

## Growth rates and differential investment in male and female Juan Fernández fur seal pups

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Male Juan Fernández fur seals (*Arctocephalus philippii*) are significantly larger than females at birth and show extreme dimorphism as adults. We investigated morphological differences among male and female pups using a cross-sectional sampling design to evaluate whether pup growth rates were sex-specific during the breeding season. We characterized growth rates using mass, length, and girth and found that length was the least variable measure of body growth (based on the coefficients of variation for the 3 measures of body size). Male pups were heavier on average than female pups on any given day of sampling but did not grow faster than females. No significant differences were noted in the body conditions of male and female pups. These findings suggest that the sexual differences among pups of *A. philippii* originate before birth and are not accentuated while suckling during the breeding season. DOI: 10.1644/09-MAMM-A-197.1.

Key words: *Arctocephalus philippii*, Juan Fernández Archipelago, Juan Fernández fur seals, maternal investment, pup growth rates, sexual dimorphism, sexual variation

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Sexual dimorphism is common among vertebrates and widespread among mammals, particularly those that have polygamous breeding systems (Derocher et al. 2005; Monakhov 2009). Differential reproductive roles played by the sexes have been documented frequently, as have the adaptive significances of the often remarkably distinct morphologies of adult males and females (Badyaev 2002). In general, large adult size is believed to increase the fitness (breeding success and survival) of males more than females (Trillmich 1986), and parents are expected to allocate more resources toward the sex that yields greater fitness returns when one sex stands to gain more from extra parental resources than the other (Trivers and Willard 1973). Applying such observations and theory to species where males have greater variability in reproductive success than females (such as in polygynous mammals) predicts that mothers in good condition should invest more in sons than in daughters (Koskela et al. 2009).

Among mammals, the taxa with the most dimorphic body sizes are the orders Primates and Proboscidea; the suborders Odontoceti, Caniformia, and Ruminantia; and the families Macropodidae and Mustelidae (Weckerly 1998). Among these taxa, fur seals (Caniformia: Otariidae) are highly polygynous and sexually dimorphic, which means that variance in lifetime reproductive success likely differs between the sexes (Guinet et al. 1999). Male-biased sexual size dimorphism generally has been attributed to sexual selection that favors larger, more-

competitive males (McKenzie et al. 2007; Trivers 1972; Weckerly 1998). Lifetime reproductive success of males also is thought to vary more widely than that of females (Clutton-Brock 1988; Trivers 1972). These conclusions lead to the prediction that males should display such phenotypic adaptations as rapid early growth and delayed maturation (Weckerly 1998). In contrast, females should invest their available resources in reproduction, rather than body growth, once a minimum size for reproduction is reached because reproductive success of females is more dependent on investment in condition and extended reproductive life span (Trivers 1972). Growth in females is therefore expected to be slower than that of males and characterized by early maturation (McKenzie et al. 2007; Weckerly 1998).

Otariids display extreme sexual dimorphism and are particularly good subjects for studying early differential growth because females bear single young that depend entirely on milk and are relatively easy to capture and handle (Arnould et al. 2003; Bonner 1984). Energy allocated to male and female offspring during nursing may provide insights into differential parental investment given the importance of size at independence for the future performance of individuals (Koskela et al.



2009; Roff 1992). Male pups should have an intrinsic capacity to grow faster than female pups (Guinet et al. 1999), not only to survive, but also ultimately to better defend territories, maintain harems, and copulate (Vargas et al. 2009).

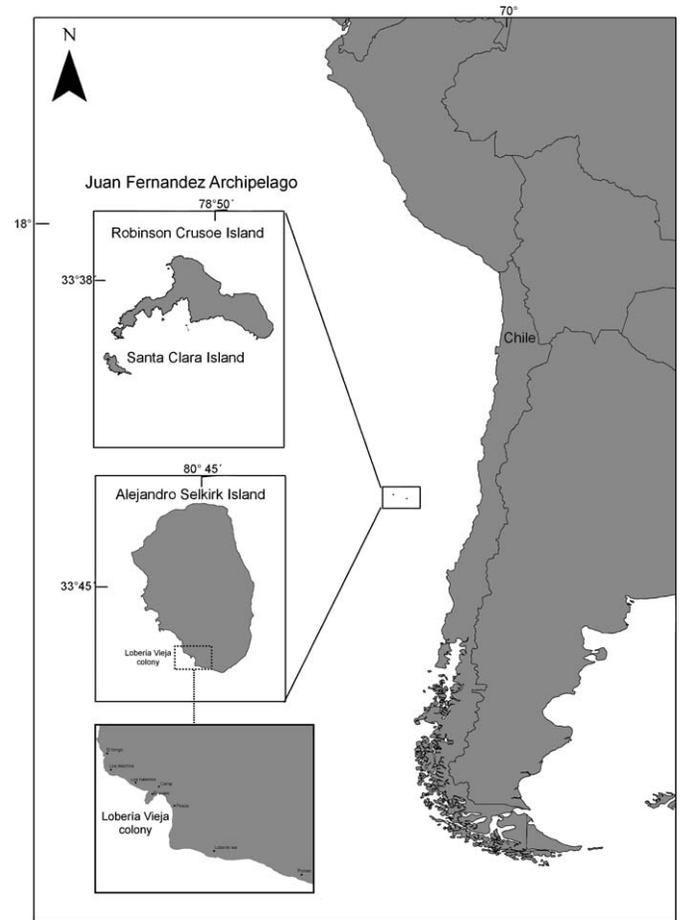
The time at which the sizes and growth rates of males and females of dimorphic species should differ is uncertain. Males may be born bigger on average than females and grow faster throughout the nursing period. However, evidence suggests that sexual differences of dimorphic species may not be too evident during their 1st year because of the physiological constraints of growth and the need to store enough energy reserves for early survival. For example, male and female goat-antelopes (alpine chamois, genus *Rupicapra*) have similar growth rates during their first 2 years of life and do not display marked between-sex differences in body growth until >1.5 years of age (Garel et al. 2009; Pioz et al. 2008). Otariids such as fur seals and sea lions could face similar constraints.

Changes in offspring mass with time can be measured either by longitudinal sampling, where the same identifiable individuals are weighed repeatedly over time, or by cross-sectional sampling, where a random sample of different individuals in the population are weighed at predefined intervals. Longitudinal sampling is particularly suited to examining the role of individual maternal strategies on pup growth. However, repeatedly locating, capturing, and weighing enough marked pups to obtain sufficiently large samples of pups throughout the lactation period is so time-consuming as to often not be practical as a routine procedure. In these circumstances cross-sectional sampling offers a more straightforward method to measure body size, because rounding up a potential sample of 100 pups every 2–4 weeks is not overly time-consuming and provides a good sample of pups that can be weighed on each sampling occasion with no requirement to locate and recapture the same pups (Reid 2002). This is especially the case in rough terrain or when the population size is large enough to make it difficult to relocate marked pups.

The goal of our study was to characterize the body growth rates of male and female *Arctocephalus philippii* (Juan Fernández fur seal) pups (measuring mass, length, and girth with a cross-sectional sampling design) and evaluate whether sexual differences in growth rates during the breeding season infer an advantage to male pups. Many studies have measured mass as an indicator of body growth in fur seal pups (Arnould et al. 1996, 2003; Doidge and Croxall 1989; Doidge et al. 1984; Goldsworthy 1995; Guinet and Georges 2000; Guinet et al. 1999; Lunn et al. 1993; Ochoa-Acuña et al. 1998; Vargas et al. 2009), but few have used length and girth as other useful indicators of growth that are not masked by the potential influences of feeding, fasting, and date of birth on recorded mass.

## MATERIALS AND METHODS

**Study area.**—*Arctocephalus philippii* is the only endemic pinniped of Chile and is restricted to the islands that make up



**FIG. 1.**—Location of the Lobería Vieja colony of Juan Fernández fur seals (*Arctocephalus philippii*) on Alejandro Selkirk Island, Juan Fernández Archipelago, Chile, South America. The other 2 islands of the archipelago that have small colonies of Juan Fernández fur seals are Robinson Crusoe and Santa Clara.

the Juan Fernández Archipelago (Robinson Crusoe, Santa Clara, and Alejandro Selkirk), one of the most unique oceanic ecosystems of Chile. *A. philippii* is one of the least known species of fur seals and is classified as Near Threatened (International Union for the Conservation of Nature 2010). Our study occurred in the sector of the breeding beach (rookery) known as El Ovalo at Lobería Vieja (Fig. 1), which is home to the largest breeding colony of *A. philippii* in the Juan Fernández Archipelago (Osman 2008; Torres 1987) on Alejandro Selkirk Island (33°45'S, 80°45'W). Pup production at Lobería Vieja increased from 548 pups in 1983 to 6,941 in 2005, and the population was in a period of high per capita growth rates during our study (Osman 2008).

**Data collection.**—Growth rates of pups of *A. philippii* were determined using a cross-sectional sampling design from January to April 2005. In a previous study, Ochoa-Acuña et al. (1998) used longitudinal sampling from the 1st to 3rd month of age (December–February, 1988–1992). Logistical problems did not allow us to begin collecting data during December when transportation to the island was difficult to obtain. Thus, our study began in January and ended in April when the pups

were 5 months of age (assuming a mean date of birth of 30 November—Francis et al. 1998). Age at sampling was assumed to equal the numbers of days between 30 November and the date of capture. Weaning date has never been determined due to the difficulty of researchers staying longer on Alejandro Selkirk Island, but Francis et al. (1998) hypothesized that lactation lasts at least 7 months.

We weighed and measured (dorsal standard length and axillary girth) random samples of 100 pups (50 males and 50 females) at about 1-month intervals. Pups were placed in a synthetic mesh bag suspended by a spring scale and weighed, wet or dry, to the nearest 0.2 kg. Dorsal standard length (nose to tail) was measured to the nearest 1 cm by holding each pup belly down, stretched on a measuring board marked in 1-cm increments. The pup’s nose was held against a block of wood attached to one end of the measuring board while the body was straightened by pulling gently on the rear flippers (Boltnev et al. 1998). Axillary girth also was measured to the nearest 1 cm after taking dorsal standard length, and a temporary mark was painted on the animal’s back to avoid measuring the pup twice. All animal handling and data collection procedures followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

*Statistical analysis.*—Mass, length, and axillary girth measurements were log-transformed to normalize the data and were compared to determine the extent of sexual dimorphism among male and female pups by age (sampling date—Chilvers et al. 1995). Growth of male and female pups was compared using multiple regression analysis, with log-mass or log-length as the response variable and sex (coded 0 for females and 1 for males), age, and the interaction between sex and age as predictor variables. The assumption of homoscedasticity was checked by visually examining the standardized residuals (the errors) plotted against predicted values. Possible differences in the body growth rates of male and female pups were assessed by testing whether the coefficients for interactions between age and sex were significant. Lack of significance implied no statistical difference between male and female growth rates (i.e., homogeneity of slopes). Equations describing the growth of male and female pups were derived subsequently by running multiple regression analyses with nonsignificant variables removed.

Body mass does not necessarily reflect the quantity of body reserves, which are mainly fat. We therefore treated the residuals of the mass (M)–length (L) relationship ( $M = aL^b$ ) as a simple body condition index for each individual pup (Guinet et al. 1998). We regressed body mass against standard length using log mass as the response variable and log length, sex, age, and the interactions between sex and log length and between sex and age as predictor variables. We recognized that age and length are highly correlated, but chose to include age in our model in the belief that body condition of pups might improve with age, independent of length. Thus, we tested whether body condition index (the residuals) differed by sex and age by assessing the significance of their respective coefficients in our multiple regression model.

**TABLE 1.**—Mean (*SD*) mass (kg), standard length (cm), and axillary girth (cm) of male and female pups of *Arctocephalus philippii* at Lobería Vieja, Alejandro Selkirk Island, Chile, during 2005 (date 1 = 16 January; 2 = 16 February; 3 = 2 March; 4 = 18 March; 5 = 4 April; 6 = 18 April). Sample size on each date consisted of 50 females and 50 males.

Body measure	Date	Females	<i>SD</i>	Males	<i>SD</i>
Mass (kg)	1	8.1	1.8	8.6	1.6
	2	9.9	2.2	11.6	2.6
	3	10.3	2.3	12.1	2.3
	4	11.6	2.3	13.5	2.6
	5	13.4	2.3	14.8	2.3
	6	143.0	2.5	15.3	2.4
Length (cm)	1	73.4	4.1	76.4	4.0
	2	77.5	5.4	81.5	6.0
	3	79.2	4.8	84.9	3.8
	4	82.9	4.3	86.8	4.3
	5	87.3	3.7	90.1	3.7
	6	88.1	3.7	90.4	3.3
Girth (cm)	1	45.4	4.4	47.0	3.6
	2	49.9	4.6	52.9	5.5
	3	50.1	4.3	53.5	4.3
	4	52.9	3.8	55.0	4.8
	5	54.2	4.2	56.6	3.9
	6	56.7	4.1	58.1	3.8

To compare our findings with those of Ochoa-Acuña et al. (1998), we calculated the mean length and mass of male and female pups at birth from the intercept of the multiple regression growth equations. Daily growth rates were calculated following Ochoa-Acuña et al. (1998) by dividing the change in body mass by the number of days between the sampling dates. All analyses were conducted using STATISTICA software (StatSoft, Tulsa, Oklahoma), with levels of statistical significance set at  $P < 0.05$ .

**RESULTS**

In total, 600 pups were measured over the course of the breeding season beginning 16 January 2005. Subsequent cross-sectional sampling occurred on 16 February, 2 and 18 March, and 4 and 18 April 2005 (Table 1). Females averaged ( $\pm SD$ )  $8.1 \pm 1.8$  kg on the 1st day of sampling and were  $14.3 \pm 2.5$  kg 3 months later. Males were heavier on average and weighed  $8.6 \pm 1.6$  kg at the beginning of our study and  $15.3 \pm 2.4$  kg at the end (Table 1). Overall, males were 6–15% heavier and 3–7% longer on average than female pups on any given day of sampling (Table 2). As assessed by the coefficient of variation, body length was the least variable measure of body size followed by girth and mass (Fig. 2).

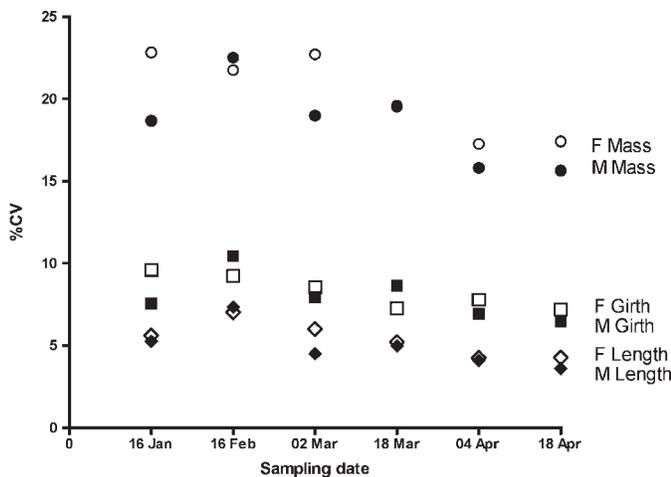
Regressing body mass against standard length (using log mass as the response variable and log length, sex, age, and the interactions between sex and log length and between sex and age as predictor variables) yielded a significant model ( $r^2 = 0.72$ ,  $F_{5,594} = 304.49$ ,  $P < 0.001$ ). However, not all variables explained the observed variation in body mass. Using the model residuals as an index of body condition and the significance of the respective coefficients in our multiple

**TABLE 2.**—Percent difference in average body size (sexual dimorphism) of male and female pups of *Arctocephalus philippii* by day in 2005 (where dimorphism is estimated as the difference between average male and female mass, standard length, and axillary girth).

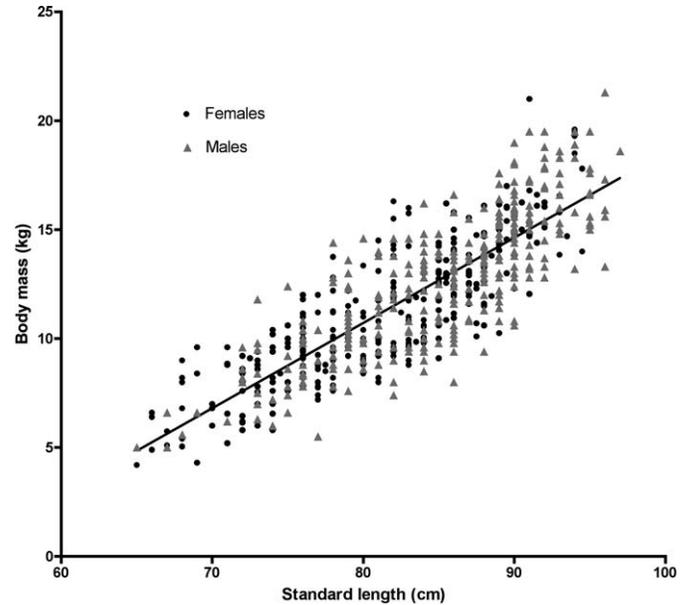
Sampling date	Mass (%)	Length (%)	Girth (%)
16 January	7	4	4
16 February	14	5	6
2 March	15	7	6
18 March	14	4	4
4 April	9	3	4
18 April	6	3	2

regression model as a measure of their contribution to body condition showed that body condition index did not differ significantly between sexes ( $t_{594} = -1.09, P = 0.28$ ; Fig. 3), but did differ with age ( $t_{594} = 3.79, P < 0.001$ ), indicating that older pups were in slightly better condition than younger pups (based on the contribution of the coefficient to estimated body mass). No interactions were found between sex and age ( $t_{594} = -1.33, P = 0.18$ ) or between sex and length ( $t_{594} = 1.11, P = 0.27$ ).

The best growth models (as determined by  $r^2$ ) predicted the logarithmic mass and lengths from the independent variables age and sex. No significant interaction occurred between age and sex, indicating that the growth rates (of mass and length) were not statistically different between male and female Juan Fernández fur seal pups (homogeneity of slopes; log mass,  $t_{596} = 0.31, P = 0.76$ ; log length,  $t_{596} = 1.31, P = 0.19$ ). Males were larger on average than females on any given date of sampling (Table 1), and mean mass and length increased significantly across sampling dates as expected (log mass,  $t_{596} = 16.07, P < 0.001$ ; log length,  $t_{596} = 18.76, P < 0.001$ ). However, mean body masses of males and females of the same lengths did not differ significantly (Fig. 3;  $t_{595} = 0.51, P = 0.61$ ). The relationship between body length (cm) and mass (kg) for male and female pups can thus be described by a



**FIG. 2.**—Coefficient of variation (%CV) of mass, standard length, and axillary girth from male and female pups of *Arctocephalus philippii* sampled in 2005 (F = females; M = males).



**FIG. 3.**—Relationship between body mass and length of male (triangles) and female (black circles) pups of *Arctocephalus philippii*. The body condition index (BCI) equaled the differences (residuals) between observed and expected masses.

single equation:  $\text{mass} = e^{-10.25} \text{length}^{2.87}$  ( $r^2 = 0.71, F_{1,598} = 1,469.72, P < 0.001$ ; Fig. 3).

Multiple regression models predicted male body mass (kg) =  $6.52e^{(a*\text{age})}$ , female body mass (kg) =  $5.78e^{(a*\text{age})}$ , male body length (cm) =  $69.5e^{(b*\text{age})}$ , and female body length (cm) =  $66.5e^{(b*\text{age})}$ , where  $a = 0.00637, b = 0.00202$ , and age is in days ( $r^2 = 0.50, F_{2,597} = 291.73, P < 0.001$  for mass of males and females;  $r^2 = 0.60, F_{2,597} = 437.20, P < 0.001$  for the male and female length equations). These loglinear models gave slightly better fits (based on  $r^2$  values) than linear regressions of the untransformed mass and lengths, and gave more reasonable estimates of mean mass and lengths at birth. They also made biological sense (given that growth is widely recognized to be a nonlinear process). Describing growth using an exponential relationship implies that the growth rate increased slightly each day; that is, the growth rate increased as a function of age such that pups grew faster as they became older. On average, however, the pups gained about 71 g and 0.17 cm per day (based on linear regressions of the untransformed data).

Our estimated masses at birth (based on the above regression models) were similar but slightly higher than those reported by Ochoa-Acuña et al. (1998); that is, 5.8 kg versus 5.5 kg for females and 6.5 kg versus 6.1 kg for males. Similarly, the average growth rate of the pups we weighed (0.071 kg per day) was similar to those reported by Ochoa-Acuña et al. (1998), but did not decrease with age (see Fig. 4).

**DISCUSSION**

In general, the maternal care of otariids consists of long periods (4 months to 3 years depending on the species) of

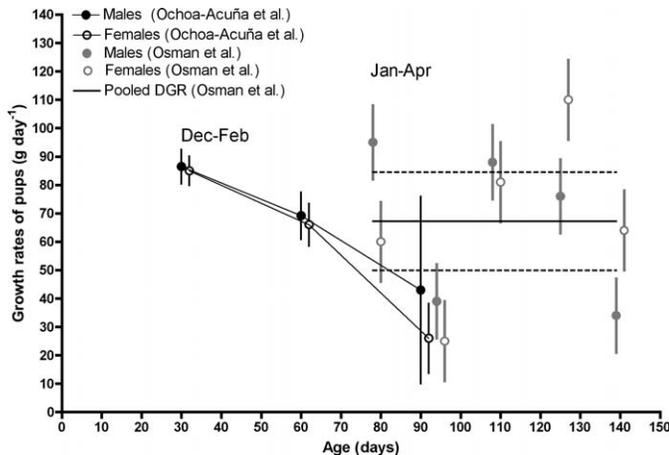


FIG. 4.—Mean daily growth rates (DGR  $\pm$  SE) of pups of *Arctocephalus philippii* at different ages estimated by longitudinal sampling (solid black circles = males; open black circles = females [Ochoa-Acuña et al. 1998]), cross-sectional sampling (solid gray circles = males; open gray circles = females [our study]), and pooled slope (horizontal solid line) with 95% confidence interval (dashed lines). Mean date of birth was assumed to be 30 November (Francis et al. 1998).

alternating between foraging trips at sea and fasting visits ashore to nurse the pups (Gentry and Kooyman 1986). Females depend on the marine environment to fulfill their energetic demands and select pupping sites that are associated with upwelling regions and continental shelf breaks with high primary productivity, zooplankton, squid, and fishes (Gentry and Kooyman 1986; Lea et al. 2006). Pup growth therefore is expected to reflect environmental conditions (e.g., prey availability) experienced by mothers as they forage (e.g., Boyd et al. 1994; Bradshaw et al. 2000; Lea and Hindell 1997; Reid 2002).

Successful pup growth depends upon the availability of food to adult females, which may differ among years or breeding colonies. Thus, variability in environmental conditions during the lactation period, or geographic differences in locations of breeding colonies relative to feeding areas, can confound simple interpretations of growth rates of pups and length of lactation. In this regard, animals inhabiting polar regions with short lactation periods and little time before weaning might have accentuated differences between male and female pups, as in Antarctic fur seals (*Arctocephalus gazella*) and northern fur seals (*Callorhinus ursinus*; Table 3). Species with longer lactation periods do not appear to have such clear-cut sexual differences during the nursing period. For example, subantarctic fur seal (*Arctocephalus tropicalis*) pups sampled longitudinally over the 10-month lactation period showed no differences in growth rates between sexes. Differences (using cross-sectional sampling) were not detected until 1 year of age (Table 3). In contrast, the growth rates of male and female New Zealand fur seal (*Arctocephalus forsteri*) pups (with 9 months of lactation) differed using both cross-sectional and longitudinal sampling designs (Table 3).

The methods employed to measure the body size of pups (longitudinal or cross-sectional sampling) may influence the

conclusion regarding whether male pups grow faster than female pups (Table 3). The growth rates of young pinnipeds and many other mammals decline with age as the energetic demands of the offspring outstrip the capacity of the mother to supply milk. In pinnipeds this equates to longer maternal feeding trips to sea and consequently less time feeding pups (leading to slower growth rates). Cross-sectional studies can be an appropriate method of measuring growth or interannual (environmental) variability in growth if length and girth measurements are included and if appropriate sample sizes are used with a random sampling technique. However, a longitudinal study specifically designed to assess differential investment between the sexes likely would attain better results relative to growth and be able to demonstrate better any declines that might occur in growth rates over time.

A protracted breeding season also can influence the interpretation of differences in body growth rates, depending on which sampling design is employed. For example, a cross-sectional sample will consist of pups with greater ranges of birth dates with each day of sampling and likely will result in lower calculated growth rates compared to growth rates calculated from longitudinal samples. This reflects later samples having greater variability due to pups that are born earlier being larger than pups born later, and the possibility that recently fed and fasted animals may have a greater likelihood of being captured. Thus, longitudinal and cross-sectional calculated growth rates are probably not comparable for species with protracted pupping seasons.

Our estimates of masses at birth and average growth rates were similar to those reported by Ochoa-Acuña et al. (1998). However, we failed to find that growth rate declined with age as they had reported (Fig. 4). We suspect this decline in growth rates reflects a handling effect associated with repeatedly capturing the same individuals and disrupting mother-pup bonds. Thus, the apparent differences in growth rates with age could be an artifact of differences in the sampling designs used in our 2 studies.

Our estimates of growth rates showed considerable variability among sampling dates, which may represent inherent variability associated with cross-sectional measurements of pups. Foraging trips of female Juan Fernández fur seals are typically between 1 and 25 days (Francis et al. 1998) but can be as long as 40 days (Osman 2008). Such variability in trip durations could explain the highly variability in growth rates we recorded because some pups might have been fed recently but others might have fasted for more than 25 days. Ochoa-Acuña et al. (1998) also recorded considerable variability in growth rates, which further suggests considerable variation in the feeding cycles of Juan Fernández fur seal pups. Interannual variability in the length of fasting periods also might explain why studies repeated in subsequent years failed to find a difference in growth rates between the sexes of other species of fur seals when differences were noted in previous years (Arnould and Hindell 2002; Chambellant et al. 2003; Table 3).

Studies using a cross-sectional design have indicated that male pups of 7 species of fur seals grow faster than females,

**TABLE 3.**—Comparison of study designs used to assess whether growth rates of males of 7 species of fur seals exceeded ( $P < 0.05$ ) those of females ( $M > F$ ) or did not differ significantly ( $M = F$ ).

Species	Lactation length	Body measure	Study design		Growth rates		Source
			Cross-sectional	Longitudinal	$M > F$	$M = F$	
Antarctic fur seal ( <i>Arctocephalus gazella</i> )	4 months	Mass	X		X		Payne (1979)
<i>A. gazella</i>	4 months	Mass	X		X		Doidge et al. (1984)
<i>A. gazella</i>	4 months	Mass		X		X	Lunn et al. (1993)
<i>A. gazella</i>	4 months	Mass	X		X		Lunn et al. (1993)
<i>A. gazella</i>	4 months	Mass		X	X		Goldsworthy (1995)
<i>A. gazella</i>	4 months	Mass		X	X		Guinet et al. (1999)
<i>A. gazella</i>	4 months	Mass	X		X		Reid (2002)
<i>A. gazella</i>	4 months	Mass		X		X	Lea et al. (2006)
<i>A. gazella</i>	4 months	Mass		X	X		Vargas et al. (2009)
New Zealand fur seal ( <i>A. forsteri</i> )	9 months	Mass		X	X		Chilvers et al. (1995)
<i>A. forsteri</i>	9 months	Mass	X		X		Goldsworthy (2006)
Subantarctic fur seal ( <i>A. tropicalis</i> )	10 months	Mass		X		X	Georges and Guinet (2000)
<i>A. tropicalis</i>	10 months	Mass		X		X	Guinet and Georges (2000)
<i>A. tropicalis</i>	10 months	Mass	X		X		Kirkman et al. (2002)
<i>A. tropicalis</i>	10 months	Mass		X	X	X	Chambellant et al. (2003)
Juan Fernández fur seal ( <i>A. philippii</i> )	>7 months?	Mass		X		X	Ochoa-Acuña et al. (1998)
<i>A. philippii</i>	>7 months?	Mass, length	X			X	Current study
Galapagos fur seal ( <i>A. galapagoensis</i> )	1–3 years	Mass		X	X		Trillmich (1986)
Australian fur seal ( <i>A. pusillus doriferus</i> )	10–11 months	Mass	X		X		Arnould and Hindell (2002)
Northern fur seal ( <i>Callorhinus ursinus</i> )	4 months	Mass		X	X		Boltnev et al. (1998)

but longitudinal studies have reported conflicting results—that males grow faster than females and also that no significant difference exists between the growth rates of males and females (Table 3). Our study is the 1st to use a cross-sectional design that shows that growth rates of male and female pups do not differ significantly from each other.

The generally accepted conclusion that male fur seal pups grow faster than female pups might be altered through further analysis of existing growth data from other fur seal species using length as a covariate to assess whether growth rates are as different as suggested by independent linear regressions of male and female body masses over time. Using loglinear growth equations, as we did, also might correct for apparent growth rate differences by better describing the growth process. Thus, the conclusion often drawn that maternal investment is greater in male than female fur seals simply might reflect that males are heavier at birth and are by default further along the exponential mass–length curve than females at the time of sampling—and not that males grew faster than female pups (Lunn et al. 1993). It may well be that physiological constraints of growth and the need to store enough energy reserves for early survival ultimately limits the extent of sexual dimorphism during the 1st year of life.

Of the 3 body measures we recorded, mass was much more variable than axillary girth and standard length. As such, standard length and axillary girth better represented the growth of the individual than did mass. We attributed the variability in mass to variability in the ages of sampled pups (differences in the timing of birth), in the maternal attendance cycle, and the delivery of milk. Pups of *A. philippii* can wait 1–22 days without suckling (Francis et al. 1998), which will

contribute to the variability of their sampled body masses. Comparing body masses of males and females adjusted for differences in body length, as we did, might show that some of the apparent differences reported in body size of other species are artifacts of variability of mass due to differences in the feeding cycles of pups and the timing of birth.

Studies of milk intake of other species of fur seals have generally found no differences in the volume of milk consumed by male and female pups of the same size. For example, Costa and Gentry (1986) reported that male northern fur seal pups received more milk than females but that, as a proportion of body mass, both sexes were provisioned equally. Donohue et al. (2002) also found the amount of milk consumed per kilogram of body mass did not differ by sex, and Arnould et al. (1996) found no difference in the milk intake of male and female Antarctic fur seal pups. Such findings are consistent with the suggestion by Guinet et al. (1999) that mothers invest equally in male and female fur seal pups, and that the faster growth rate of males reflects females losing a greater proportion of their mass during fasts rather than males receiving more maternal resources.

Examination of our data shows that male and female Juan Fernández fur seal pups have the same mass–length relationship. Trites and Bigg (1996) similarly showed that male and female northern fur seals have the same mass–length relationship until males reach the age of 4–5 years, when males experience accelerated growth. Sexual size dimorphism in New Zealand fur seals was most apparent after the age of 5–7 years (McKenzie et al. 2007). Thus, the only real difference between young male and female fur seals could be their size at birth. Trites (1991) showed that growth differential between

the sexes of northern fur seals begins shortly after implantation and increases to the time of birth. This suggests that males grow faster than females during the fetal period and upon attaining sexual maturity.

Estimates of body size are subject to biases related to mobility of animals of different ages and sizes and the movement of older pups to the water's edge as the breeding season progresses (Reid 2002). Pups of different ages and sizes therefore may not be distributed randomly on breeding beaches and thus may not be selected randomly for weighing. Trites (1993) found that the 1st northern fur seal pups captured for weighing tended to be smaller and younger than subsequent captures, possibly because smaller pups were easier to handle and were segregated to the peripheral rookery regions where sampling begins. Such hidden biases related to sampling error and fur seal biology were addressed in our study by having at least 2, and often 3, of the same observers capture all pups at the same location (El Ovalo) without differentiating size and condition of the pups. Only pups that were clearly in extremely poor condition (i.e., starving) were excluded from our analysis. All of the pups we measured were released with a paint mark on their backs to avoid recapturing the same individuals.

Juan Fernández fur seals show extreme sexual dimorphism that begins during the fetal stage and results in males being noticeably larger than females at birth (Ochoa-Acuña et al. 1998). However, we failed to find any indication that males grew proportionally faster than females or were in better body condition while pups. Our findings are consistent with those of Ochoa-Acuña et al. (1998), who used a longitudinal sampling design during the first 2 months of life and found that male and female Juan Fernández pups grew at the same rates. Differences in the growth rates were noted only between years during the 1st month (Ochoa-Acuña et al. 1998). Thus, the sexual differences among pups of *A. philippii* appear to originate before birth given that pup growth rates did not differ in our cross-sectional study or in the longitudinal study of Ochoa-Acuña et al. (1998). Similarities between our studies in daily growth rates further suggest that the growing population of *A. philippii* might have experienced similar environmental conditions in the 2 time periods (1988–1992 versus 2005).

In conclusion, differences among the growth rates of male and female Juan Fernández fur seal pups appear to originate before birth and are not accentuated during the nursing period. We found no sexual differences among the body condition and growth rates of male and female pups of *A. philippii* during mid-lactation using a cross-sectional sampling method. On average, males were heavier and longer than females on any given day of sampling but were not heavier than females of the same length.

## RESUMEN

Los machos de los lobos finos de Juan Fernández (*Arctocephalus philippii*) son significativamente más grandes que las hembras al nacer, mostrando un dimorfismo extremo como adultos. Investigamos las diferencias morfológicas entre

crías machos y hembras usando un muestreo al azar con el fin de evaluar si las tasas de crecimiento de las crías durante la temporada reproductiva son específicas del sexo. Caracterizamos las tasas de crecimiento usando medidas corporales de peso, largo y ancho, encontrando que el largo fue la medida corporal menos variable (basado en los coeficientes de variación de las 3 medidas corporales). Los machos fueron más pesados en promedio que las hembras durante todo el periodo de estudio, pero no crecieron más rápido que las hembras. Tampoco se encontraron diferencias en el índice de condición corporal de crías machos y hembras. Estos hallazgos sugieren que las diferencias sexuales entre las crías de *A. philippii* se originan durante la gestación y no se ven acentuadas durante la crianza.

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