2004; Clutton-Brock and Iason 1986; Sheldon and West 2004). The strongest evidence of environmentally mediated offspring sex-ratio adjustment resulted from the novel metric of change in maternal condition between previous birth and conception (Cameron and Linklater 2007).

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Northern elephant seals (*Mirounga angustirostris*) have many traits that make them excellent for examining sex-ratio theory. They are a highly polygynous, sexually dimorphic species where body size is important in winning fights (Armitage 1987; Clutton-Brock et al. 1981; Clutton-Brock and Iason 1986; Le Boeuf 1974). Variance in lifetime reproductive success is approximately 4 times greater among males than females (Le Boeuf and Reiter 1988). Estimation of parental investment is simple because male elephant seals invest nothing in their offspring except DNA (Le Boeuf et al. 1989). Single pups are born annually and receive all preweaning nourishment from their mother's milk; females fast completely during the 24- to 28-day lactation period. No postweaning investment occurs; females go to sea immediately after weaning their pups, and no subsequent contact occurs (Le Boeuf and Briggs 1977; Reiter et al. 1978). Weanling mass in both sexes is a function of mother's size, which increases with age (Le Boeuf 1994; Reiter et al. 1981) but varies interannually (Le Boeuf et al. 2000), and interannual variability is more important in determining the mass of a weaned pup than its sex. Offspring sex ratio does not vary with maternal age, the main determinant of female size and dominance (Le Boeuf et al. 1989). Although males on average weigh more than females at weaning, there is no evidence of differential maternal investment relative to sex of pups in northern elephant seals, nor in its Southern Hemisphere congener (Deutsch et al. 1994; Fedak et al. 1994; Le Boeuf et al. 1989; McCann et al. 1989). Furthermore, sons are not more costly to produce than daughters when cost is measured in units of the mother's future reproduction: the sex of the pup raised the previous year has no effect on the mother's survival, pregnancy rate, sex of the next pup, or weaning success the following year (Le Boeuf et al. 1989). The reproductive success of 1st-time breeding females is no different in this regard than that of experienced females (Le Boeuf et al. 1989). Moreover, because females rapidly recover energy lost during lactation when they return to sea (LeBoeuf et al. 1989), the best maternal strategy apparently is to feed the pup as much as possible, whatever its sex. There also is no evidence that females giving birth early in the season (cf. Coulson and Hickling 1961; Stirling 1971) bias the sex of their offspring (Reiter et al. 1981). In the RC model framework, males can be considered the dispersing sex because sexually distinct foraging grounds exist (Le Boeuf et al. 2000), and based on dive profiles, sexes seem to exploit different prey resources (Le Boeuf 1994), so competition for food resources occurs predominately within sex.

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 Tahiti High and Darwin (Australia) Low. Therefore, ENSO events are often examined relative to the Southern Oscillation Index (SOI—Trenberth 1984). A positive SOI is related to strong Pacific trade winds, westward intensification, and thermocline shoaling in the eastern tropical Pacific. 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 influence the North Pacific High and other pressure cells of the North Pacific. A relatively new indicator of atmospheric pressure gradients is the Northern Oscillation Index (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. In this case, positive values of the NOI are reflective of productive La Niña–like variability in ocean productivity, and strong winds associated with upwelling along the west coast of North America.

During El Niño events, warm water intrusion up the west coast of North America to British Columbia and southeastern Alaska shifts the usual foraging area of females northward and farther away from California rookeries (Fulton and LeBrasseur 1985). Under these conditions, female elephant seals spend more time foraging, gain less mass than usual, begin breeding later, and show lower fecundity (Crocker et al. 2006; Huber et al. 1991; Le Boeuf et al. 2000; Le Boeuf and Reiter 1991). Warm-water years, such as during an El Niño characterized by a negative NOI, clearly constitute low prey resource conditions for breeding female elephant seals (Le Boeuf and Crocker 2005).

We investigated the annual variation in offspring sex ratio of northern elephant seals born at Southeast Farallon Island, California, between 1976 and 2006 in relation to ocean climate and large-scale atmospheric pressure cell oscillations. The atmospheric conditions were indexed by the SOI and NOI. Ocean conditions in the foraging realm of the northern elephant seal were provided by the Pacific Decadal Oscillation (PDO, see below). We hypothesized that climate variability affects sex-ratio variation as follows: In high-resource (La Niña) years, the TW model predicts more male pups. In low-resource (El Niño) years, the RC model predicts more male pups, whereas the TW model predicts more female pups.

Materials and Methods

Biologists from PRBO Conservation Science (formerly Point Reyes Bird Observatory) collected data on the sex of northern elephant seal pups born on the Farallon National Wildlife Refuge, 43 km west of San Francisco, California (37.6°N, 123°E), over 31 years (1976–2006). Breeding female elephant seals were individually marked with hair dye (Clairol, Stamford, Connecticut) upon arrival and monitored daily during the breeding season (~15 December–15 March each year). Pups were marked with hair bleach 24 h after birth and monitored daily. Sex of pups was determined during the nursing period, at pup death, or after weaning. There is no difference in observability of pups according to sex, or in relation to fate of the pup (weaned or not weaned), although the sex of some pups that disappeared before weaning was not determined. Sex was determined for 3,107 pups, with a mean annual

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sample of 100 (minimum = 22, maximum = 220), over the 31-year period. Sex was not determined for all pups every year; the mean proportion of total pups for which sex was determined was 0.59 (minimum = 0.19, maximum = 1.0). Table 1 presents the data used in this analysis. We considered our sample to be representative of sex ratio at birth. We do not believe there were significant biases affecting which pups had their sex determined and treated the known-sex group of pups as a random sample of pups each year. Our field protocol followed the guidelines of the American Society of Mammalogists (Gannon et al. 2007).

We examined 17 environmental covariate models relative to a constant model and a year-specific model of annual variation in sex ratio, defined as the probability a given pup was male. The probability that an individual pup was male was analyzed using a generalized linear model procedure with binomial error structure and a logit link function in program STATA 8.2 (STATACorp, College Station, Texas). Model structure was: sex ratio, or probability a given pup was male = exp(covariate × coefficient)/[1 + exp(covariate × coefficient)]. We ranked and selected models using Akaike's information criterion (AIC). We used analysis of deviance (ANODEV) to determine significance of covariate models and the amount of variation they explained (Skalski et al. 1993).

Our 17 environmental covariate models were derived from 3 ocean climate indices that are metrics of the atmosphere, the ocean, ENSO phenomena, and the northeastern Pacific where female elephant seals forage: SOI, NOI, and PDO. The SOI and NOI are physical forcing mechanisms because changes in pressure gradients influence winds and primary productivity in the ocean. Positive SOI values indicate strong Pacific trade winds (La Niña); negative values indicate the reversal of Pacific trade winds (El Niño). NOI is the difference in sea level pressure between the North Pacific High off the California coast and the Equatorial Pacific Low off Darwin, Australia. NOI relates to strength of prevailing wind patterns for the northeastern Pacific (Schwing et al. 2002). 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. The PDO is the 1st principal component of monthly sea surface temperature anomalies in the North Pacific Ocean poleward of 20°N. The monthly mean global average sea surface temperature anomalies are removed to separate this pattern of variability from any ''global warming'' signal that may be present in the data (Mantua et al. 1997; Zhang et al. 1997). The PDO reflects ocean climate conditions (North Pacific sea surface temperature anomalies) but is not based on the physical atmospheric–oceanographic mechanisms that produced the signal. The marine ecological response to PDO-related environmental changes starts with phytoplankton and zooplankton at the base of the food chain and works its way up to top-level predators (Francis and Hare 1994; Francis et al. 1998; Hare and Francis 1995; Roemmich and McGowan 1995).

Our model set included annual values for each index (the average of 12 monthly values), seasonal averages of monthly values (winter = January–March, spring = April–June, summer = July–September, autumn = October–December), as well as a constant and year-specific model for a total of 17 climate index environmental covariate models. We chose to examine seasonal values with the expectation that if a seasonally specific model best explained annual variation in sex ratio, the timing of sex-ratio adjustment (pre- or postfertilization), and thus the underlying mechanism, could be determined. Based on the literature and existing theory, we also examined 3 additional covariates that may have influenced offspring sex ratio: adult sex ratio during conception, median age of the female breeding population, and population density (measured as total population size from National Oceanic and Atmospheric Administration stock assessments, and local population size at Southeast Farallon Island). We considered these to be ''nuisance'' variables to our main interest in climate–sex ratio covariation.

Table 1.—Number of known-sex pups, number of male pups, and sex ratio of northern elephant seal (*Mirounga angustirostris*) pups born at the Farallon Islands, California, 1976–2006.

Year	Known-sex pups	Males	Sex ratio (males/total)
1976	56	26	0.464
1977	97	60	0.619
1978	107	57	0.533
1979	104	41	0.394
1980	92	48	0.522
1981	96	59	0.615
1982	115	60	0.522
1983	144	66	0.458
1984	152	78	0.513
1985	167	88	0.527
1986	154	82	0.532
1987	116	64	0.552
1988	120	69	0.575
1989	220	127	0.577
1990	184	83	0.451
1991	144	78	0.542
1992	128	53	0.414
1993	116	59	0.509
1994	61	33	0.541
1995	22	13	0.591
1996	20	11	0.550
1997	38	20	0.526
1998	30	24	0.800
1999	89	44	0.494
2000	24	12	0.500
2001	46	28	0.609
2002	30	16	0.533
2003	19	12	0.632
2004	42	22	0.524
2005	86	45	0.523
2006	115	61	0.530

Results

Offspring sex ratio across the study was slightly male-biased (probability of male pup = 0.523, *SE* = 0.012, 2-sided binomial test $P = 0.034$). Annual variation in the probability that a pup was male was best modeled by the environmental covariate of summer NOI (Table 2; Fig. 1). Summer NOI was statistically significant (ANODEV, $F = 6.83$, *d.f.* = 1, 30,

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TABLE 2.—Model selection results for ocean climate covariates of offspring sex ratio of northern elephant seal (*Mirounga angustirostris*) pups born at the Farallon Islands, California, 1976–2006. Asterisks indicate significant (ANODEV $P < 0.05$) covariates.

Model[a]	k	AIC	ΔAIC	Deviance
NOI summer*	2	4,298.14	0.00	4,294.1
PDO*	2	4,301.41	3.27	4,297.4
PDO summer	2	4,302.24	4.10	4,298.2
PDO spring	2	4,302.25	4.11	4,298.3
NOI winter	2	4,304.00	5.86	4,300.0
PDO winter	2	4,304.17	6.03	4,300.2
SOI spring	2	4,304.38	6.24	4,300.4
NOI spring	2	4,304.66	6.52	4,300.7
Constant	1	4,304.66	6.52	4,302.7
PDO autumn	2	4,304.93	6.79	4,300.9
SOI autumn	2	4,305.64	7.50	4,301.6
SOI summer	2	4,306.24	8.10	4,302.2
SOI winter	2	4,306.43	8.29	4,302.4
NOI	2	4,306.56	8.42	4,302.6
NOI autumn	2	4,306.63	8.49	4,302.6
SOI	2	4,306.66	8.52	4,302.7
Year	31	4,321.26	23.12	4,259.3

[a] NOI = Northern Oscillation Index; PDO = Pacific Decadal Oscillation; SOI = Southern Oscillation Index.

$P = 0.014$), and the negative relationship explained 20% of the annual variation in pup sex ratio (ANODEV; Fig. 2). Negative summer NOI values (El Niño; weak North Pacific High relative to Darwin Low) resulted in a higher probability of male pups born at the Farallon Islands 4–6 months later. The 2nd-ranked model, average PDO during the entire year leading up to the breeding season (Table 2), also was a significant covariate (ANODEV, $F = 4.57$, $d.f. = 1, 30$, $P = 0.041$), and the positive relationship (warm sea surface temperature and higher probability of male pup) explained 12% of the annual variation in pup sex ratio. No other covariate models were significant, although several were ranked above the constant (null) model. We found that adult sex ratio during conception, population density, and maternal age were not ranked above the null model. These nuisance covariates also did not significantly improve our top 2 climate models as additive effects, and were thus not confounding our ocean climate results.

DISCUSSION

We documented significant overall male bias and temporal variation in sex ratio of northern elephant seal pups born at the Farallon Islands between 1976 and 2006. Sex ratio of pups varied with atmospheric–oceanographic conditions. Years of weak NOI or warm water temperatures in the North Pacific are low-resource years for breeding females (Crocker et al. 2006), and these poor foraging seasons apparently resulted in a higher proportion of male pups born at the Farallon Islands. This result is more consistent with the predictions of the RC model of sex-ratio adjustment than with the TW model because the sexes exploit different foraging resources, and sons are not likely to compete with their mothers for forage resources as they mature. This is a relatively novel finding. Le Boeuf and Crocker (2005) found that sex ratio at weaning for another California northern elephant seal rookery did not deviate significantly from parity over the past 4 decades; however, marginally more males were weaned there during a warm period in the Pacific Decadal climate regime (1990–1999) when weaning mass also was lower due to poor foraging conditions for pregnant females. The annual ENSO pattern we detected may be revealing a trait that is adaptive over longer-period cycles. PDO cycles are much longer than ENSO and give ample time for reproductive females to compete with their daughters during warm periods, and our PDO model was the only other significant correlate of offspring sex ratio in our model set. Our results indicate that offspring sex ratio is clearly affected by climatically induced nutritional stress in gestating females, but the exact nature and timing of the signal that females respond to requires further investigation.

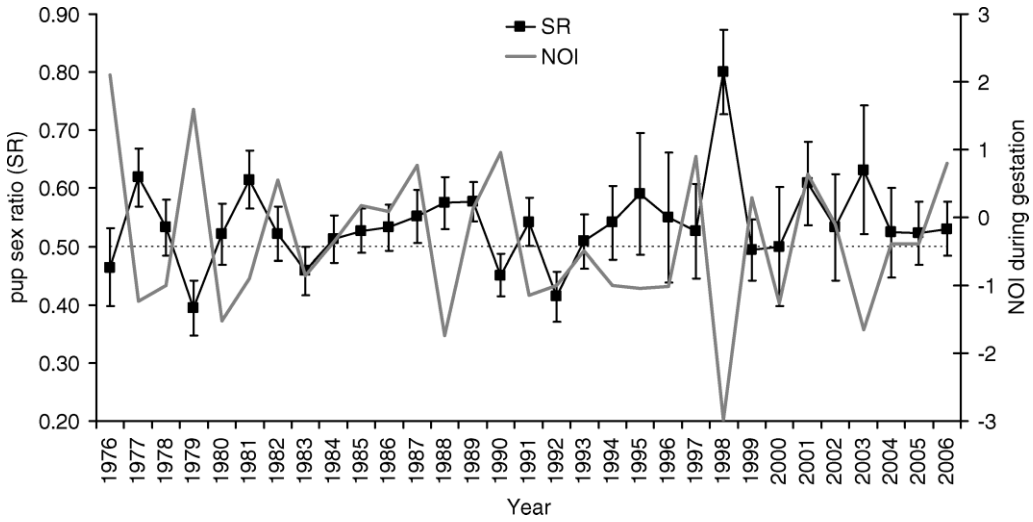


FIG. 1.—Annual values of summer Northern Oscillation Index (NOI), the primary El Niño signal in northern latitudes, and offspring sex ratio (SR) of northern elephant seals (*Mirounga angustirostris*) born at the Farallon Islands, California, 1976–2006.

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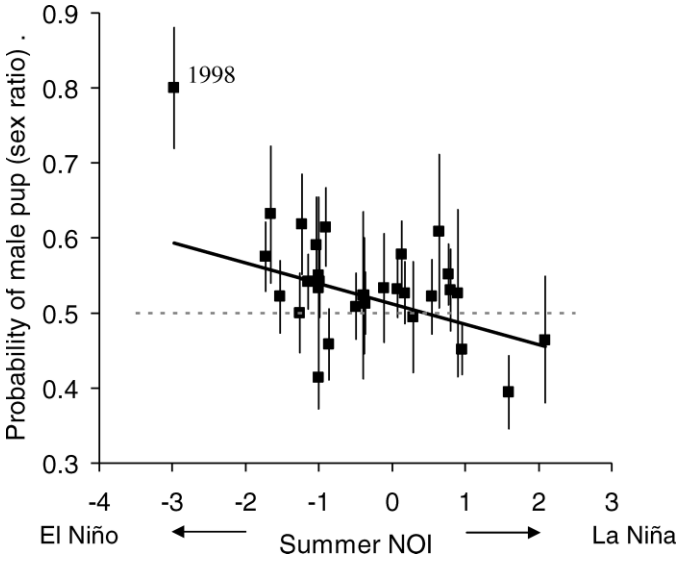


Fig. 2.—Relationship between offspring sex ratio in northern elephant seals (*Mirounga angustirostris*) and summer values of the Northern Oscillation Index (NOI). Annual probabilities (black squares) and their standard errors are shown. Dashed line at 0.5 on y-axis designates an equal sex ratio. Regression coefficient: −0.109 (± 0.037 *SE*), $z = -2.91$, $P = 0.004$. NOI explained 20% of the annual variation in sex ratio (ANODEV). The relationship remains significant with the 1998 data point removed. Data are from the Farallon Islands, California, 1976–2006.

Previous workers have reported how environmental conditions and maternal nutrition affect offspring sex-ratio patterns in other species. Vergani et al. (2004) found that the sex ratio of pups of southern elephant seals (*M. leonina*) was in accordance with the TW model, with a female bias in poor forage years and a male bias during good and ''normal'' years as determined by a sea surface temperature index of the South Pacific. Kruuk et al. (1999) found the proportion of red deer (*Cervus elaphus*) calves born each year that were males declined with increasing population density and winter rainfall, both environmental variables associated with maternal nutritional stress during pregnancy. Thomas et al. (1989) also found support for the TW model among caribou (*Rangifer tarandus pearyi* and *R. t. groenlandicus*) with differential maternal condition. Conversely, several other studies of ungulates found female-biased offspring sex ratios when maternal nutrition was high (Hoefs and Nowlan 1994; Pederson and Harper 1984; Sachdeva et al. 1973; Verme 1969).

Mechanisms proposed to explain the skewing of sex ratios in mammals are of 2 classes, those that operate before conception, and those that favor 1 sex over the other after fertilization (Rosenfeld and Roberts 2004). Northern elephant seals have delayed implantation, where fertilization occurs 12 months before birth, whereas gestation lasts only 8 months. Because sex ratio was best explained by conditions 4–6 months before birth, we consider the 2 mechanisms that operate post-conception. First, differences between XX and XY embryos in the rate of development or in sensitivity to conditions within the female reproductive tract can cause a selective loss of embryos of 1 sex before placentation. Second, mothers also may be able to selectively resorb or abort fetuses according to sex (Rosenfeld and Roberts 2004).

Selective resorption–abortion or sensitivity of embryos to maternal condition seem the most likely mechanisms of sex-ratio adjustment in this case, rather than differences in developmental rate. The overall slightly male-biased sex ratio of northern elephant seal pups is expected for sexually dimorphic species because male juveniles are generally less viable than females (Clutton-Brock et al. 1985). If the sex-specific mortality of juveniles applies to fetuses (McMahon and Burton 2005), the opposite of the observed climate-related sex-ratio bias should be present. Male pups are larger, thus male fetuses have a faster rate of growth requiring more food, and should, therefore, be more adversely affected by food limitations. Male fetuses should be more vulnerable than female fetuses to nutritional stress during gestation (Kruuk et al. 1999), resulting in more females during El Niño, not fewer as we observed. Thus, energetic demands seem not to be the underlying sex-ratio adjustment mechanism, but female embryos may be more sensitive to maternal nutritional stress via hormonal or nutrient signals (Rosenfeld and Roberts 2004). Any number of physiological signals could function as the proximate cue for sex-specific fetal resorption. For example, male and female conceptuses are sexually dimorphic in their response to glucose (Gutierrez-Adan et al. 2001) and sex ratio can be affected by different glucose concentrations during development (Larson et al. 2001).

An alternative explanation of our results is possible based on differential breeding propensity (natality) and mass-specific offspring sex ratios. Because elephant seals exhibit largely indeterminate growth, older females are larger and have significantly greater resources available for investment in reproduction than do young, small females (Le Boeuf 1994). In southern elephant seals, larger females produce more male pups (Wilkinson and van Aarde 2001). Ocean climate impacts breeding propensity (Crocker et al. 2006; Huber et al. 1991), with small females less likely to breed than large females. This could lead to male-biased sex ratios in years with impacts to breeding propensity. In other words, more male pups are born in years when only the older, large females give birth. However, we found no effect of maternal age and population density in our models, so these intrinsic variables may provide less-than-compelling interpretations of our results.

Some climate models have indicated significant increases in variability, and in the magnitude of ENSO extremes, as the Earth warms due to anthropogenic global warming (Intergovernmental Panel on Climate Change 2001). An increase in El Niño variability should not shift the population sex ratio of northern elephant seals, so long as the frequency and intensity of El Niño relative to La Niña years remains close to parity. However, anthropogenic global warming may result in an increasingly warm North Pacific similar to an extremely warm, long-term PDO regime (Overland and Wang 2007), which could result in generally decreased productivity with an overabundance of males that may adversely affect this and other similarly regulated mammalian populations.

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Appendix I

Model assumptions.—The TW model is dependent upon 3 assumptions: 1) maternal condition during the period of parental investment is correlated with the condition of offspring at the end of parental investment; 2) differences in the condition of young at the end of parental investment endure into adulthood (thus potentially affecting reproductive success); and 3) slight advantages in condition should have a greater effect on male reproductive success in polygynous species wherein males compete for mates while females do not (see reviews in Clutton-Brock and Iason 1986; Cockburn 1990; Hewison and Gaillard 1999). The RC model requires that: 1) a limited resource exists; 2) access to this resource affects reproductive success; and 3) philopatry of 1 sex results in competition with mothers (Silk 1983). Both models assume that our sample of pups was random, and represented the true sex ratio of all pups born.

Data are lacking to know if northern elephant seals explicitly meet TW model assumptions. Although the condition of weanlings at the end of the period of parental investment is

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correlated with maternal condition (TW assumption 1—Crocker et al. 2006; Deutsch et al. 1994), it is unclear whether differences in the condition of males at the end of parental investment endure into adulthood (TW assumption 2—Le Boeuf et al. 1994), and condition of male weanlings has not been proven to affect reproductive success (TW assumption 3). There is apparently no survival benefit of increased weanling mass in northern elephant seals (Le Boeuf et al. 1989, but see McMahon and Burton [2005] for southern elephant seals), but the relationship of weanling mass to all lifetime fitness components has not been fully examined. An alternative TW model holds that if condition at weaning confers advantage on females but not males, the ''advantaged daughter'' (AD) model is applicable (Hewison and Gaillard 1999; Hiraiwa-Hasegawa 1993; Simpson and Simpson 1982). The advantaged daughter model predicts that mothers in good condition should invest more in daughters than in sons if maternal care affects the fitness of daughters more strongly than the fitness of sons, for example through inheritance of social rank (see Leimar 1996). The fact that dominance of females is largely explained by age-related mass increases, yet female age does not affect pup sex argues against the advantaged daughter model. However, the effects of dominance and maternal condition should be integrated in future analyses where both data are known (Dittus 1998). Northern elephant seals meet the requirements of the RC model because during El Niño, food can be considered a limited resource (Crocker et al. 2006), access to this resource affects reproductive success (Le Boeuf and Reiter 1991), and females are most likely to compete for forage with their mothers (Le Boeuf et al. 2000). Further research into the inheritance of female dominance is needed to determine definitively whether the sex-ratio adjustment we documented is entirely attributable to the RC model, or if the advantaged daughter model also is applicable.

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