Ontogeny of body size and shape of Antarctic and subantarctic fur seals

Sebastián P. Luque, Edward H. Miller, John P.Y. Arnould, Magaly Chambellant, and Christophe Guinet

Abstract: Pre- and post-weaning functional demands on body size and shape of mammals are often in conflict, especially in species where weaning involves a change of habitat. Compared with long lactations, brief lactations are expected to be associated with fast rates of development and attainment of adult traits. We describe allometry and growth for several morphological traits in two closely related fur seal species with large differences in lactation duration at a sympatric site. Longitudinal data were collected from Antarctic (*Arctocephalus gazella* (Peters, 1875); 120 d lactation) and subantarctic (*Arctocephalus tropicalis* (Gray, 1872); 300 d lactation) fur seals. Body mass was similar in neonates of both species, but *A. gazella* neonates were longer, less voluminous, and had larger foreflippers. The species were similar in rate of preweaning growth in body mass, but growth rates of linear variables were faster for *A. gazella* pups. Consequently, neonatal differences in body shape increased over lactation, and *A. gazella* pups approached adult body shape faster than did *A. tropicalis* pups. Our results indicate that preweaning growth is associated with significant changes in body shape, involving the acquisition of a longer, more slender body with larger foreflippers in *A. gazella*. These differences suggest that *A. gazella* pups are physically more mature at approximately 100 d of age (close to weaning age) than *A. tropicalis* pups of the same age.

Résumé : Il y a souvent un conflit entre les demandes fonctionnelles d'avant et d'après le sevrage sur la taille et la forme corporelles chez les mammifères, particulièrement chez les espèces chez lesquelles le sevrage implique un changement d'habitat. Contrairement aux allaitements prolongés, on s'attend à ce que les allaitements courts soient associés à des taux rapides de développement et d'acquisition des caractéristiques adultes. Nous décrivons l'allométrie et la croissance de plusieurs variables morphologiques chez deux espèces fortement apparentées d'otaries à fourrure vivant dans un même site, mais possédant des périodes d'allaitement de durée différente. Nous avons récolté des données longitudinales sur des otaries à fourrure antarctiques (*Arctocephalus gazella* (Peters, 1875); allaitement de 120 j) et subantarctiques (*Arctocephalus tropicalis* (Gray, 1872); allaitement de 300 j). La masse corporelle est semblable chez les nouveau-nés des deux espèces, mais les nouveau-nés d'*A. gazella* sont plus longs et moins volumineux et ils possèdent des nageoires antérieures plus grandes. Les taux de croissance de la masse corporelle avant le sevrage sont similaires chez les deux espèces, mais les taux de croissance des variables linéaires sont plus rapides chez les petits d'*A. gazella*. En conséquence, les différences de forme corporelle à la naissance augmentent au cours de l'allaitement et les petits d'*A. gazella* acquièrent la forme adulte plus rapidement que les petits d'*A. tropicalis*. Nos résultats indiquent que la croissance avant le sevrage est associée à une importante modification de la forme corporelle, ce qui se traduit chez *A. gazella* par l'acquisition d'un corps plus long et plus élancé avec des nageoires antérieures plus grandes. Ces différences laissent croire que les petits d'*A. gazella* âgés d'environ 100 j (près de l'âge de sevrage) ont une maturité physique plus grande que les petits d'*A. tropicalis* du même âge.

[Traduit par la Rédaction]

Introduction

Magnitude, rate, and pattern of mammalian growth determine adult body size and shape (Brody 1964; McNab 2002). Adult body size and shape, in turn, have major influences on viability and reproduction, among other life-history traits (Stearns 1992; Arendt 1997; Lindström 1999). Growth must be optimized relative to other demands, therefore it varies across individuals, populations, and species (Mangel and Stamps 2001; Caley and Schwarzkopf 2004). Some trade-offs occur in offspring, while others are imposed by different trade-offs acting on their mothers, which may alter the quality and quantity of milk that the mothers deliver. Interspecifically, milk composition and energy content are related to duration of lactation, so differences in the latter do not necessarily reflect total energy transferred to the offspring. Tilden and Oftedal (1997) noted that the energy den-

sity of milk is inversely related to duration of lactation in primates. Similarly, slowly growing and highly mobile offspring typify ungulate and macropod (kangaroos, wallabies, etc.) species with long lactations (Sæther and Gordon 1994; Fisher et al. 2002). However, body size is an important complicating factor, as lactation typically lasts longer in larger species (Peters et al. 1983; Clutton-Brock 1991; Ross 1998). Because of these confounding factors, reasons for interspecific variation in growth with respect to lactation duration remain poorly understood.

Pinnipeds are an attractive model for studying preweaning development because they undergo a transition from suckling on land to foraging at sea, involving major physical, physiological, and behavioural changes in preparation for that transition. The success of the transition ultimately depends on the acquisition of sufficient oxygen stores in relation to energy expenditure while diving (Burns and Castellini 1996; Burns 1999; Thorson et al. 1994; Horning and Trillmich 1997a, 1997b). However, increased physiological diving capacity must be closely coordinated with physical growth and the gradual development of swimming skills (Jørgensen et al. 2001; Bowen et al. 1999). Recent studies suggest that oxygen storage capacity across a broad range of marine mammal species does not reach adult levels before independent foraging (Noren et al. 2001; Burns et al. 2004). Therefore, lactation duration is an important factor affecting the ontogeny of physical and behavioural traits of offspring.

Relationships between life-history traits have been extensively studied in pinnipeds because they are ecologically and reproductively diverse and display a wide range of body sizes (Stirling and Kleiman 1983; Bonner 1984; Oftedal et al. 1987; Costa 1993; McLaren 1993; Boyd 1998). For instance, lactation lasts from <4 d (hooded seal, *Cystophora cristata* (Erxleben, 1777)) to 2–3 years (walrus, *Odobenus rosmarus* (L., 1758)). Quality of knowledge, however, varies across species; good estimates of lactation duration are available for only eight species — three otariids and five phocids (Schulz 2004). Good quantitative estimates of growth rate and duration of lactation for the same species are available for even fewer. Considering the difficulty in obtaining comprehensive and precise data, and given the widespread effects of spatiotemporal environmental variability on one-time estimates (Trillmich et al. 1991; Lunn et al. 1993), an alternative approach for comparing ecologically different and related species might be profitable. Two otariid species that have recently been used in the context of foraging and growth studies are the Antarctic (*Arctocephalus gazella* (Peters, 1875); AFS hereinafter) and subantarctic (*Arctocephalus tropicalis* (Gray, 1872); SFS hereinafter) fur seals (Kerley 1985; Goldsworthy et al. 1997; Klages and Bester 1998; Goldsworthy and Crowley 1999; Robinson et al. 2002).

We investigated comparative growth in AFS and SFS pups to determine the presence and nature of differences that may influence how the species cope with the critical postweaning period as pups become independent foragers. These species have similar adult body mass and length (Payne 1979; Bester and Van Jaarsveld 1994), yet exhibit a large disparity in lactation duration: 116 d in AFS (Costa et

al. 1988; Lunn et al. 1993) and 300 d in SFS (Kerley 1987; Guinet and Georges 2000), respectively. Therefore, the time required to acquire the physical and physiological characteristics enabling pups to become independent foragers may differ between the species. Comparisons between two species cannot be used to elucidate the relationship between lactation duration and growth patterns, but they offer an advantage that is rarely found in multispecies comparisons — the ability to control for confounding factors, such as environmental differences between populations of different species, in syntopic (locally sympatric) populations. AFS and SFS breed syntopically at a few locations where habitat differences between species are likely to be minimal, facilitating the interpretation of comparative analyses.

In previous research, Arnould et al. (2003) found that daily pup energy expenditure was higher in AFS than in SFS breeding syntopically at Ile de la Possession, Crozet archipelago, in the Southern Indian Ocean. In contrast, earlier reports from other syntopic sites suggested higher growth rates in body mass of AFS (Kerley 1985; Goldsworthy and Crowley 1999). We suggest that the reported disparity may reflect differences in body shape, which commonly differs adaptively between related species (Dodson 1975; Carrier 1983; Alatalo et al. 1984; Atchley 1984; Creighton and Strauss 1986; Gisbert 1999; Hochuli 2001).

Functional demands on body size and shape may change sharply between pre- and post-weaning ages in young pinnipeds, especially in otariids because of their long preweaning terrestrial existence (Koehler and Barclay 2000). Within the otariids, AFS and SFS differ substantially in this regard, so we predicted that these species would differ in growth trajectories and in the rate at which they acquire adult body form or shape (e.g., in foreflippers; Fish 1998; Fish et al. 2003). Specifically, we predicted that AFS pups should acquire adult flipper size and shape relatively sooner than would SFS pups, assuming that this allows them to make a successful transition to independent foraging at an earlier age.

Materials and methods

Fur seal colonies and identification procedures

Research was carried out at La Mare aux Elephants (46°22′29″S, 51°40′13″E), at the western end of Ile de la Possession, Crozet archipelago, Southern Indian Ocean, during the 2001–2002 (4 December – 25 March) and 2002–2003 (1 December – 16 March) breeding seasons (2001 and 2002 hereinafter). The site consists of two adjacent AFS and SFS colonies on different types of substrate — AFS on the northern part of the beach, which is composed of small to medium-sized pebbles, with gentle slopes behind; SFS on the southern part of the beach, which is composed of large boulders that have fallen from the steep hinterlands. Both species give birth close to shore, but the AFS colony grows in size as the season progresses, while the other species tends to remain close to shore during the same period.

Pups were individually marked (Georges and Guinet 2000; Arnould et al. 2003; Bailleul et al. 2005) over a 6 d (2001) or 13 d (2002) period (Table 1). Pup production and mean pupping date were estimated using (i) total pup counts (both years; including dead and living pups) on a weekly ba-

Table 1. Summary of numbers of Antarctic (*Arctocephalus gazella*; AFS) and subantarctic (*Arctocephalus tropicalis*; SFS) fur seal used in the study, broken down by year, species, and sex.

	Breeding season		
	2001	2002	Both
AFS			
Female	47 (10)	29 (24)	76
Male	48 (6)	29 (19)	77
Both	95	58	153
SFS			
Female	31 (27)	36 (32)	67
Male	27 (22)	30 (28)	57
Both	58	66	124

Note: Values indicate total number, including newborn pups; the number of newborn pups is shown in parentheses.

sis until no more births were observed and (*ii*) mark–recapture methods (2001 only). Peak pupping dates were 5 and 15 December (2001: 164 pups; 2002: 167 pups) for AFS, and 25 and 30 December (2001: 80 pups; 2002: 91 pups) for SFS. Populations of both species have been increasing at an annual rate of approximately 18% annually at least until 1994 (Guinet et al. 1994).

Morphometric measurements

Body mass (BM) of pups was measured to the nearest 0.05 at first capture, and every 5–9 d thereafter, on a 25 kg capacity digital suspension balance (ElectroSamson; Salter Brecknell, Fairmount, Minnesota). The following variables were also measured on pups upon first capture and every 12–16 d thereafter: body length (BL; nearest 0.5 cm, straight line from the tip of the nose to the flesh tip of the tail) with a tape measure, while animals were manually restrained over a board and positioned straight and flat on their ventral surface. In 2002, we also measured the following variables (nearest 0.5 cm) taken the same way and on the same schedule: body girth at levels of pinna, mid-neck, axillae, and umbilicus (G1–G4 hereinafter); distance from the tip of the nose to each of these points (see next; RL1–RL4 hereinafter). BL and RL1–RL4 were measured with a straight tape measure glued onto the board on which the animals were placed. Length, width, and surface area of foreflippers were measured as follows. First, the right foreflipper was extended and held to the side of and perpendicular to the body, and was placed on a wooden board with horizontal

and vertical scales (20 cm, marked every 5 cm). Second, a photograph was taken (Nikon Coolpix E885) in dorsal aspect from a distance of approximately 1.25 m. Finally, measurements were made from the photographs: (*i*) length (FL), defined as the distance from proximal end of the humerus (estimated by palpation) to the tip of foreflipper through the midline of the flipper; (*ii*) width (FW), defined as the largest distance perpendicular to the foreflipper length; and (*iii*) area (FA), estimated from the traced outline of the foreflipper using Object-Image version 2.11 (US National Institutes of Health, available from http://simon.bio. uva.nl/Object-Image/object-image.html [accessed 12 December 2007]). FL and FW were also measured directly on the foreflipper for cross-validation and subsequent analyses.

The relationship between direct measurements on flippers, and those taken photogrammetrically, were tested for linearity to detect outliers or invalid estimates. This led to the exclusion of FA estimates for pups with FL >27 cm, as the corresponding relationship became asymptotic beyond this value, indicating decreasing accuracy.

We also took all measurements on 63 AFS and 70 SFS adult females, but BM was measured to the nearest 0.5 kg. For comparisons with pups, each female was measured at least twice, and the median value for each variable was used to set adult body measurements. Estimates for some variables on adult males were included using data taken at South Georgia for AFS (Payne 1979) and at Marion Island (about 950 km west of Crozet) for SFS (Bester and Van Jaarsveld 1994).

Body volume (BV; ±0.01 L) of pups was obtained by using model B in Luque and Aurioles-Gamboa (2001), in which the body was modelled as two cones plus two truncated cones. Volumes of cones ($\frac{1}{3}\pi h(r_1^2 r_2^2 + r_1^2 r_2^2)$) and truncated cones ($\frac{1}{3}(\pi r^2 h)$) were calculated using the lengths (h) of cones estimated from RL1 and RL4, and lengths of truncated cones were estimated from RL2 and RL3, respectively. Girth was used to calculate radius (r).

Analyses

Interspecific differences in neonatal and adult body size were assessed using double classification analyses of variance, with a term for sex effects, including only data for which accurate ages were available. However, adult females were assigned to a single age category because their ages were unknown.

To determine whether growth trajectories varied according to species or sex, a linear mixed effects model (Raudenbush and Bryk 2002) was designed for the *j*th observation on the *i*th individual:

$$[1] \quad y_{ij} = (\beta_{00} + \beta_{01}\text{species}_i + \beta_{02}\text{sex}_i + \beta_{03}\text{species}_i\text{sex}_i + b_{i0}) + (\beta_{10} + \beta_{11}\text{species}_i + \beta_{12}\text{sex}_i + \beta_{13}\text{species}_i\text{sex}_i + b_{i1})x_{ij} + \varepsilon_{ij}$$

where β_{00} and β_{10} refer to the population intercept and slope, respectively, for AFS female pups, which is the baseline group. β_{01}, β_{02}, and β_{03} are fixed effects for the change in population intercept associated with the species, sex, and their interaction in relation to the baseline group. β_{11}, β_{12},

and β_{13} are the changes in population slope associated with the same effects. b_{i0} and b_{i1} are the random intercept and slope effects for the *i*th individual, respectively, and ε_{ij} is a within-subject residual term. Other terms were added to test for year effects and their interactions with body mass and

body length, but they were subsequently dropped if they were nonsignificant here and elsewhere at $\alpha = 0.05$.

Based on exploratory analyses and because ages were <300 d, a linear model was assumed, rather than a more complicated one. No assumptions were made regarding the autocorrelation structure of the ε_{ij} values. However, it was assumed that these were independent and normally distributed, regardless of the b_i values. In this model, species$_i$ and sex$_i$ take on values of zero and one, to indicate whether y_{ij} refers to AFS or SFS, and to a female or a male pup, respectively. We fitted the model using a restricted log-likelihood method, as described in Pinheiro and Bates (2000), and implemented in the NLME R package (Pinheiro et al. 2004). We subsequently estimated linear equations from this model, collapsing across and (or) within fixed effects that were not significantly different from zero. Only pups that were measured more than twice throughout the study period were considered for these analyses.

Because absolute age was not known for all individuals (Table 1), relative age was defined as the number of days elapsed since seals were first seen, which was taken as day zero. The difference in peak pupping dates between species was taken into account by adding the corresponding value from each breeding season (2001: 20 d; 2002: 15 d) to the relative age of AFS pups. Relative age was then used as the regressor x in eq. 1. Relative age was logarithmically transformed (logarithm base 10) and a constant was added to it to achieve linearity before using it as the regressor for BL in eq. 1. This transformation was chosen because BL changed faster in young pups (<30 d) than in older pups.

To address the question of whether growth trajectories gave rise to interspecific differences in the rate at which pups acquired adult body shape, two allometric relationships that might influence aquatic locomotory performance (e.g., Feldkamp 1987; Fish et al. 1988; Stelle et al. 2000) were studied: (1) foreflipper span (FS) squared vs. total FA (TFA) and RL3 vs. BL. FS was calculated as $2 \cdot FL + G3 \cdot \pi^{-1}$ and TFA was calculated as $2 \cdot FA$. The first relationship is the foreflipper aspect ratio expressed allometrically, whereas the second was used as an index of the position of foreflippers along the body axis relative to BL. One random measurement per female pup, where 80 d < age < 120 d, was selected for this analysis to eliminate any dependence between observations while maintaining a large enough sample size with valid foreflipper measurements (i.e., <27 cm). For adult females, the median value for each variable was used, assuming their growth was negligible.

To investigate how allometric relationships 1 and 2 compared between species and age groups (female pups vs. adult females), we used analysis of covariance (Zar 1996). We were interested in the interaction between age group (adult or pup) and species to test whether pups of one species were more allometrically similar to adults than the other. This approach avoided known biases associated with ratios between the variables from each relationship (Packard and Boardman 1999).

All statistical analyses were performed in the GNU R system (R Development Core Team 2006). The Shapiro–Wilks statistic and the Fligner–Killeen test were used to evaluate assumptions of normality of data distributions and homo-

geneity of variances, respectively, in analyses of variance and covariance. Results show SE as the measure of dispersion, unless stated otherwise.

Results

Neonatal and adult body size

There was no evidence of interannual effects on neonatal BM ($F_{[1,160]} = 1.70$, $P = 0.19$) or body length ($F_{[1,157]} = 2.03$, $P = 0.16$) when species and sex were taken into account. Therefore, measurements were pooled across years for subsequent analyses.

Male neonates were larger than females in most measurements (Table 2). AFS neonates were significantly longer than SFS neonates, had longer head and neck regions (RL1 and RL2), longer and narrower foreflippers, and greater FA (Table 2). Other interspecific differences were detected among females only; AFS female pups were larger in girth and BV than SFS pups. Adult female AFS were significantly heavier than adult female SFS. AFS adult females were larger in all flipper measurements than SFS adult females (Table 3).

Growth

Growth trajectories for each variable showed differing patterns of growth between species. No main effects or interactions of year with species or sex effects were significant in the models of mass and body length growth ($P > 0.5$, all cases), so the data were pooled. The magnitude and SE of interspecific and intersexual effects, in terms of eq. 1, are shown in Table 4. Estimated growth rates for each variable, with results of interspecific comparisons, are shown in Table 5.

In both species, sexual differences in BM increased steadily throughout lactation owing to the faster growth of male pups ($t_{[2822]} = 4.0$, $P < 0.01$). However, pups grew at a similar rate in both species ($t_{[2822]} = -0.04$, $P > 0.90$) after the sex effects were removed (Fig. 1). Neonatal BM did not differ between species, but the intercept of the relationship between BM and relative age was higher in AFS pups. No interactions were significant between species ($t_{[264]} = -1.34$, $P > 0.1$) and sex (; $t_{[2822]} = 0.18$, $P > 0.8$). A similar pattern was found for BV (Fig. 1), which is consistent with faster rates of growth in SFS girth (Table 5).

Growth in BL was faster in AFS pups ($t_{[1321]} = -2.57$, $P = 0.01$), as well as in males of both species ($t_{[1321]} = 2.21$, $P = 0.03$) (Fig. 1). There were no interactions between species and sex for slope ($t_{[1321]} = -0.05$, $P > 0.9$) or intercept ($t_{[260]} = -0.93$, $P > 0.3$). RL1 and RL2 showed faster rates of growth in AFS ($t_{[441]} = -4.65$, $P < 0.01$ and $t_{[441]} = -2.80$, $P < 0.01$, respectively), irrespective of sex ($t_{[441]} = 1.49$, $P > 0.1$ and $t_{[441]} = 1.53$, $P > 0.1$, respectively) (Table 5).

All foreflipper measurements increased in size faster in AFS: FL ($t_{[441]} = -10.50$, $P < 0.02$), FW ($t_{[441]}$ -2.45, $P < 0.02$), and FA ($t_{[208]} = -5.13$, $P < 0.01$) (Fig. 2). There were no significant interactions with sex (FL: $t_{[441]} = 0.96$, $P > 0.3$; FW: $t_{[441]} = 1.92$, $P > 0.3$; FA: $t_{[208]} = 0.47$, $P > 0.6$).

Allometry

Pup growth trajectories along individual variables led to differing allometric relationships between species and age

Table 2. Summary of morphometric differences between species and sexes in neonatal Antarctic (AFS) and sub-antarctic (SFS) fur seals.

Variable	Female		Male		F ratio[a]
	AFS	SFS	AFS	SFS	
Body mass (BM; kg)	4.90±0.150	4.60±0.080	5.40±0.210	5.45±0.100	0.98; **35.28**
Body length (BL; cm)	60.3±0.54	58.8±0.32	63.8±0.75	61.7±0.40	**11.34; 46.63**
Girth (G; cm)					
G1	30.4±0.30[b]	28.9±0.14	30.6±0.26	30.4±0.15	**9.57**
G2	29.5±0.32[b]	27.4±0.26	28.6±0.48	29.2±0.27	**16.22**
G3	39.6±0.54[b]	37.2±0.33	39.3±0.71	39.6±0.43	**7.87**
G4	39.1±0.64[b]	36.7±0.41	39.1±0.72	40.2±0.55	**9.27**
Reference length (RL; cm)					
RL1	8.3±0.13	7.8±0.11	8.8±0.17	8.1±0.11	**25.33; 9.24**
RL2	12.9±0.15	12.1±0.16	13.6±0.30	12.8±0.19	**16.86; 14.16**
RL3	30.3±0.41	29.0±0.37	31.1±0.62	30.9±0.43	2.45; **11.15**
RL4	43.8±0.43	40.2±0.34	45.0±0.59	41.9±0.37	**62.84; 13.99**
Foreflipper length (FL; cm)	22.2±0.23	21.1±0.14	23.0±0.45	22.0±0.18	**21.66; 13.77**
Foreflipper width (FW; cm)	8.0±0.11	8.2±0.10	8.4±0.17	8.8±0.10	**10.95; 24.10**
Foreflipper surface area (FA; cm^2)	142.1±3.57[b]	126.6±2.41	145.4±5.99	144.1±2.50	**4.30**
Body volume (BV; L)	4.5±0.15[b]	3.6±0.08	4.5±0.21	4.2±0.11	**4.93**

Note: For all variables, sample sizes (n) were 22 females and 17 males (AFS) and 32 females and 28 males (SFS), except for body mass and body length, where the sample sizes were 34 females and 25 males (AFS) and 59 females and 50 males (SFS). Values are means ± SE.

[a]Values for interspecific and intersexual comparisons, respectively, are shown. Significant effects are in boldface type. For significant interactions, only the value for the interaction is shown.

[b]For significant interactions, this is the species and sex with the highest mean.

Table 3. Summary of morphometric differences between adult Antarctic (AFS) and sub-antarctic (SFS) fur seal females.

Variable	AFS	SFS	F ratio[a]
Body mass (BM; kg)	32.7±0.36 (63)	30.5±0.45 (70)	**6.88**
Body length (BL; cm)	118.0±0.49 (63)	117.0±0.51 (70)	1.07
Axillary girth (G3; cm)	75.0±0.70 (24)	73.8±1.12 (22)	0.44
Reference length (RL3; cm)	63.3±0.52 (24)	61.6±0.55 (18)	2.74
Foreflipper length (FL; cm)	40.3±0.25 (62)	33.9±0.23 (70)	**179.80**
Foreflipper width (FW; cm)	12.9±0.08 (62)	11.9±0.07 (70)	**43.8**
Foreflipper surface area (FA; cm^2)	431.5±11.46 (16)	348.1±6.4 (11)	**17.67**

Note: Values are means ± SE, with sample size (n) in parentheses.

[a]Significant effects are in boldface type.

groups. A two-way analysis of covariance indicated that age-group differences in the slope of the relationship between FS^2 and TFA were dependent on species (slope interaction term: $F_{[1,43]} = 5.00$, $P = 0.03$). The age group did not significantly affect the allometric slope in AFS ($F_{[1,27]} = 2.83$, $P = 0.10$), but it did in SFS ($F_{[1,16]} = 5.29$, $P = 0.04$); female SFS pups had a higher allometric slope than adult females (Fig. 3A). Among pups, the allometric slope showed large differences between species ($F_{[1,25]} = 11.4$, $P = 0.002$), but it was similar between species among adults ($F_{[1,18]} = 0.36$, $P = 0.55$). In agreement with this trend, differences in the allometric slope between pups and adults were larger in SFS. Foreflipper size differences between pups and adults were also much larger in SFS.

RL3 scaled with BL differently between species ($F_{[1,69]} = 6.01$, $P = 0.02$), but similarly between age groups ($F_{[1,69]} = 0.29$, $P = 0.59$), without any interaction between these factors ($F_{[1,65]} = 1.08$, $P = 0.30$). The allometric slope of the relationship was higher in AFS, particularly among female pups (Fig. 3B).

Discussion

Neonatal and adult body size

Based on multiple traits, we documented many interspecific differences in neonatal body size, preweaning growth, and changes in body growth between two otariid species, AFS and SFS. We hypothesized that AFS pups should mature physically faster than SFS pups, given their younger weaning age. Neonates of the two species differed little on any measurements, but differed greatly in rates of growth. However, if adults show larger differences between species than neonates, then the results may simply reflect intrinsic morphological differences between species rather than different development patterns. Therefore, we begin our discussion by comparing neonate and adult body size of AFS and

Table 4. Summary of the effects of species (β_{01} and β_{11}), sex (β_{02} and β_{12}), and their interactions (β_{03}) on the growth of Antarctic and subantarctic fur seal pups, estimated using eq. 1.

Variable	Intercept effect			Slope effect	
	β_{01}	β_{02}	β_{03}	β_{11}	β_{12}
Body mass (BM)	**−0.950 (0.180)**		ns	ns	**0.010 (0.003)**
Body length (BL)[a]			ns	**−1.740 (0.680)**	**1.410 (0.640)**
Foreflipper length (FL)		**0.880 (0.330)**	ns	**−0.040 (0.004)**	ns
Foreflipper width (FW)	ns	**0.570 (0.140)**	ns	**−0.004 (0.001)**	ns
Foreflipper surface area (FA)		ns	ns	**−0.410 (0.080)**	ns
Body volume (BV)	**−1.030 (0.230)**		ns	ns	**0.010 (0.004)**
Girth (G)					
G1	**−1.400 (0.300)**	**0.860 (0.310)**	ns	ns	ns
G2		ns	**1.700 (0.750)**	**0.040 (0.008)**	ns
G3		ns	ns	**0.030 (0.010)**	ns
G4		ns	ns	**0.060 (0.015)**	ns
Reference length (RL)					
RL1		**0.550 (0.190)**	ns	**−0.010 (0.003)**	ns
RL2		**1.150 (0.310)**	ns	**−0.020 (0.006)**	ns
RL3	**−2.770 (0.580)**	**1.530 (0.590)**	ns	ns	ns
RL4	**−4.070 (0.590)**		ns	ns	ns

Note: The interactions in slope β_{13} were nonsignificant, therefore they were omitted. Significant effects are in boldface type; nonsignificant effects are indicated by ns; meaningless effects owing to interactions are blank. Standard errors are in parentheses.

[a]Relative age (d) was log-transformed to linearize this relationship.

Table 5. Comparison of growth rates of Antarctic (AFS) and subantarctic (SFS) fur seal pups, using the estimated slope (lower–upper 95% confidence limits) from eq. 1.

Variable	Female		Male	
	AFS	SFS	AFS	SFS
Body mass (BM; kg·d^{-1})	0.06 (0.06–0.07)[a]		0.08 (0.07–0.08)[a]	
Body length (BL; cm·log(d^{-1}))	17.58 (16.68–18.47)	15.83 (14.85–16.82)	18.99 (18.11–19.86)	17.19 (16.15–18.23)
Girth (G; cm·d^{-1})				
G1	0.04 (0.04–0.05)[b]			
G2	0.07 (0.06–0.08)	0.10 (0.09–0.11)	0.09 (0.07–0.10)	0.10 (0.09–0.1)
G3	0.14 (0.13–0.15)	0.17 (0.15–0.18)	0.14 (0.13–0.15)	0.17 (0.15–0.18)
G4	0.09 (0.08–0.11)	0.15 (0.13–0.18)	0.09 (0.08–0.11)	0.15 (0.13–0.18)
Reference length (RL; cm·d^{-1})				
RL1	0.05 (0.05–0.06)	0.04 (0.03–0.04)	0.05 (0.05–0.06)	0.04 (0.03–0.04)
RL2	0.10 (0.10–0.11)	0.09 (0.08–0.10)	0.10 (0.10–0.11)	0.09 (0.08–0.10)
RL3	0.10 (0.09–0.11)[b]			
RL4	0.13 (0.13–0.14)[b]			
Foreflipper length (FL; cm·d^{-1})	0.08 (0.08–0.08)	0.04 (0.03–0.05)	0.08 (0.08–0.08)	0.04 (0.03–0.05)
Foreflipper width (FW; cm·d^{-1})	0.02 (0.02–0.02)	0.02 (0.02–0.02)	0.02 (0.02–0.02)	0.02 (0.02–0.02)
Foreflipper surface area (FA; cm·d^{-1})	0.99 (0.89–1.09)	0.58 (0.45–0.72)	0.99 (0.89–1.09)	0.58 (0.45–0.72)
Body volume (BV; L·d^{-1})	0.04 (0.03–0.04)[a]		0.04 (0.04–0.05)[a]	

[a]Growth rate was common to both species.

[b]Growth rate was common to both species and both sexes.

SFS at Iles Crozet with other populations, and then focus on the factors that could have given rise to species differences in development.

We found no species differences in neonatal body mass at Iles Crozet, as Kerley (1985) also found for seven animals at Marion Island. No comparable data are available from Macquarie Island, the third site where the two species coexist. However, body mass alone cannot be used to compare body size between the species, because neonatal body shape differs — at birth, AFS pups are longer, have longer heads and necks, and have larger foreflippers. Therefore, the simi-

larity between species in body mass may indicate differences in body composition rather than similarities in body size. Based on a small sample of our pups from 2001, Arnould et al. (2003) showed that AFS pups had lower total body lipid stores than SFS pups at approximately 2 months of age, and our results suggest that the difference may also be present at birth.

Neonates of both species from our study were about a kilogram heavier than those weighed by Sparrow and Heywood (1996), although the difference cannot readily be attributed to any ecological factor because of the small
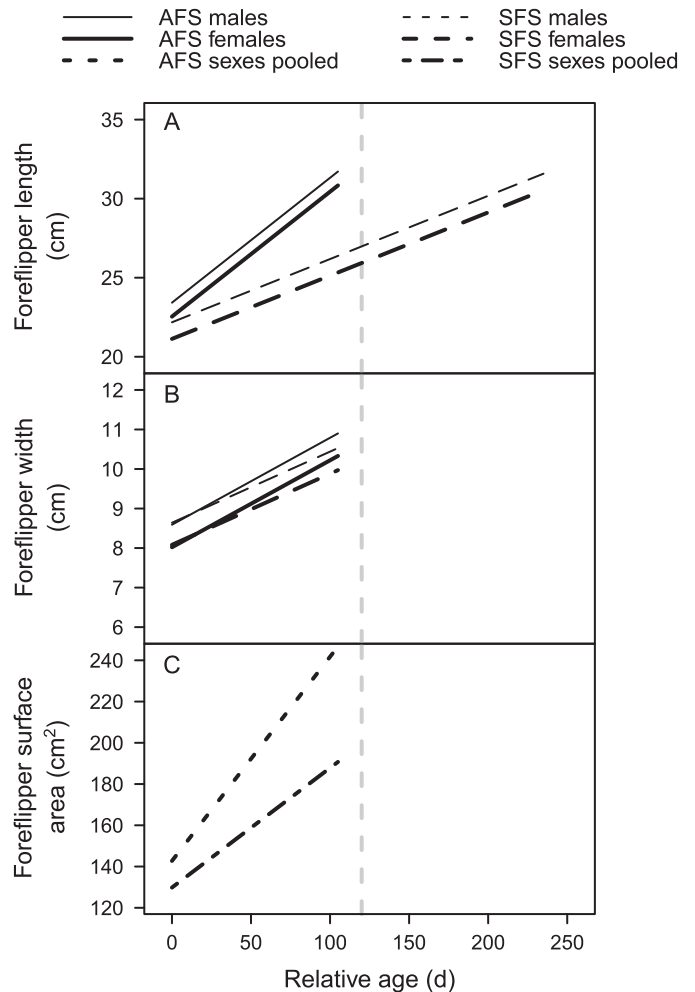
Fig. 1. Rates of growth in body mass (A) and body volume (B) did not differ between Antarctic (*Arctocephalus gazella*; AFS) and subantarctic (*Arctocephalus tropicalis*; SFS) fur seal pups during lactation, but growth in body length (C) was faster in AFS pups, based on eq. 1. The vertical broken line indicates weaning age of AFS pups. See Table 5 for estimated growth rates.

Fig. 2. Foreflipper length (A), width (B), and surface area (C) grew faster in Antarctic (AFS) compared with subantarctic (SFS) fur seal pups during lactation, based on eq. 1. The vertical broken line indicates weaning age of AFS pups. See Table 5 for estimated growth rates.
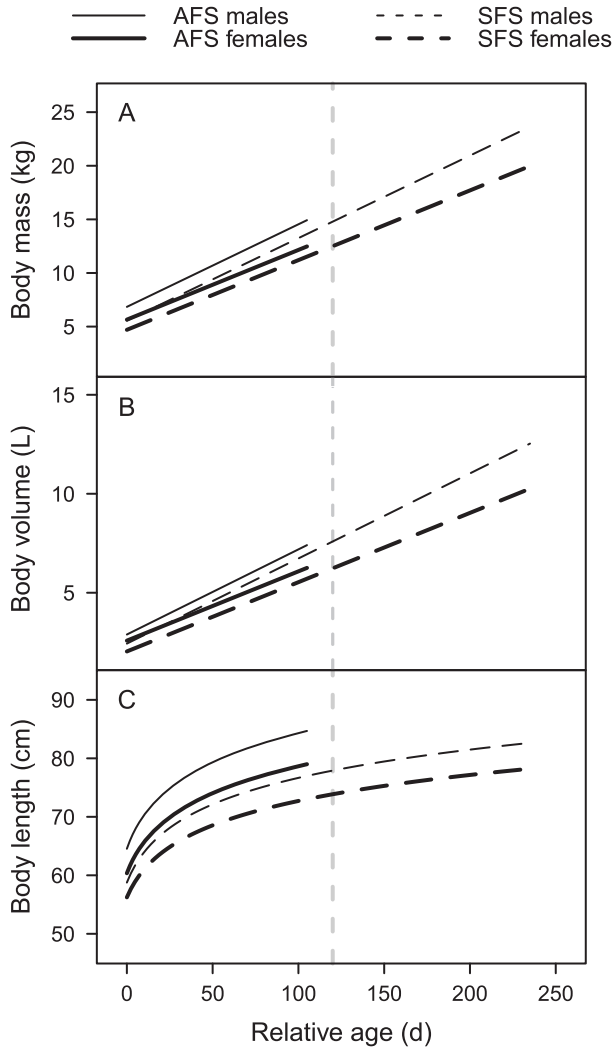
sample size in the latter study. Estimated pup birth dates in our study were similar to those reported by Kerley (1985) on Marion Island and were consistent with Sparrow and Heywood (1996), who showed that the two archipelagoes have a similar marine environment. The body mass of neonatal SFS pups in our study is comparable with that obtained from allopatric sites at Amsterdam Island (Georges and Guinet 2000) and Gough Island (Bester 1987; Bester and Van Jaarsveld 1994) for SFS and at Bird Island, South Georgia (Lunn et al. 1993), for AFS, suggesting that adult females are equally able to meet the demands of gestation in these environments, or can compensate for any differences without a cost to the newborn offspring.

Sexual differences in neonatal body size occur in all otariids, including in our species (Bester 1987; Kerley 1985; Lunn et al. 1993). However, pup sex did not influence most interspecific comparisons of neonatal body size in our analyses; sexual size differences were similar for both species,

except for girth measurements, body volume, and foreflipper surface area. For the latter three variables, AFS pups were larger than their congenerics only among females. The larger axillary girth and body volume of female AFS pups may reflect sex-specific differences in relative body lipid stores. Several authors have reported higher total body lipid stores in female pups compared with male pups belonging to several species (e.g., Arnould et al. 1996; Donohue et al. 2002; Beauplet et al. 2003), including those in this study. Therefore, everything else being equal, female pups would be expected to be more voluminous than male pups (Luque and Aurioles-Gamboa 2002).

Intraspecifically in pinnipeds, large mothers tend to give birth to large pups (Costa et al. 1988; Arnbom et al. 1997; Mellish et al. 1999). Boltnev and York (2001) found that neonatal mass increases at a decelerating rate with maternal mass in northern fur seals (*Callorhinus ursinus* (L., 1758)). The same relationship appears to hold interspecifically (Costa 1991), but whether the relationship is linear or not is unclear. Adult female AFS did not give birth to heavier pups in our study, despite being heavier than adult female SFS.

Fig. 3. Body shape of pups at approximately 100 d of age shows more similarities with that of adults in Antarctic (AFS) than in subantarctic (SFS) fur seals, based on (A) aspect ratio (relationship between foreflipper span^2 to foreflipper surface area) and (B) relationship between distance from tip of nose to axillae (RL3) and body length. The slopes (b) of the relationship (lower, upper 95% confidence limits) are shown.
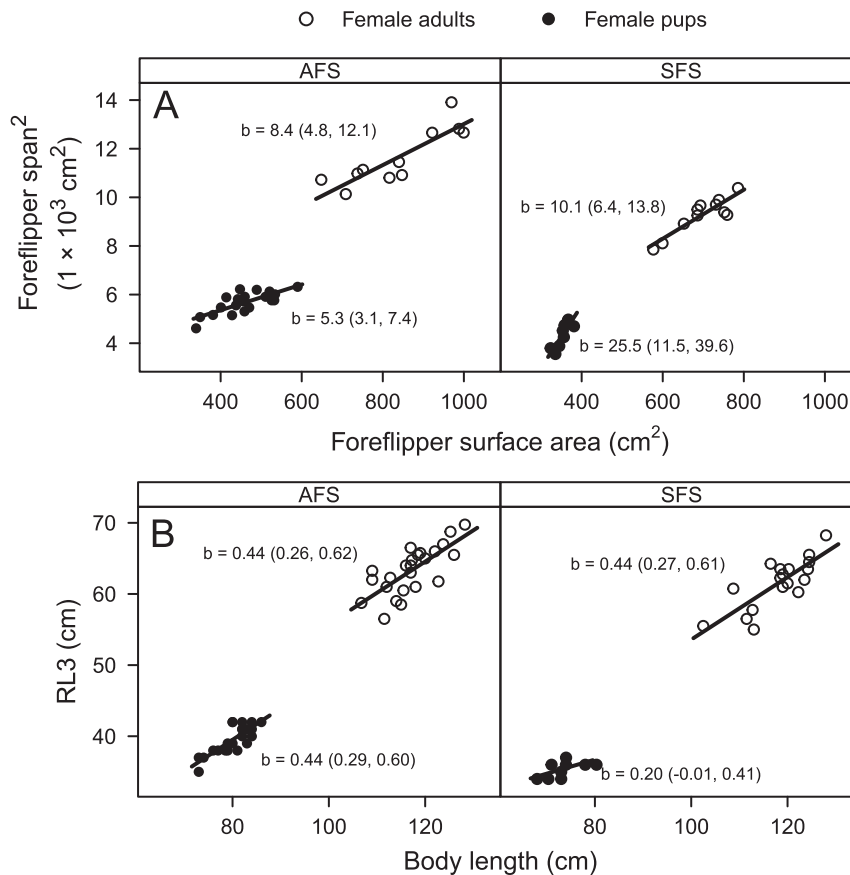
Compared with body mass, linear measurements (body length, axillary girth, and RL3) of physically restrained fur seals include larger measurement errors, reducing the statistical power of interspecific comparisons. Therefore, comparisons of pup body size in relation to maternal body size require more accurate measurements.

Both adult females and neonates differed in body shape between species, so interspecific differences in growth of body size may simply reflect morphological differences between AFS and SFS. We did not measure adult males of both species at La Mare aux Elephants, so we cannot generalize the argument to both sexes. However, if growth rates of individual variables were mainly determined by species-specific morphometric traits, then interspecific differences in these traits would be expected to be similar in neonates and adults, and body shape would be expected to remain relatively constant with age. Both expectations from this argument were not supported by our results. The magnitudes of morphometric differences between species were considerably larger among adult females than among neonates, and more similarities in body shape between adult females and 80–120 d old pups were found in AFS than in SFS. Therefore, the growth patterns exhibited by each species may not be only related to intrinsic morphometric differences between them.

Preweaning growth and allometry

We found no interspecific differences in rate of growth in body mass. This contrasts with previous studies of these species where they are sympatric (Marion Island: Kerley 1985; Macquarie Island: Goldsworthy and Crowley 1999). Our estimates of growth rates in body mass also were lower at Ile de la Possession than at those two sites. The reasons for such discrepancy are not clear, but methodological differences in pup sampling protocol (longitudinal vs. cross-sectional) and period of lactation covered hinder the comparison of results among these studies.

In our study, SFS and AFS pups had similar rates of growth in body mass and body volume. However, AFS pups had (*i*) faster rates of growth in body length, length of anterior portions of the body (RL1–RL2), and foreflipper dimensions, and (*ii*) lower rates of growth in body girth. These differences lead to a more streamlined body with relatively large foreflippers in AFS and a stockier body in SFS.

Two-species comparisons cannot provide general conclusions about relations between lactation duration and growth pattern (Garland and Adolph 1994) in otariids, but by minimizing other confounding factors, such a comparison can provide insights into possible mechanisms (Fisher et al. 2002). We hypothesized that AFS pups would exhibit more precocial growth than SFS pups. In AFS, differences be-

tween pup and adult foreflipper shape, as well as their position along the body, differed more than in SFS, which supports this hypothesis. These differences were reflected in the relationship between foreflipper span^2 and foreflipper surface area, which defines an important measure (aspect ratio) of aquatic locomotory ability (e.g., Feldkamp 1987; Fish et al. 1988; Norberg et al. 1993). For instance, low aspect ratio flippers are associated with increased costs of transport during steady swimming, but are better suited for rapid accelerations during quick turns in open water (Fish and Nicastro 2003; Fish et al. 2003). A similar argument can be made for the relationship between RL3 and body length, which is an index of the position of the foreflippers along the body. Relative position of the foreflippers along the body may have functional significance in aquatic stability and maneuverability, which is favoured when foreflippers are located far from the center of gravity (Fish et al. 2003).

Allometric analysis (Figs. 3A, 3B) suggests that AFS pups have foreplippers positioned more posteriorly along the body, as well as lower foreflipper aspect ratio, than SFS pups, and hence potentially greater aquatic turning abilities at 100 d (±20) of age. However, while AFS pups are near the end of lactation at this age, SFS pups are in mid-lactation, so increased aquatic turning abilities may be more critical for the former. Indeed, the largest foreflipper surface areas of female AFS pups were close to adult values, which was not the case for female SFS pups. Further studies are needed to assess the effect of differences in flipper size and structure for terrestrial locomotion, as well as the acquisition of foraging skills at sea, of these two species. Other factors that are likely to influence this process, such as the timing and pattern of moulting, should also be considered because they are known to affect pup thermoregulatory ability (Donohue et al. 2000).

To summarize, we found many differences in growth of AFS and SFS pups at Iles Crozet, where the species breed sympatrically, but maintain species-specific differences in lactation duration. Compared with SFS pups, AFS pups adopted a growth strategy that favours the acquisition of a longer, more slender body with larger foreflippers. The growth differences between species led to different allometric relationships between female pups and adult females, whereby AFS pups showed more similarities in foreflipper shape and position along the body with their adult counterparts than SFS pups. These interspecific comparisons of allometric relationships suggest AFS pups are physically more mature at approximately 100 d of age (close to weaning age) than SFS pups of the same age. Whether SFS pups achieve a similar level of physical maturity close to their weaning age, and whether different morphological development patterns affect the ontogeny of foraging skills, remain to be determined.

Acknowledgements

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