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ARTICLE

Male and female pups of the highly sexually dimorphic northern elephant seal (*Mirounga angustirostris*) differ slightly in body size

E. Salogni, F. Galimberti, S. Sanvito, and E.H. Miller

Abstract: In mammals, males generally are larger than females, though such sexual-size differences have been documented primarily in adults and are relatively poorly known in early life. We studied sexual-size differences in pups of the northern elephant seal (*Mirounga angustirostris* (Gill, 1866)), which in adulthood is one of the most sexually dimorphic mammals. We studied body size at birth and weaning, at Islas San Benito, Mexico, at the southernmost limit of the species' breeding range. Males were 10% heavier and 2% longer than females at birth. Sexes did not differ significantly in either measure of body size at weaning, although males were slightly heavier (4%) and longer (1%) than females. Neither growth rate nor suckling duration differed between the sexes. In previous studies in California, USA, pups at weaning were heavier than in our study, and males were heavier than females. These differences may reflect ecological, temporal, or life-history differences across populations. The modest difference in sexual-size dimorphism early in life in this species compared with the great difference in adulthood likely reflects multiple selective forces, including constraints on neonatal size set by body size of females, and the weakness of sexual selection at that stage of life.

Key words: sexual-size dimorphism, early growth, neonatal body mass, northern elephant seal, *Mirounga angustirostris*, pinnipeds, Islas San Benito, Baja California.

Résumé : Chez les mammifères, les mâles sont généralement plus grands que les femelles, de telles différences entre les sexes ayant toutefois été documentées principalement chez des adultes, leur présence aux premières étapes du cycle de vie n'étant pas très bien établie. Nous avons étudié les différences de taille associées au sexe chez des chiots d'éléphants de mer boréaux (*Mirounga angustirostris* (Gill, 1866)), une espèce dont les adultes sont parmi les mammifères présentant le plus important dimorphisme sexuel. Nous avons étudié la taille du corps à la naissance et au moment du sevrage dans les îles San Benito (Mexique), à l'extrémité sud de l'aire de reproduction de l'espèce. À la naissance, la masse des mâles était de 10 % supérieure et leur longueur, de 2 % supérieure à celles des femelles. Au moment du sevrage, il n'y avait pas de différence significative entre les sexes pour l'une ou l'autre de ces mesures, les mâles étant toutefois légèrement plus lourds (4 %) et plus longs (1 %) que les femelles. Aucune différence du taux de croissance ou de la durée de l'allaitement n'a été observée entre les sexes. Dans des études précédentes en Californie (États-Unis), les chiots au moment du sevrage étaient plus lourds que dans l'étude actuelle, et les mâles étaient plus lourds que les femelles. Ces différences pourraient refléter des différences écologiques, temporelles ou associées au cycle biologique entre les populations. Le dimorphisme sexuel modeste de la taille tôt durant la vie chez cette espèce comparée à la grande différence chez les adultes reflète vraisemblablement différentes forces de sélection, dont des contraintes sur la taille des nouveau-nés imposées par la taille du corps des femelles, et la faiblesse de la sélection sexuelle à cette étape du cycle biologique. [Traduit par la Rédaction]

Mots-clés : dimorphisme sexuel de la taille, croissance précoce, masse corporelle des nouveau-nés, éléphant de mer boréal, *Mirounga angustirostris*, pinnipèdes, îles San Benito, Basse-Californie.

Introduction

Secondary sexual differences have evolved in relation to life history, ecology, mating system, and sexual selection (Willner and Martin 1985; Weckerly 1998; Lindenfors et al. 2007; González-Suárez and Cassini 2014). In mammals, sexual dimorphism in body size is common, and males typically are the larger sex (Lindenfors et al. 2007; McPherson and Chenoweth 2012). Male-biased dimorphism in body size can be high in polygynous species (Weckerly 1998), in which males compete physically among themselves to get access to breeding females, and hence large size can be important for winning contests or extending a male's breeding tenure (Bartholomew 1970; Clutton-Brock 1989; Mesnick and Ralls 2018). Evolutionarily, sexual-size differences can arise before polygyny, however, as a result of natural selection related to foraging and resource use (Cullen et al. 2014; Krüger et al. 2014; Berta et al. 2018). Information about body size and growth in early life is important for understanding the evolution and characteristics of sexual-size differences in breeding adults (Willner and Martin 1985; Badyaev 2002). As those differences are the result of growth processes that may differ between the sexes, it is important to

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E. Salogni. Department of Biology, Memorial University of Newfoundland, St. John's, NL A1B 3X9, Canada; Elephant Seal Research Group, Sea Lion Island, Falkland Islands, FIQQ 1ZZ.
F. Galimberti and S. Sanvito. Elephant Seal Research Group, Sea Lion Island, Falkland Islands, FIQQ 1ZZ.
E.H. Miller. Department of Biology, Memorial University of Newfoundland, St. John's, NL A1B 3X9, Canada.

Corresponding author: E. Salogni (email: es0773@mun.ca).

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know what affects growth rate and duration, how they change through time, and how selection acts on them (Badyaev 2002).

For polygynous species in which the sexes differ in body size, mothers that are large or in good condition should allocate more resources to sons than to daughters, because sons may have higher reproductive success (Trivers and Willard 1973; Cockburn et al. 2002; Bowen 2009; Lukas and Clutton-Brock 2014). Maternal investment has two energetically expensive components: gestation and lactation (Gittleman and Thompson 1988). Neonatal mass can be viewed as a proxy of a female's gestational effort, as it is related to her costs in producing and carrying the fetus, and to her foraging success throughout pregnancy (Gittleman and Thompson 1988; Smith and Leigh 1998; McMahon and Hindell 2003). However, neonatal mass can be constrained by the size of the mother (Badyaev 2002). Mass of a litter at weaning is influenced not only by the quantity and quality of a mother's milk (Badyaev 2002), but also by maternal body size, age, social rank, and external factors such as the site and timing of parturition (Reiter et al. 1981; Côté and Festa-Bianchet 2001; Weladji et al. 2006; Bowen 2009).

Pinnipeds are well suited for studies of sexual-size dimorphism because species vary substantially in mating system, body size, sexual-size differences, and maternal care (Lindenfors et al. 2002; Schulz and Bowen 2004; Ferguson 2006; Ferguson and Higdon 2006), and they include the most polygynous and sexually size dimorphic species of all mammals (Weckerly 1998; Lindenfors et al. 2007). Moreover, some pinniped species are used as classic examples of the evolution of large size in males through intrasexual selection (Weckerly 1998; Lindenfors et al. 2007).

Young pinnipeds vary greatly in body size at birth and weaning, and in the quality and quantity of milk provided by mothers, which is related to body size (Fedak et al. 1996; Schulz and Bowen 2004). This is especially true of phocids, which are capital breeders that usually produce one offspring at a time and in which offspring rely solely or mainly on energy obtained through nursing (Crocker et al. 2001).

Sexual-size differences have been well studied in adult pinnipeds (McLaren 1993; Lindenfors et al. 2002; Fitzpatrick et al. 2012). In fur seals and sea lions (Otariidae), as well as in walruses (Odobenidae), adult males are larger than females, a difference that is already present at birth (Fay 1982; Kovacs and Lavigne 1992*b*; Mesnick and Ralls 2018). For example, for otariid species reported on by Kovacs and Lavigne (1992*b*), males were 9%–23% larger than females in neonatal body mass. In contrast, sexual-size differences in adult seals (Phocidae) are weak to moderate, with the exception of the two species of elephant seal: northern elephant seal (*Mirounga angustirostris* (Gill, 1866)) and southern elephant seal (*Mirounga leonina* (Linnaeus, 1758)) (Mesnick and Ralls 2018). In the latter species, where differences in early life are well documented, males tend to be larger than females at birth (McMahon et al. 1997; Wilkinson and van Aarde 2001) and at weaning (Arnbom et al. 1993; McMahon et al. 1997, 2017; Wilkinson and van Aarde 2001; Oosthuizen et al. 2015; Clausius et al. 2017*a*).

Sexual-size dimorphism early in life in northern elephant seal pups has been studied less. For example, little information about neonatal body size is available, and most comes from studies of the northernmost breeding colonies in central California, USA, which may not be representative of the entire breeding range. A few reports suggest that males are larger than females at birth at Año Nuevo State Park (California) (Reiter et al. 1981; Le Boeuf et al. 1989). Studies also report a male-biased sexual-size dimorphism at weaning, but published results vary, even within related data sets (Reiter et al. 1978; Le Boeuf et al. 1989; Kretzmann et al. 1993; Le Boeuf and Crocker 2005). Information on body length at birth and weaning is scarce and rarely addresses sexual-size dimorphism (Stewart 1989; Deutsch et al. 1994; Noren et al. 2003).

The great sexual-size dimorphism in adult elephant seals led us to hypothesize that the sexes may also differ substantially in body size as pups. Our main goals were to (*i*) study neonatal and weaning body size of northern elephant seals in the southernmost breeding colony of the species, at Islas San Benito (Baja California, Mexico), and reduce the gap in the literature about the Mexican colonies; (*ii*) analyze sexual differences in body mass, body length, and growth of pups to improve knowledge about sexual-size dimorphism in early life in this species; and (*iii*) compare our results with existing literature on northern Californian colonies to determine whether differences exist across colonies in body size and sexual-size dimorphism, as expected from observations on southern elephant seals.

For common and scientific names of pinnipeds, we follow The Society of Marine Mammalogy (2018).

Materials and methods

Study area and demography of the colony

We studied elephant seals at the Islas San Benito (28°18′N, 115°35′W), an archipelago of three islands located ~25 km west of Isla de Cedros (Baja California, Mexico). Our study areas were located on two islands: Isla San Benito Medio (hereafter SBM) and Isla San Benito Oeste (hereafter SBO). Data were collected during two breeding seasons (2006–2007, 2007–2008) at SBM and during one breeding season (2006–2007) at SBO, as a part of a long-term study on behavioural ecology of the species (http://www.eleseal.org/).

The population of northern elephant seals in Baja California has been declining since the 1990s (Elorriaga-Verplancken et al. 2015; García-Aguilar et al. 2018). At Islas San Benito, the population has been declining since 2000 (Elorriaga-Verplancken et al. 2015) and, during the period of our study (2001–2010), the population decreased at SBM but changed little at SBO (F. Galimberti, unpublished data). We monitored all harems in the study area, which varied in size from 2 to 329 females at the peak of female numbers on shore.

We marked females and pups by placing a numbered tag (Jumbo Rototags, Dalton Supplies Ltd.) in the interdigital membrane of each rear flipper and by painting names and codes on their flanks with a 4:1 mixture of hydrogen peroxide and commercial hair bleach (Decolorante Anven Premium 350 g, Anven, http://anven.mx/). We carried out daily counts by walking along all breeding beaches at low tide and recording all marked individuals. We recorded arrivals and departures of females, plus births, weaning, abandonments, and deaths of pups. The research protocol for fieldwork was approved under a research licence granted by the Secretaría de Medio Ambiente y Recursos Naturales (see Acknowledgements) and it was in accordance with established guidelines (Gales et al. 2009; Sikes and Gannon 2011).

Weighing and measuring

We weighed 207 newborn pups and 248 weanlings and measured the body length of 176 pups at birth and 56 pups at weaning. Of these pups, measurements of body mass at both birth and weaning were obtained for 85 pups, whereas body lengths at both times were obtained for 18 pups. We restrained pups by hand and weighed them with a weighing bag suspended to a 500 kg digital dynamometer (precision ±0.1%; DIN1ETS, CAMI Paviglianiti, http://www.cami-it.com/). At birth we lifted pups by hand, attaching the dynamometer to an aluminum pole; at weaning we lifted them using a winch with the dynamometer attached to an aluminum tripod. Dynamometer accuracy was checked before and after each weighing session by weighing an object of known mass (120 kg). We measured newborn body length as the straight-line distance from nose to tail, with pups on the venter on a measuring board (ventral body length (VBL)); we measured weaned pups only on SBM in 2007–2008, by laying them on their back and using a measuring tape (standard body length (SBL)).We converted VBL at birth to SBL using a relationship obtained on a sample of dead pups (linear regression: SBL = 10.63 + 0.93·VBL, n = 35, R^2 = 0.96,

$b = 0.93$, SE(b) = 0.032, 95% CI(b) = 0.87, 1.00 (where 95% CI is 95% confidence interval)). Repeatability was calculated from three measurements of the same individual and was high for all variables (birth mass: $n = 23$, $R = 0.998$; birth length: $n = 28$, $R = 0.980$; weaning mass: $n = 43$, $R = 1.000$). Repeatability was not calculated for weaning length.

Selection of individuals for analysis

We included only newborn pups measured within 4 days from the date of birth in our analyses and excluded twins. We determined the date of birth by direct observation of births or from the daily identifications of females, in which we noted their reproductive status (pregnant; with pup; without pup). For females for whom parturition was not observed, we excluded all individuals that had gaps greater than 2 days in their serial identifications. We observed the births of 70% of the 207 pups weighed at birth (56% in 2006–2007 and 82% in 2007–2008) and 44% of 248 pups weighed at weaning (14% in 2006–2007 and 57% in 2007–2008). For mother–pup pairs in which birth was not observed, we assumed that a female was the mother of a pup if she was seen with that pup in more than 80% of her identifications in which a pup was present, and if the pup was seen with that female in more than 80% of its identifications in which it was with a female.

For analysis of weaned pups, we considered only pups with known weaning dates. We excluded all pups that were abandoned, dead, adopted, nursed by more than one female, or twins. We also excluded three pups with nursing periods <20 days, because this is an unusually short suckling period (mean ~4 weeks; Le Boeuf and Laws 1994), and a single pup with a nursing period of 48 days. The date of weaning was based on the date of the observed return to sea of the mother or the serial identifications of the pups, in which the pup status was recorded (i.e., with mother or weaned). If we had information only from serial identifications of a pup, then we considered the first day it was observed as a weaned pup to be the weaning date and we excluded pups with gaps greater than 2 days in their serial identifications.

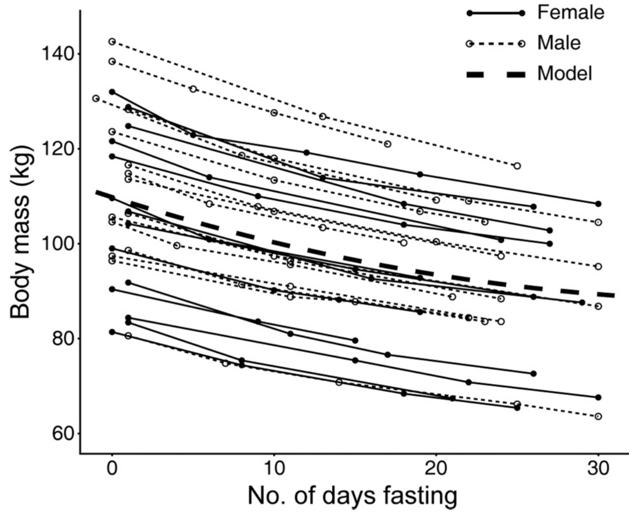
We determined the sex of pups from two sources: daily identification records and handling records. We attributed sex to pups only if there were at least two identical sex determinations. In cases of conflicting data, we attributed the sex that was recorded in at least 80% of observations.

Data analysis

We used linear models to analyze body mass and body length, with different fixed effects. We included the combination of island and year as a categorical variable (island–year) with three levels (SBO 2006–2007, SBM 2006–2007, and SBM 2007–2008). We checked residuals for homogeneity and normality. In the analysis of newborn body mass and body length, weaning mass, and duration of nursing, we modelled the effects of sex, island–year, and the number of days from the peak number of females on land. In the estimation of growth rate in body mass, calculated by subtracting neonatal mass from weaning mass and dividing by the number of days of nursing, we modelled the effects of birth mass, sex, and the number of days from the peak number of females on land. In estimating growth in body length, we modelled the effects of birth length and sex. In the estimation of weaning length, we modelled the effects of sex, duration of lactation, and the number of days from the peak number of females on land. The duration of lactation was not included in the model of weaning mass because, from an exploratory graph (Supplementary Fig. S1)[1], there was no evidence of an effect and including it in the linear model would have greatly reduced sample size.

Weaning mass was measured within 1 week after weaning (of 248 weaned pups, 42 were weighed at weaning, 57 were weighed 1 day after weaning, and 149 were weighed during the 1st week after weaning). We modelled the decline in body mass after weaning using a mixed-effects model (Laird and Ware 1982), and we predicted body mass at weaning for those individuals weighed the first time within 7 days after the date of weaning to include them in the analysis. The initial data for this model included only individuals weighed at least three times during the first 30 days of fasting and comprised 29 individuals (14 females and 15 males; 15 were weighed three times, 12 were weighed four times, and 2 were weighed five times). We limited our analysis to this period of time, as a previous study reported a decrease in mass loss after the first 4 weeks of fasting (Rea and Costa 1992). Mixed models were compared by maximum likelihood. Based on Akaike's information criterion (AIC; Johnson and Omland 2004), the mixed model that best predicted the decrease of weaning mass in pups in the first 30 days of fasting was quadratic, with days of fasting as a fixed factor and a random intercept represented by the identity of the individuals ($y = 109.79 - 1.0869x + 0.0135x^2$; $b = -1.0869$, SE(b) = 0.0511, 95% CI(b) = −1.1885, −0.9854; $c = 0.0135$, SE(c) = 0.0018, 95% CI(c) = 0.0098, 0.0171; Fig. 1). This model showed a better fit to the data than did linear and exponential mixed models (Table 1), whereas models that included sex did not increase the fit. We cross-validated the quadratic model with another data set of 12 individuals weighed twice, once at weaning and once within 14 days after weaning, obtaining a mean difference from actual weaning mass of 1.6 kg (range: 0.1–5.4 kg).

Fig. 1. The decrease in body mass of fasting weaned pups of northern elephant seals (*Mirounga angustirostris*) is best predicted by a quadratic model. Data and individual curves refer to 29 pups (14 females and 15 males) during the first 30 days of fasting. The boldface broken line represents the quadratic model: $y = 109.79 - 1.0869x + 0.0135x^2$.



We conducted analyses with R version 3.4.3 (R Core Team 2018). To calculate the effect size, represented by Cohen's d and 95% CI, for differences between the sexes in body size and growth rate at Islas San Benito, we used the function cohen.d in the R package effsize (Torchiano 2017). In the case of summary data from previous literature, we calculated the effect size for differences between the sexes within different studies using the function ci.smd from the R package MBESS (Kelley 2018). We used the Hochberg method to control experimentwise error when conducting multiple pairwise comparisons (Hochberg 1988). To test for differences in variation in mass of neonatal and weaning pups in our study,

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[1] Supplementary tables and figure are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2018-0220.

Table 1. The decrease in postweaning body mass of northern elephant seal (*Mirounga angustirostris*) pups in the first 30 days of fasting is predicted best by a quadratic model; model selection based on Akaike's information criterion (AIC) scores, calculated using maximum likelihood.

Model structure	Model	df	Log likelihood	AIC	ΔAIC	AIC weight
Quadratic model	$W_i = \beta_0 + \beta_1 D_i + \beta_2 D_i^2 + \upsilon_i + \varepsilon_i$	5	–272.96	555.93	0.00	0.81
Exponential model	$W_i = \beta_0\, e^{\beta_1 D_i} + \upsilon_i + \varepsilon_i$	7	–272.44	558.89	2.96	0.19
Linear model	$W_i = \beta_0 + \beta_1 D_i + \upsilon_i + \varepsilon_i$	4	–293.01	594.02	38.09	0.00

Note: W_i is body mass of individual *i*; D_i is days of fasting by individual *i*; β is model coefficients of fixed effect (days of fasting); υ_i is random effect (identity of individual *i*); ε_i is an error term.

we compared the coefficients of variation (CV) using the R package cvequality (Marwick and Krishnamoorthy 2018).

We used the sexual-size dimorphism index proposed by Lovich and Gibbons (1992). This size dimorphism index (SDI) is commonly used to quantify sexual-size dimorphism and is calculated by dividing the mean of the larger sex by the mean of the smaller sex and subtracting 1. The index is negative if the male is the larger sex and positive if females are larger (Fairbairn 2007).

Comparison with other colonies

We reviewed literature on northern elephant seals that included information on body mass or body length of pups at birth or at weaning. We found information on the following colonies: South Farallon Islands; Año Nuevo State Park (composed of Año Nuevo State Reserve on the mainland plus Año Nuevo Island); San Miguel Island, currently the largest breeding colony (Lowry et al. 2014); and San Nicolas Island. We included only papers that reported means, standard deviations (SD) (or standard errors (SE)), and sample sizes. Several publications on elephant seals at Año Nuevo State Park seemed to have overlapping data or data based on different kinds of samples (e.g., measurements of dead or live pups). In such cases, we used the most complete data when available and excluded measurements of dead pups. We also excluded data for which the time frame of data collection was not clear. Finally, when data from a publication were included subsequently in a more comprehensive publication, we used the latter.

To compare breeding colonies, we carried out one-way ANOVAs and two-tailed Student's *t* tests using the summary statistics (mean and SD) from the original papers, pooled and weighted by sample sizes as appropriate. Sexual-size dimorphism across colonies was compared using the effect size, i.e., Cohen's *d* measures and 95% CI. When there was more than one study per colony, we used the pooled data for each sex to calculate effect size and the 95% CI of the pooled data.

Results

Sexual-size differences in newborn pups

At birth, males were 10% heavier than females (Table 2; Fig. 2A). Body mass differed significantly across the island–year factor: SBO 2006–2007, SBM 2006–2007, and SBM 2007–2008 (Table 2; $F_{[2,188]}$ = 8.98, $p < 0.001$), but neonatal mass did not vary significantly over the breeding season ($F_{[1,188]}$ = 0.03, p = 0.86). Newborn males also were longer than females by ~2% (Table 2; Fig. 2B) and body length differed significantly across the levels of the island–year factor ($F_{[2,161]}$ = 9.99, $p < 0.0001$). For body length, the difference between the sexes was driven by one year and island (SBO 2006–2007) where males were 5% longer than females ($F_{[1,39]}$ = 11.60, Hochberg corrected p = 0.01), whereas the sexes did not differ significantly on the other island (SBM 2006–2007: $F_{[1,40]}$ = 0.03, Hochberg corrected p = 0.87; SBM 2007–2008: $F_{[1,81]}$ = 1.40, Hochberg corrected p = 0.48). Neonatal body length did not differ significantly over the breeding season ($F_{[1,161]}$ = 1.24, p = 0.27).

Sexual-size differences at weaning

At weaning, males were slightly heavier (4%) than females, but the difference was not statistically significant (Table 2; Fig. 2A). Body mass differed significantly across the levels of the island–year factor ($F_{[2,238]}$ = 3.59, p = 0.03) and decreased significantly over the breeding season (–0.2 kg/day; $F_{[1,238]}$ = 8.09, $p < 0.01$). Body length at SBM in 2007–2008 did not differ significantly between the sexes (Table 2; Fig. 2B), but pups born later in the season were shorter than those born earlier (–0.2 cm/day; $F_{[1,37]}$ = 9.12, $p < 0.01$). Body length at weaning was not significantly related to the duration of the nursing period ($F_{[1,37]}$ = 0.19, p = 0.67).

Pups measured both at birth and at weaning

Those pups weighed both at birth and at weaning increased, on average, in mass over the nursing period by 71.5 ± 14.14 kg (n = 85, 95% CI = 68.5 kg, 74.6 kg), whereas the mean increase in length was 14 ± 4.1 cm (n = 18, 95% CI = 13.6 cm, 16.0 cm). Sexes did not differ significantly in growth rate or in the duration of the nursing period (Table 2). Duration of the nursing period did not change over the breeding season ($F_{[1,158]}$ = 1.11, p = 0.29), but differed significantly between SBO 2006–2007, SBM 2006–2007, and SBM 2007–2008 ($F_{[2,158]}$ = 3.94, p = 0.021; Table 2). This result seems to have been driven by a difference between years at SBM ($F_{[1,142]}$ = 5.93, Hochberg corrected p = 0.032) and not by islands ($F_{[1,37]}$ = 0.98, Hochberg corrected p = 0.329).

Pups that were heavier and longer at birth were also heavier (birth mass: $F_{[1,81]}$ = 54.96, $p < 0.0001$; sex: $F_{[1,81]}$ = 2.12, p = 0.15) and longer (birth length: $F_{[1,14]}$ = 13.69, $p < 0.01$; sex: $F_{[1,14]}$ = 1.00, p = 0.33) at weaning, with no differences between the sexes. Smaller pups grew slightly more in size than bigger pups in relation to initial body mass, although the relationship was weak (linear regression: n = 85, R^2 = 0.05, b = –1.62, SE(b) = 0.70, 95% CI(b) = –3.02, –0.22).

Body mass at birth was 21–53 kg (CV = 13%) and at weaning was 68–155 kg (CV = 15%). This increase in variation was slight but statistically significant (Feltz and Miller's asymptotic test, n = 455, p = 0.02; Fig. 2A).

Comparison with other populations

A summary of our literature review for body mass and body length is in Supplementary Tables S1 and S2.[1] Neonatal mass did not differ significantly between Islas San Benito and Año Nuevo State Park ($t_{[307]}$ = 0.65, p = 0.52; Table 3; Fig. 3A). In contrast, weaning mass differed significantly among Año Nuevo State Park, Islas San Benito, San Miguel Island, and South Farallon Islands ($F_{[3,1489]}$ = 58.68, $p < 0.0001$; Table 3; Fig. 3A). In particular, all pairwise comparisons between colonies were significant (Hochberg corrected $p < 0.001$), except that between Año Nuevo State Park and San Miguel Island ($t_{[1213]}$ = 1.67, Hochberg corrected p = 0.10; Table 3). Pups were significantly heavier at Año Nuevo State Park than at Islas San Benito (17%; $t_{[1401]}$ = 11.43, Hochberg corrected $p < 0.001$). Moreover, excluding years immediately following El Niño events and for body mass measured at 22 days, the lowest weaning mass recorded in 2000 at Año Nuevo State Park (125.9 ± 3.8 kg, n = 30; Noren et al. 2003) was significantly greater than at Islas San Benito (14%; $t_{[276]}$ = 4.88, $p < 0.0001$).

Neonatal length at Islas San Benito was significantly greater (4%) than at Año Nuevo State Park ($t_{[209]}$ = 4.88, $p < 0.0001$; Table 3; Fig. 3B); no data on neonatal body length are available for other colonies. On the contrary, weaning length differed significantly among colonies ($F_{[2,268]}$ = 5.82, $p < 0.01$; Table 3; Fig. 3B). Weaning

Table 2. Descriptive statistics for body measurements, growth rates, and nursing periods of northern elephant seal (*Mirounga angustirostris*) pups at Islas San Benito, Mexico, in the 2006–2007 and 2007–2008 breeding seasons.

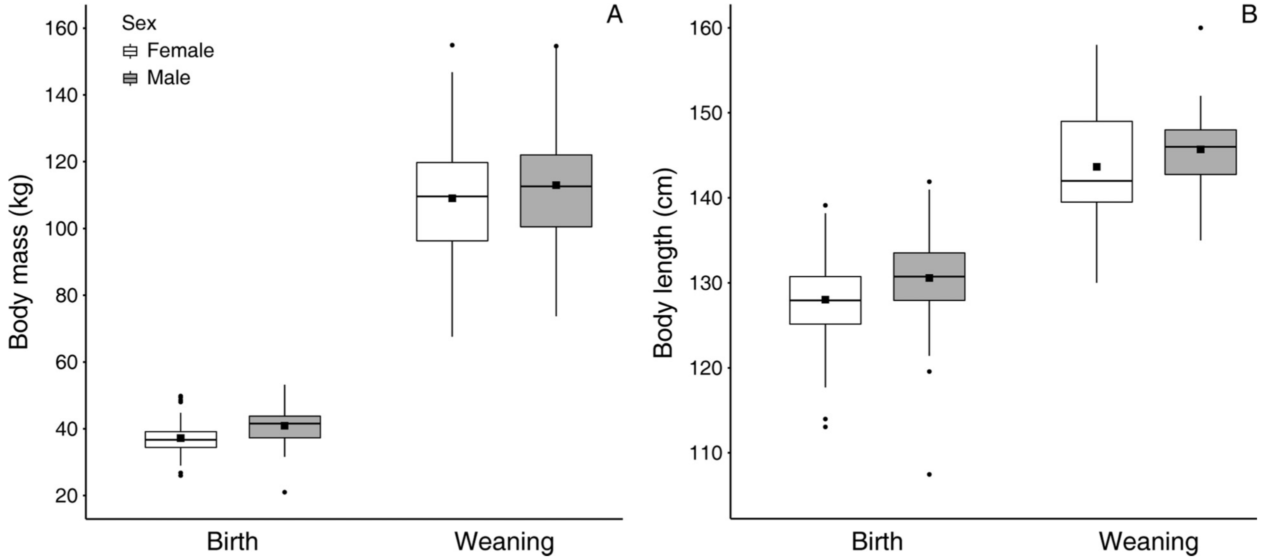
	Sexes combined[a]		Male		Female						Effect size	
Variable	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD	*n*	DI[b]	*F*	df	*p*	Estimated Cohen's *d*	95% CI
Birth mass (kg)	38.9±5.08	207	40.9±4.91	96	37.2±4.57	97	−0.10	31.88	1, 188	<0.0001	0.78	0.49, 1.08
SBO 2006–2007	41.3±5.16	43	43.4±3.43	25	38.9±6.08	16	−0.12				0.97	0.30, 1.63
SBM 2006–2007	36.6±4.56	53	39.0±5.94	20	35.3±2.74	28	−0.10				0.85	0.25, 1.44
SBM 2007–2008	39.1±4.85	111	40.5±4.70	51	37.7±4.56	53	−0.07				0.60	0.21, 1.00
Weaning mass (kg)	110.7±17.00	248	113.0±16.09	123	109.0±17.29	120	−0.04	3.54	1, 238	0.06	0.24	−0.02, 0.49
SBO 2006–2007	113.7±18.66	38	116.4±17.03	21	112.2±19.85	16	−0.04				0.23	−0.42, 0.88
SBM 2006–2007	104.4±14.95	35	104.9±10.67	16	104.1±18.09	19	−0.01				0.05	−0.61, 0.72
SBM 2007–2008	111.2±16.78	175	113.7±16.35	86	109.6±16.59	85	−0.04				0.25	−0.05, 0.55
Birth length (cm)	129±5.5	176	131±5.5	77	128±5.1	89	−0.02	10.63	1, 161	0.001	0.48	0.17, 0.79
SBO 2006–2007	131±5.8	43	134±3.7	25	128±6.6	16	−0.05				1.20	0.51, 1.87
SBM 2006–2007	126±4.7	45	126±6.5	16	126±3.6	26	0.00				0.00	−0.62, 0.62
SBM 2007–2008	130±5.2	88	130±4.9	36	129±5.0	47	−0.01				0.20	−0.23, 0.64
Weaning length (cm)	144±6.5	56	146±6.3	23	144±6.7	33	−0.01	0.49	1, 37	0.49	0.32	−0.23, 0.86
Growth rate in mass (kg/day)	2.8±0.56	85	2.8±0.52	40	2.8±0.60	45	0.00	1.17	1, 81	0.28	0.00	−0.43, 0.43
Growth rate in length (cm/day)	0.54±0.15	18	0.46±0.11	5	0.57±0.15	13	0.24	1.48	1, 15	0.24	0.78	−0.30, 1.83
Nursing period (days)	26±2.1	166	26±2.2	86	26±1.8	77	0.00	0.18	1, 158	0.68	0.00	−0.31, 0.31
SBO 2006–2007	27±1.6	22	27±1.7	16	26±0.7	5	−0.04				0.65	−0.39, 1.66
SBM 2006–2007	27±1.9	17	27±1.8	10	27±2.2	7	0.00				0.00	−0.97, 0.97
SBM 2007–2008	26±2.1	127	26±2.4	60	26±1.9	65	0.00				0.00	−0.35, 0.35

Note: Lengths measured as standard body lengths, calculated from the ventral body lengths in case of birth measures (see text); SBM is Isla San Benito Medio and SBO is Isla San Benito Oeste. The *p* values refer to the covariate sex in the linear model and 95% CI is the 95% confidence interval.

[a] Sexes combined includes pups of unknown sex.

[b] DI is the difference index (for body mass and length, this is the size dimorphism index (SDI); see text).

Fig. 2. Body mass (A) and body length (B) at birth and weaning in northern elephant seals (*Mirounga angustirostris*) at Islas San Benito, Mexico. Squares represent mean values. The line inside the box represents the median, whereas the box represents the 25th and 75th percentiles. Whiskers extend from the edges to the points within 1.5 interquartile range of the lower and upper quartiles. Points represent outliers.



length was greater at San Nicolas Island than at Año Nuevo State Park and Islas San Benito (San Nicolas–San Benito: $t_{[147]} = 2.52$, Hochberg corrected $p = 0.03$; San Nicolas–Año Nuevo: $t_{[213]} = 2.74$, Hochberg corrected $p = 0.02$), but weaning length at Año Nuevo State Park did not differ significantly from weaning length at Islas San Benito ($t_{[176]} = 1.06$, Hochberg corrected $p = 0.29$).

Sexual differences in neonatal mass varied across colonies (Año Nuevo: Cohen's $d = 0.34$, 95% CI = −0.21, 0.89; San Benito: Cohen's $d = 0.78$, 95% CI = 0.49, 1.08; Table 3), but effect sizes had very broad and overlapping 95% CI. At weaning, sexual dimorphism in body mass tended to vary between the colonies (Año Nuevo: Cohen's $d = 0.35$, 95% CI = 0.24, 0.47; San Miguel: Cohen's $d = 0.64$, 95% CI = 0.12, 1.16; San Benito: Cohen's $d = 0.24$, 95% CI = −0.02, 0.49; Table 3), but sexual dimorphism in body length was similar (San Nicolas: Cohen's $d = 0.30$, 95% CI = −0.11, 0.71; San Benito: Cohen's $d = 0.32$, 95% CI = −0.23, 0.86; Table 3).

Discussion

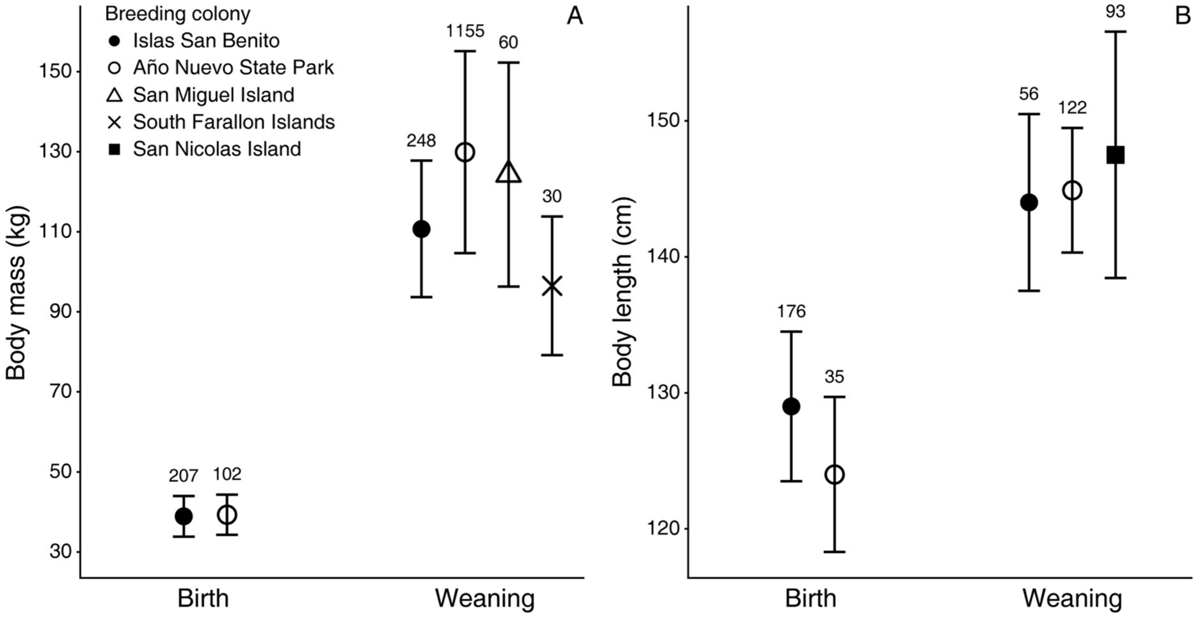
Adult male and female northern elephant seals differ greatly in body size, with males ~3.5 times as heavy as females (Deutsch et al. 1994), but sexual differences in size are modest though ap-

Table 3. Summary statistics from studies of different breeding colonies of the northern elephant seal (*Mirounga angustirostris*).

	Sexes combined		Male		Female		
Variable	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD	*n*	Sources
Neonatal mass (kg)							
Año Nuevo State Park	39.3±5.09	102					Le Boeuf et al. 1989; Deutsch et al. 1994; McDonald and Crocker 2006; Habran et al. 2010
			41.6±5.02	23	39.8±5.48	30	Le Boeuf et al. 1989; Kretzmann 1990
Islas San Benito	38.9±5.08	207					This study
Weaning mass (kg)							
Año Nuevo State Park	129.9±25.24	1155					Le Boeuf et al. 1989; McDonald and Crocker 2006; Habran et al. 2010; Reiter et al. 1978; B.J. Le Boeuf (unpublished data) in Kretzmann et al. 1993; Crocker et al. 2001; Noren et al. 2003
			134.8±26.52	546	126.0±23.19	571	Le Boeuf et al. 1989; Reiter et al. 1978; B.J. Le Boeuf (unpublished data) in Kretzmann et al. 1993; Noren et al. 2003
San Miguel Island	124.3±27.98	60					Reiter et al. 1978
South Farallon Islands	96.5±17.31	30					Lee 2006
Islas San Benito	110.7±17.00	248					This study
Neonatal length (cm)							
Año Nuevo State Park	124±5.7	35					Deutsch et al. 1994; Habran et al. 2010
Islas San Benito	129±5.5	176					This study
Weaning length (cm)							
Año Nuevo State Park	145±4.6	122					Deutsch et al. 1994; Habran et al. 2010; Noren et al. 2003
San Nicolas Island	148±9.1	93					Stewart 1989
			149±9.2	42	146±10.8	51	Stewart 1989
Islas San Benito	144±6.5	56					This study

Note: Pooled mean and pooled SD were calculated from summary statistics in the original sources.

Fig. 3. Comparison of body mass (A) and body length (B) at birth and weaning in northern elephant seals (*Mirounga angustirostris*) at several breeding colonies. Data from the colonies of Año Nuevo State Park, San Miguel Island, and South Farallon Islands are pooled data obtained from published literature (see the Materials and methods). Symbols are mean values and lines represent standard deviations. Numbers on top represent sample sizes.



parent early in life. In both species of elephant seal, newborn males generally are heavier than females. In our study at Islas San Benito, male northern elephant seal pups were 10% heavier than females at birth, similar to estimates for Año Nuevo Island (8%; Le Boeuf et al. 1989; no data on neonatal body mass are available for other colonies). This pattern also is seen in the southern elephant seal, where newborn male pups were ~8%–22% heavier than females in several colonies (Guinet 1991; Burton et al. 1997; McMahon et al. 1997; Wilkinson and van Aarde 2001); only a few studies depart from this trend, but their sample sizes were small

(Guinet 1991; Campagna et al. 1992). Similar or smaller sexual differences in neonatal body mass occur in other phocids. In species with moderate sexual-size differences as adults, such as gray seal (*Halichoerus grypus* (Fabricius, 1791)) and hooded seal (*Cystophora cristata* (Erxleben, 1777)), newborn pups do not differ significantly in body mass (4%–5%; Kovacs and Lavigne 1992*a*; Pomeroy et al. 1999), with the exception of gray seal pups in Canada in which males are the larger sex (Baker et al. 1995; Coltman et al. 1998). Sexes do not differ significantly in neonatal mass in species with weak or reversed sexual-size dimorphism as adults, such as harp seal (*Pagophilus groenlandicus* (Erxleben, 1777)) (Kovacs and Lavigne 1985; Chabot and Stenson 2000), harbor seal (*Phoca vitulina* Linnaeus, 1758) (Cottrell et al. 2002; Dubé et al. 2003), and Weddell seal (*Leptonychotes weddellii* (Lesson, 1826)) (Kovacs and Lavigne 1986). Overall, these findings contrast with the expectation of a positive correlation between sexual-size dimorphism in adults and newborn pups in phocids, as in other highly dimorphic mammals (Kovacs and Lavigne 1986; Smith and Leigh 1998). Moreover, the similarity in sexual-size dimorphism at birth across species of phocids and other mammals with varying dimorphism as adults suggests the presence of size-related constraints acting on mothers during gestation or parturition. In otariids, which are the most sexually size dimorphic group of mammals (Weckerly 1998), male-biased dimorphism in neonatal mass is 9%–23% (Kovacs and Lavigne 1992*b*). Similarly, in primates, sexual-size differences in neonatal body mass can reach 19% (Smith and Leigh 1998) and, in adult-dimorphic cervids, sexual differences in neonatal mass are ~6%–18% (Dubost 2016).

Patterns of body size at weaning are more inconsistent than those for birth in the northern elephant seal, showing a greater variation across studies. We found a nonsignificant sexual-size difference for pups at weaning, although males were slightly heavier than females (4%). In contrast, at Año Nuevo State Park, weaned males were 8%–15% heavier than females (Le Boeuf et al. 1989; Noren et al. 2003), but some short-term studies reported no difference between the sexes (Reiter et al. 1978; B.J. Le Boeuf (unpublished data) in Kretzmann et al. 1993), or even reported reversed sexual dimorphism (females larger than males by ~4%; Noren et al. 2003). In the southern species, most studies report a male-biased difference in body size, varying from 4%–6% (Arnbom et al. 1993; McMahon et al. 1997; Oosthuizen et al. 2015) to 15%–16% (Wilkinson and van Aarde 2001; McMahon et al. 2017), with a few exceptions (McCann et al. 1989; Campagna et al. 1992; Galimberti and Boitani 1999). Two long-term studies, over about 30 years, reported a male-biased difference of 5% for both northern and southern species (Le Boeuf and Crocker 2005; Oosthuizen et al. 2015). Other species of phocid have a similar degree of dimorphism at weaning, again suggesting that sexual dimorphism in adults and in early life are not positively correlated. In phocids with male-biased dimorphism in adulthood, sexual differences in body mass at weaning are generally weak and mostly not significant, e.g., hooded seal (Kovacs and Lavigne 1992*a*), gray seal (Hall et al. 2001; Noren et al. 2008*a*), harp seal (Kovacs and Lavigne 1985), and harbor seal (Muelbert and Bowen 1993; Bowen et al. 2001). Sexes also do not differ in weaning body mass in the Weddell seal (Proffitt et al. 2008), a species with reversed sexual-size dimorphism in adults.

In pinnipeds, weaning mass is generally assumed to affect adult mass (McCann et al. 1989). In the short-term, there is some evidence of a positive effect of greater offspring body mass on survival (Bowen 2009), but the effect is not consistent across the two species of elephant seal. In the northern elephant seal, there is no relationship of weaning body mass to survival in the first year of life (Le Boeuf et al. 1994), but there is a positive relationship in the southern species (McMahon et al. 2000; Oosthuizen et al. 2018). There are no studies linking sexual differences in early life to adult body size or reproductive success in northern elephant seals, unlike for other mammals (Kruuk et al. 1999). In the southern elephant seal, the only long-term study refers to females and reports no positive correlation between weaning mass and survival after the first 2 years of life (Oosthuizen et al. 2018). Some researchers (McCann et al. 1989; Trillmich 1996) have suggested that differences in body size early in life have a negligible effect on body size of adult male pinnipeds, which depends more on rapid pubertal growth (McLaren 1993). This is in agreement with the decline of maternal effects over years in long-lived species, where other factors later in life, such as environmental conditions, may affect growth and adult phenotype (Wilson and Festa-Bianchet 2009). We recommend long-term studies on the relationship of body size early in life and in adulthood and reproductive success to clarify these matters for pinnipeds.

Body length differs little or not at all between the sexes at birth and weaning in phocids. We found a slight but significant difference between the sexes in neonatal body length of northern elephant seals at one island (5%; San Benito Oeste 2006–2007), and no comparable data exist from other colonies of this species. In the southern elephant seal and harbor seal, sexes do not differ in neonatal body length (Little et al. 1987; Cottrell et al. 2002). At weaning, the sexes do not differ significantly in body length in northern elephant seals at Islas San Benito and Año Nuevo State Park (Stewart 1989), or in the southern elephant seal (Little et al. 1987; Clausius et al. 2017*b*). Similarly, sexes do not differ in body length at approximately 2 weeks of age in the harbor seal (Trumble and Castellini 2002) or at 3–5 weeks in the Weddell seal (Noren et al. 2008*b*).

Sexual-size dimorphism can result from differences in rate and duration of growth (Badyaev 2002), but contrary to what we expected from the great difference in body size between the sexes in adult elephant seals, sexes were similar in growth rate and duration of nursing. In the northern species, growth rates in body mass and body length, and duration of nursing, did not differ significantly between the sexes at Islas San Benito or Año Nuevo State Park (Le Boeuf et al. 1989; Kretzmann et al. 1993; Deutsch et al. 1994). However, the magnitude of the increase in body mass differed between the breeding colonies (2.8 kg/day at Islas San Benito and 3.4–4.4 kg/day at Año Nuevo State Park; Le Boeuf et al. 1989; Deutsch et al. 1994; Houser et al. 2001), suggesting a difference between the colonies in postnatal investment by the mothers. In the southern elephant seal, a similar trend is present across several colonies, where sexes do not differ in growth rates in body mass (3.2–4.0 kg/day) or duration of nursing (McCann et al. 1989; Campagna et al. 1992; Fedak et al. 1994; Arnbom et al. 1997; McMahon et al. 1997; Wilkinson and van Aarde 2001). A lack of sexual difference in growth rate also occurs in the harbor seal (Boulva and McLaren 1979), harp seal (Kovacs and Lavigne 1986), and gray seal (Bowen et al. 1992). This lack of difference in length of nursing and growth rates in both species of elephant seal may be due to a similar investment in the sexes by the mothers during lactation, as a differential investment may not affect reproductive success in adults (Trillmich 1996).

Overall body size in pups of the southern elephant seal can vary across colonies and through time (Burton et al. 1997; Vergani et al. 2001; Clausius et al. 2017*a*). In the northern elephant seal, full assessment of geographic variation through the breeding range is limited by the scarce information available for most colonies. Moreover, the distribution in time of previous studies, with data collected in varying years at different breeding colonies, limit the comparison, as body mass can vary over time (Noren et al. 2003; Le Boeuf and Crocker 2005). Furthermore, studies may have differed in methodologies, especially in the measurement of body length. Despite these complications, we found differences in body size among colonies. Californian and Mexican colonies belong to different stocks with little exchange of individuals (Carretta et al. 2015). Adult females, and probably also males (Clinton 1994; Sanvito and Galimberti 2003), at Islas San Benito are smaller than adults at Año Nuevo State Park (Robinson et al. 2012). We recommend further studies to verify the presence of a structural difference between the colonies, which may affect body mass of pups at weaning.

In conclusion, neonatal mass is generally male-biased in both species of elephant seal, whereas weaning mass is male-biased but more variable, across breeding colonies and over time. Further studies at different breeding colonies are desirable to clarify geographic and temporal variation in overall body size and sexual dimorphism. Modest differences between the sexes in weaning size, growth rates, growth duration, and mass decrease over postweaning fasting raise the question of whether body size in early life is more important for short-term survival than it is for adult size and reproductive success. In contrast to primates (Smith and Leigh 1998) and ungulates (Wilson and Festa-Bianchet 2009), maternal effects in elephant seals may not persist much later in life, due to their important growth at puberty (Clinton 1994; Oosthuizen et al. 2018). Longitudinal studies on the relationships between early life, body size, and lifetime reproductive success are needed to verify the assumptions that have been made about the effect of sexual selection on maternal investment in these long-living and highly polygynous mammals.

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