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BACULAR AND TESTICULAR GROWTH AND ALLOMETRY IN THE CAPE FUR SEAL *ARCTOCEPHALUS P. PUSILLUS* (OTARIIDAE)

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ABSTRACT

The baculum in *Arctocephalus p. pusillus* reaches up to 14.1 cm in length, 13.5 g in mass, and 1.3 g/cm in density (= mass/length). A pubertal growth spurt occurs between 2 and 3 yr of age, when bacular length increases by 28%, mass by 124%, and density by 77%; concurrently, body length increases by 14%. A second, weaker spurt occurs at social maturity (9–10 yr of age). Testes grow most rapidly between 1 and 2 yr of age, when testicular length increases by 29%. After 3 yr of age, growth in bacular and testicular length slows, and bacular mass continues to increase approximately linearly. Bacular and testicular lengths average 6.8% and 3.4% (respectively) of body length in adults, compared with 9.9% and 5.7% in the promiscuous harp seal (*Pagophilus groenlandicus*). Bacular length, mass, and density, and testicular length, are positively allometric to body length over growth; bacular length is isometric to testicular length. Among animals of the same age, bacular length and mass are positively allometric to body length in young animals, with negative allometry or isometry thereafter; testicular length is isometric to body length in young animals and negatively allometric thereafter. Patterns of early growth and allometry of the baculum and testes are interpreted as adaptations for mating opportunities, years before territoriality is possible. The baculum and testes of adult Cape fur seals and other otariids are small compared with those of most phocids, because sperm competition among male otariids is weak.

Key words: growth, allometry, sexual selection, reproduction, Cape fur seal, *Arctocephalus pusillus*.

The baculum is a large bone in pinnipeds but varies greatly in absolute and relative size across species, being large in the walrus (*Odobenus rosmarus*) and most phocids but small in elephant seals (*Mirounga* spp.) and fur seals and sea lions (Otariidae) (Scheffer and Kenyon 1963). Reasons for interspecific variation in size are not known, though Dixson (1995) suggested that the duration of copulation may select for large bacula in Carnivora, and Scheffer and Kenyon (1963) noted that large bacula occur in aquatically mating of pinnipeds. Comparative approaches are valuable for identifying general interspecific trends, but to understand their adaptive basis, detailed studies on single species are needed (Arnqvist 1997).

For this reason, we undertook a quantitative analysis of bacular growth and allometry in a typical species of otariid, the Afro-Australian fur seal (*Arctocephalus pusillus*). We included analysis of testicular measurements because testicular size is correlated with sperm production, which in turn is adapted to reproductive ecology and mating system (Kenagy and Trombulak 1986, Harcourt *et al.* 1995, Kappeler 1997, Short 1997). Our study was carried out on the African subspecies *A. p. pusillus,* hereafter termed Cape fur seal. The biology of the Cape fut seal has been intensively studied because of its commercial exploitation and its conflicts with commercial fisheries in southern Africa (Rand 1959, Shaughnessy 1985, David 1987, Punt and Butterworth 1995, Wickens 1996). In the course of these studies many specimens have been collected, providing the opportunity for the present investigation.

METHODS

Specimens (n = 827) were collected randomly at sea during 24 research cruises from 1974 to 1992 throughout the species' range in southern Africa. Collections were made in all months except December. Seals were collected by shooting with a 12-gauge shotgun. Specimens were processed immediately on board after being shot, and standard measurements were taken (American Society of Mammalogists 1967). Body length (nose-to-tail in a straight line, with the seal on its back) was used to represent body size, because body mass (and mass-related measures, like axillary girth) in marine mammals varies greatly through the annual cycle, in relationship to health, *etc.* The epididymides were removed from the testes, then both testes were measured (length, width, height) to the nearest mm. Only testicular length was analyzed in this study, because it had the least measurement error. Mean testicular length per individual was used in analyses. Penes were frozen on board ship, then later thawed and boiled for approximately 1 h; the bacula wete cleaned by hand. Bacula were air-dried at room temperature for several weeks before being measured (length to 1 mm, mass to 0.1 g). Bacular "density" per unit length was computed as (bacular mass/bacular length). Uppet canines wete used fot age determination. Longitudinal ground sections were prepared, and age was estimated by counting growth-layer-groups in the dentine (Oosthuizen 1997). Five independent estimates were made, and their mean was taken as the estimated age. Sections that gave variable estimates were excluded from analyses.

Seals were assumed to have a birth date of 1 December (Warneke and Shaughnessy 1985). Statistical analyses were conducted on ages estimated to the nearest 0.1 yr and on age (year) classes (age class 1 = 0.5–1.4 yr, age class 2 = 1.5–2.4 yr, *etc.*); specimens younger than 0.5 yr of age were excluded.

To control for seasonal variation in testicular growth (Rand 1956*a,* Stewardson *et al.* 1998), analyses of testicular data were restricted to the large sample of animals ($n = 270$) collected in March and April. This was after the breeding season, but we assumed that trends in relative size were unaffected. Testicular volume was estimated as (length × depth × breadth)($\pi/6$), and is reported below per testis (*i.e.,* not per seal).

Changes in growth rate with age can be quantified in several ways, *e.g.,* by the instantaneous or geometric growth rate (= instantaneous rate of increase) in size y between ages 0 and t $[\log_e(y_t/y_0)]$. Alternatively, the relative rate of increase $[(y_t - y_0)/y_0]$ (usually expressed as a percentage) can be used (Ricker 1975, Simpson *et al.* 1960). These approaches yielded nearly identical results in our study. We employed the latter measure and refer to it hereafter as the relative growth rate.

Allometric relationships among body, bacular, and testicular size were explored in the usual manner, with the allometric equation $Y = b{\cdot}X^a$. In allometric analysis there is properly no distinction between dependent and independent variables, so it is appropriate to use geometric mean regression (also termed reduced major axis regression) (Teissier 1960). This is similar to simple linear regression when the correlation r between Y and X is high, and is identical when $r = 1$ (the slope in reduced major axis regression $= m/r$, where m is the slope in simple linear regression, and r is Pearson's product-moment correlation coefficient). Thus, for practical purposes, simple linear regression is usually acceptable for quantifying relative size and has the desirable property of being statistically well known. In addition, for allometric analyses of body parts relative to overall body size, it is reasonable to use simple linear regression (Teissier 1960). Geometric mean regression is normally more suitable for analyses involving body parts, but we assumed that testicular hormones influence bacular growth and so treated bacular size as a variable dependent on testicular size.

For analysis of size-related allometry, data within age classes were used. Growth was apparent within age classes 1 through 6, so only subsamples of specimens aged 1.3 and 1.4, 2.3 and 2.4, *etc.* (which did not differ significantly from one another) were used for those age classes. For all regressions, residuals were examined for normality, homogeneity of variance, and independence.

Except for regression slopes and intercepts, data and statistical results are reported to two decimal places for values <1, one decimal place for values <100, and no decimal places for higher values; standard deviations are given with one more decimal place than their associated means (Sokal and Rohlf 1981); slopes and intercepts are reported to two decimal places for values <10.

Data screening and statistical and graphical analyses were done with DataDesk 5.0, Kaleidagraph 3.0, SuperAnova 1.11, and Statview 4.5.

RESULTS

General patterns of body, bacular, and testicular growth—Relative growth rates (RGRs) between years revealed two spurts in growth before males first became territorial at approximately 10 yr of age: between 2 and 3 (RGR = 14.3%), and between 9 and 10 yr of age (RGR = 6.3%; Table 1, Fig. 1A). Little growth occurred after that age (for seals >10 yr old, mean body length = 186 cm, SD = 12.2, n = 36). Using the estimate for males >10 yr of age as an asymptote, 69% of growth in body length was reached at 3 yr of age, and 96% at 10 yr; 90% was reached between 8 and 9 yr.

The baculum similarly showed spurts in growth between 2 and 3 and between 9 and 10 yr of age (Table 1, Fig. 1B, C). Between 2 and 3 yr of age, bacular length increased by 28%, mass by 124%, and density by 77%. The longest baculum was 14.1 cm in length (in a 10.9-yr-old male); for males >10 yr old, mean length = 12.1 cm (*SD* = 0.70, n = 35). Bacular mass increased rapidly with age, as expected for a cubic measure; the heaviest baculum was 13.5 g in mass, in a 12.4-yr-old male (mean mass for males >10 yr old = 9.9 g, SD = 1.76, n = 34). Reflecting the patterns of growth for bacular length and mass, bacular density also increased rapidly throughout life, with highest density being 1.1 g/cm in a male aged 12.0 yr (mean density for males >10 yr old = 0.82 g/cm, SD = 0.134, n = 34). Again using the values for males >10 yr old as an asymptote: 61% of growth in bacular length, 15% in bacular mass, and 24% in bacular density were reached at 3 yr of age; and 99%, 90%, and 90%, respectively, were reached at 10 yr. All measures of bacular size reached 90% of asymptotic values by 8–9 yr of age.

Growth in testicular length was rapid from 1 to 3 yr of age and then slowed, reaching an asymptote at approximately 6.0–6.5 cm (Table 1, Fig. 1D). The pattern of relative growth differed from that for body and baculum, being highest between 1 and 2 (28.8%) and 2 and 3 (21.5%) yr of age, declining to 8.8% between 3 and 4 yr, and fluctuating thereafter at a low level. Trends for males >8 yr of age were not apparent because of small sample sizes, though there was a suggestion of continued growth throughout life. Testicular length averaged 6.3 cm for males >10 yr old (*SD* = 0.47, n = 8). At 2 yr of age, length was 63% of this value, and at 10 yr it was 92%; 90% of asymptotic size was reached between 6 and 7 yr of age.

Testicular volume ranged from 1 to 26 ml^3 per testis for specimens collected in March and April (Table 1). For males >10 yr old collected in those months, volume averaged 18.4 ml^3 (*SD* = 4.48, n = 8) per testis. Specimens collected closer to the breeding season had larger testes: for males >10 yr old collected from 30 August to 19 October, volume averaged 26.5 ml^3 (*SD* = 6.35, n = 7) per testis. As noted, no data are available for the breeding period.

General relationships of bacular and testicular size to body length—Relative to body length, bacular length increased quickly up to 5 yr of age, increased slowly to 9–10 yr, then declined (Fig. 2A). For age classes 5–10, bacular length exceeded 6.5% of body length, peaking in 9-yr-old males at 6.8% (n = 45); in males >10 yr old, bacular length averaged 6.5% of body length (n = 34).

Growth spurts in bacular and body length were approximately concurrent but differed in magnitude; rates of bacular growth and body growth differed

Table 1. Statistics on body length, bacular size, and testicular length (testicular data from March and April only). Data shown as mean ± SD (range; *n*).

Age class (yr)	Body length (cm)	Bacular length (cm)	Bacular mass (g)	Bacular density (g/cm)	Testicular length (cm)	Testicular volume (cc)[a]
1	103 ± 7.7 (86.5–121; 64)	5.1 ± 0.60 (4.0–6.7; 57)	0.38 ± 0.195 (0.20–1.1; 56)	0.07 ± 0.028 (0.04–0.16; 56)	3.1 ± 0.54 (2.2–4.3; 21)	1.9 ± 1.25 (0.85–6.3; 20)
2	112 ± 8.5 (94.5–136; 151)	5.8 ± 0.87 (4.2–8.3; 150)	0.69 ± 0.371 (0.30–1.9; 150)	0.11 ± 0.043 (0.06–0.24; 150)	4.0 ± 0.53 (2.9–4.8; 44)	4.3 ± 1.84 (1.2–8.3; 44)
3	128 ± 9.5 (104–148; 78)	7.4 ± 0.97 (5.2–9.8; 69)	1.5 ± 0.63 (0.4–3.7; 69)	0.20 ± 0.059 (0.08–0.38; 69)	4.8 ± 0.59 (3.7–6.2; 38)	7.2 ± 2.28 (3.2–13.7; 38)
4	138 ± 9.1 (121–161; 89)	8.6 ± 1.09 (6.3–11.2; 82)	2.4 ± 0.85 (0.9–4.2; 82)	0.27 ± 0.074 (0.12–0.46; 82)	5.3 ± 0.47 (4.5–6.2; 33)	10.6 ± 3.05 (5.8–20.5; 32)
5	145 ± 7.3 (129–163; 93)	9.4 ± 0.74 (7.6–11.7; 89)	3.2 ± 0.90 (1.6–5.8; 88)	0.33 ± 0.077 (0.17–0.59; 88)	5.4 ± 0.62 (4.2–6.6; 37)	11.5 ± 3.17 (5.4–18.3; 36)
6	154 ± 8.3 (135–180; 95)	10.1 ± 0.68 (8.4–12.1; 90)	4.0 ± 1.02 (2.1–7.3; 89)	0.39 ± 0.085 (0.24–0.67; 89)	5.5 ± 0.48 (4.8–6.5; 33)	12.7 ± 3.18 (8.1–20.6; 32)
7	161 ± 7.2 (147–178; 74)	10.8 ± 0.74 (8.8–12.7; 69)	5.1 ± 1.08 (2.9–8.1; 70)	0.47 ± 0.092 (0.28–0.77; 69)	5.8 ± 0.43 (5.0–6.6; 24)	13.1 ± 3.99 (8.8–26.4; 24)
8	165 ± 9.7 (146–186; 71)	10.9 ± 0.79 (8.9–12.5; 68)	5.8 ± 1.66 (2.9–12.9; 68)	0.53 ± 0.145 (0.32–1.3; 68)	5.8 ± 0.51 (5.0–7.0; 18)	14.7 ± 3.69 (7.7–24.6; 18)
9	168 ± 9.8 (150–191; 47)	11.3 ± 0.82 (10.0–13.3; 45)	6.8 ± 1.43 (4.2–11.6; 44)	0.60 ± 0.115 (0.41–1.0; 44)	5.8 ± 0.71 (5.2–7.0; 9)	14.7 ± 3.38 (10.7–20.5; 9)
10	179 ± 8.8 (162–193; 20)	12.0 ± 0.77 (10.6–13.8; 20)	8.7 ± 1.42 (5.8–11.1; 20)	0.72 ± 0.106 (0.48–0.86; 20)	5.8 ± 0.41 (5.4–6.4; 5)	14.5 ± 2.53 (12.1–18.4; 5)

Table 1. Continued.

Age class (yr)	Body length (cm)	Bacular length (cm)	Bacular mass (g)	Bacular density (g/cm)	Testicular length (cm)	Testicular volume (cc)[a]
11	184 ± 11.6 (162–208; 19)	12.0 ± 0.76 (10.7–14.1; 19)	9.3 ± 1.54 (6.9–12.8; 19)	0.78 ± 0.115 (0.57–1.0; 19)	6.2 ± 0.27 (6.0–6.6; 4)	19.4 ± 3.40 (14.7–22.8; 4)
12	184 ± 9.7 (168–197; 7)	12.0 ± 0.56 (11.4–12.8; 7)	10.5 ± 1.98 (8.4–13.5; 7)	0.88 ± 0.144 (0.71–1.1; 7)	6.2 ± 1.06 (5.4–7.0; 2)	15.9 ± 8.91 (9.6–22.2; 2)
13	188 ± 15.5 (172–209; 4)	12.5 ± 0.70 (12.0–13.5; 4)	10.3 ± 1.64 (7.9–11.6; 4)	0.82 ± 0.111 (0.66–0.92; 4)	6.6 (*n* = 1)	16.8 (*n* = 1)
14	191 ± 9.8 (174–199; 5)	12.3 ± 0.60 (11.6–12.8; 4)	11.2 ± 2.08 (8.4–12.9; 4)	0.91 ± 0.184 (0.66–1.1; 4)	6.6 (*n* = 1)	21.2 (*n* = 1)
16	215 (*n* = 1)	13.2 (*n* = 1)				

[a] Per testis.

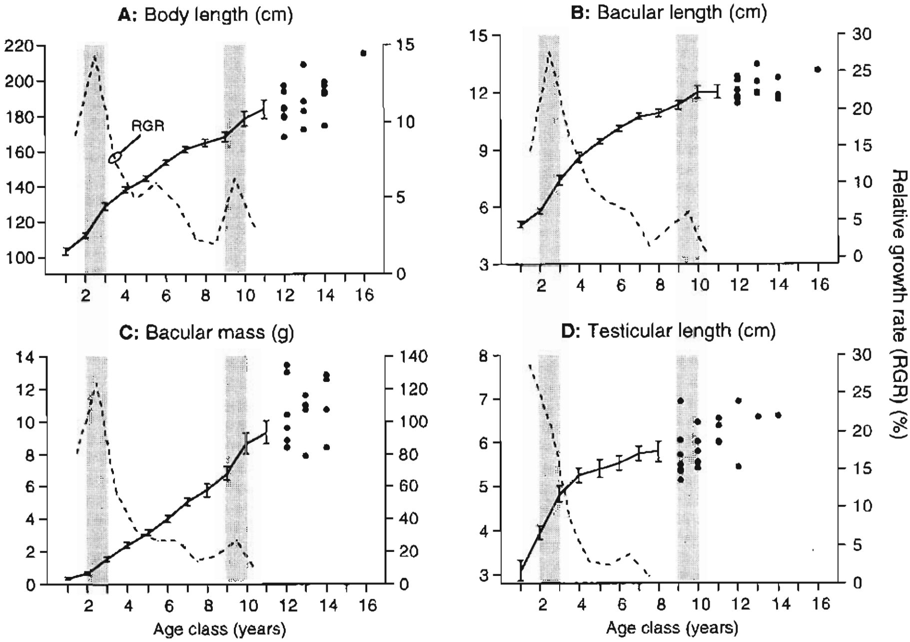

Figure 1. Growth in body length, bacular length and mass, and testicular length. Means and 95% confidence intervals on means shown for age classes with $n > 10$; raw data shown for other age classes. Relative growth rates (RGRs) plotted as dashed curves. Transitions between 2 and 3, and between 9 and 10 yr of age, represented by shaded rectangles. Testicular data from March and April only. For sample sizes, see Table 1.

most between 1 and 5 yr of age, particularly between 2 and 3 yr when absolute growth rates were also highest (Table 1, Fig. 1A, B).

Testes grew quickly relative to body size between 1 and 3 yr of age, peaking at 4 yr when testicular length averaged 3.7% of body length (3.9% when adjusted for seasonal variation; Fig. 2B). Relative testicular length declined after that age, averaging only 3.3% of body length in seals >8 yr old (seasonally adjusted estimate = 3.4%).

Patterns of relative testicular and body growth were not concordant (Fig. 1A, D). High relative growth in testicular length occurred in age classes 1–4, followed by a sharp decline and then a levelling-off (Table 1, Fig. 1D).

Growth-related allometry of bacula, testes, and body—Over all age classes, bacular length, mass, and density, and testicular length, were positively allometric to body length; bacular length was isometric to testicular length (Table 2, Fig. 3). In postpubertal growth the positive allometry of bacular size to body length weakened, and negative allometry characterized both testicular length in relation to body length and bacular length in relation to testicular length.

Size-related allometry of bacula, testes, and body—Bacular allometry in relation to body length varied across age classes (*i.e.,* the ratio of specific growth rates in bacular and body size changed with age; Simpson *et al.* 1960, Shea 1985). For example, bacular length and mass exhibited mainly positive allometry in

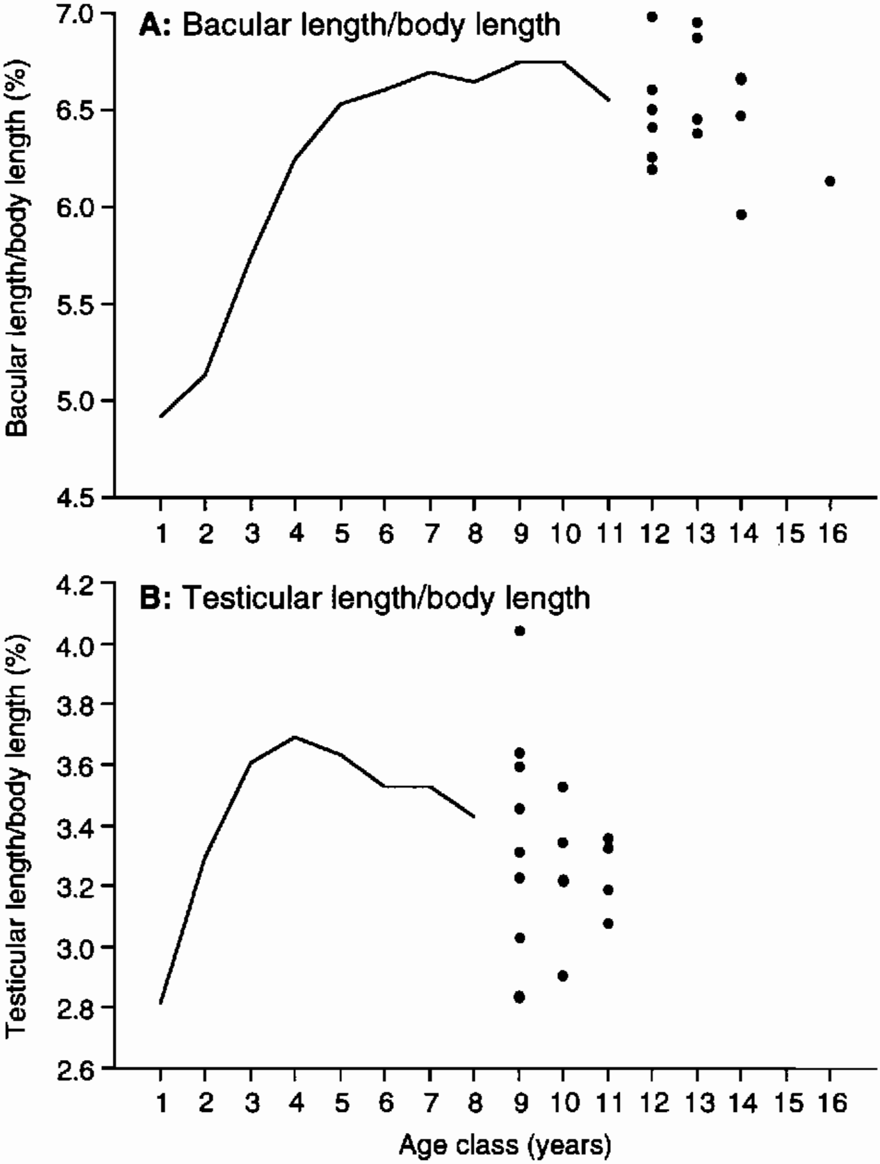

Figure 2. Changes with age in (A) bacular and (B) testicular length in relation to body length.

young age classes and mainly negative allometry thereafter (up to age class 11; Fig. 4A, B). Size-related allometry of testes also changed with age; positive allometry characterized 1-yr-old animals, followed by isometry in older age classes (up to age class 8; Fig. 4C). Bacular length was negatively allometric to testicular length in all age classes (Fig. 4D).

Variation in body length, bacular size, and testicular length—Body length was

Table 2. Summary of results for allometric (log-log) regressions related to growth (for regressions involving testes, only data from March and April used). $P < 0.001$ for all regressions.

Age	*n*	Slope (95% CI)	Intercept (95% CI)	r^2
Bacular length (cm) *vs.* body length (cm)				
<4	273	1.60 (1.51, 1.69)	−2.52 (−2.70, −2.34)	0.82
≥4	492	1.12 (1.07, 1.18)	−1.46 (−1.59, −1.33)	0.74
All	765	1.59 (1.56, 1.62)	−2.48 (−2.55, −2.41)	0.92
Bacular mass (g) *vs.* body length (cm)				
<4	272	5.68 (5.37, 6.00)	−11.9 (−12.5, −11.2)	0.82
≥4	489	4.40 (4.20, 4.61)	−9.02 (−9.47, −8.58)	0.79
All	761	5.59 (5.48, 5.70)	−11.6 (−11.9, −11.4)	0.93
Bacular density (cm/g) *vs.* body length (cm)				
<4	272	4.08 (3.82, 4.34)	−9.33 (−9.86, −8.80)	0.78
≥4	488	3.28 (3.09, 3.46)	−7.56 (−7.96, −7.16)	0.72
All	760	4.00 (3.91, 4.09)	−9.15 (−9.34, −8.96)	0.91
Testicular length (cm) *vs.* body length (cm)				
<3	64	1.82 (1.39, 2.25)	−3.20 (−4.08, −2.32)	0.54
≥3	201	0.72 (0.60, 0.84)	−0.83 (−1.10, −0.57)	0.41
All	265	1.22 (1.12, 1.31)	−1.94 (−2.14, −1.73)	0.71
Bacular length (cm) *vs.* testicular length (cm)				
<3	60	0.59 (0.47, 0.72)	0.46 (0.39, 0.53)	0.62
≥3	186	0.78 (0.63, 0.93)	0.42 (0.31, 0.53)	0.36
All	246	0.97 (0.89, 1.04)	0.28 (0.23, 0.33)	0.74

most variable in young animals, with the coefficient of variation (CV) being 7%–8% for age classes 1–4, but only 4%–6% thereafter (Table 3). The same pattern occurred in bacular size and testicular length, but variation was much greater. For example, CVs for bacular length were 13%–15% for age classes 1–4 and 5%–8% thereafter; CVs for testicular length declined from 18% in age class 1 to 8%–9% in age classes 6–7.

DISCUSSION

General patterns of size and growth—A few estimates of bacular size in the Cape fur seal have been made by other workers. Mohr (1963) measured a baculum that was 11.8 cm long and 8 g in mass (density = 0.68 g/cm). In his study, based on collections made from 1947 to 1951, Rand (1956*a*) reported mean (and maximal) length as 12.6 cm (13.5 cm) and mass as 12.0 g (15.2 g) (mean density = 0.95 g/cm). Due to the lack of techniques for age determination at the time, Rand (1956*a*) could not determine ages, so his analyses of bacular growth are not comparable to ours.

Our data can be compared with those for the subantarctic (*Arctocephalus tropicalis*) and northern (*Callorhinus ursinus*) fur seals (Scheffer 1950; Rand 1956*b*; Murphy 1969, 1970; Bester 1990; McLaren 1993; Bester and van

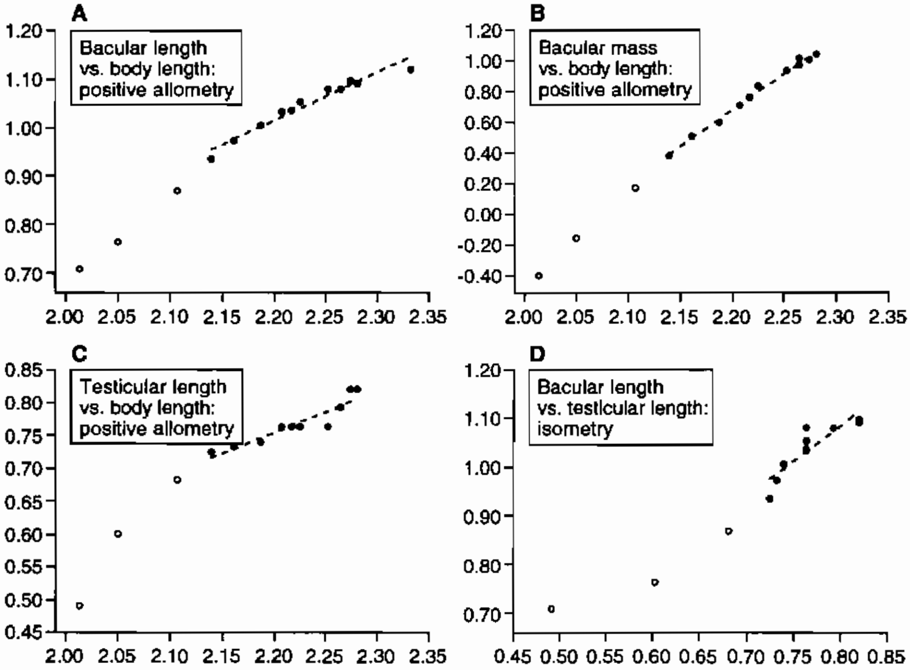

Figure 3. Allometric relationships of bacular length and mass, and testicular length, to body length, and between bacular and testicular lengths. Regression lines for seals >3 yr old shown (regressions based on age-class means, for graphical purposes). Testicular data from March and April only.

Jaarsveld 1994). In the Cape fur seal, growth in bacular length averages 17% per year between 1 and 5 yr of age (maximum = 28%), compared with 20% and 18%, respectively, for the subantarctic and northern fur seals (maximum for the latter species = 24%) (unpublished data[2]; Scheffer 1950). Over the same ages, growth in body length averages 9% in the Cape fur seal, and 12% and 10% in the other species, respectively (Scheffer and Wilke 1953, Bester and van Jaarsveld 1994). Only one sea lion has been studied; bacular length increases by a third between 1 and 3 yr of age in the California sea lion (*Zalophus californianus*) [Morejohn 1975; unfortunately, information on rates of body growth in young males is poor (McLaren 1993)]. In the best-studied phocid (harp seal, *Pagophilus groenlandicus*), much faster bacular growth occurs than in otariids: bacular length increases by 48% between 3 and 4 yr of age (concurrently, body length increases by 7%; Miller *et al.* 1998). The pattern of rapid pubertal growth in bacular size in the Cape fur seal and other pinnipeds suggests that there are appreciable adaptive advantages to large bacular size in young males. For the Cape fur seal, this interpretation is strengthened

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[2] Personal communication from M. N. Bester, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa, September 1997.

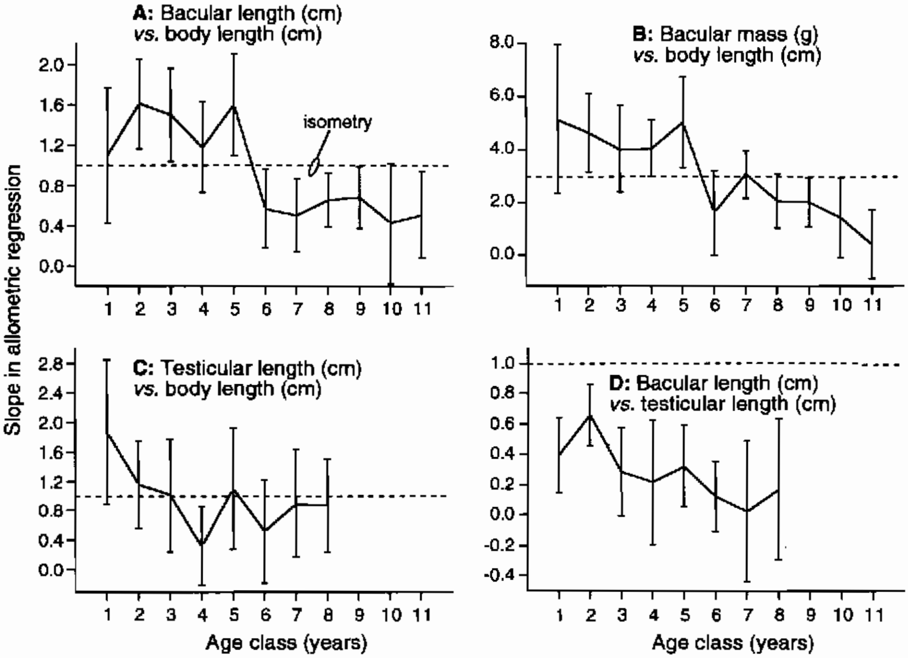

Figure 4. Allometric relationships of bacular and testicular size varied with age: slopes and 95% confidence intervals from allometric regressions of (A) bacular length, (B) bacular mass, and (C) testicular length on body length shown for age classes with $n > 15$. Similar graph shown for allometric regression of (D) bacular length on testicular length. Isometry represented as horizontal dashed lines.

Table 3. Summary of variation in body length, bacular length and mass, and testicular length in relationship to age. Data shown as coefficient of variation (CV, in per cent), for age classes with $n > 15$. CVs for the sample from March and April, corresponding to last column, shown in parentheses. For sample sizes, see Tables 1 and 2.

Age class (yr)	Body length (cm)	Bacular length (cm)	Bacular mass (g)	Testicular length (cm)
1	7.5 (6.2)	11.9 (10.6)	50.9 (48.5)	17.6
2	7.6 (6.2)	15.1 (12.9)	53.7 (35.6)	13.3
3	7.4 (5.0)	13.1 (10.0)	40.9 (32.8)	12.3
4	6.6 (5.9)	12.7 (9.5)	35.4 (26.6)	8.9
5	5.0 (4.7)	7.8 (8.9)	28.6 (30.0)	11.5
6	5.4 (4.4)	6.7 (5.6)	25.5 (19.8)	8.6
7	4.5 (4.0)	6.9 (7.1)	21.3 (23.2)	7.5
8	5.9 (5.7)	7.2 (7.2)	28.6 (21.7)	8.7
9	5.8 (–)	7.2 (–)	20.9 (–)	—
10	5.0 (–)	6.4 (–)	16.4 (–)	—
11	6.3 (–)	6.3 (–)	16.5 (–)	—

by the observation that most testicular growth occurs by 3 yr of age, when most males first exhibit spermatogenesis (Stewardson *et al.* 1998).

Male Cape fur seals start to become territorial during the breeding season at 8–10 yr of age, which coincides with the second spurt in body and bacular growth that we observed. Rapid body growth at this time seems clearly adaptive in terms of the advantage of large size in esrablishing and holding territories. The concurrent spurt in bacular growth suggests that increased bacular size becomes adaptively significant around the same time, though reasons for this are unclear.

Variation—Young Cape fur seals are more variable in body, bacular, and testicular size than are adults, which is the norm in mammals (Yablokov 1974). In the northern fur seal, Scheffer (1950) estimated CV in bacular length as 7.8% from 1 to 5 yr of age, and 4.6% from 6 to 8 yr (older animals were not studied); CV in testicular mass averaged 34% and 17%, respectively. An identical trend occurs in the harp seal, in which CV in body length averages 6.5% from 1 to 5 yr of age, and 5.1% from 6 to 20 yr; CV in bacular length averages 21% and 9.1%, respectively (Miller *et al.* 1998). Variation in the attainment of physiological sexual maturity depends on growth rate and body size, which must contribute to the high variation that occurs in young pinnipeds (Scheffer 1950; Kenyon *et al.* 1954; Hewer 1964; Murphy 1969, 1970; Sergeant 1973). Fast growth early in life is important to fitness and so is generally selected for (Clutton-Brock 1988, Baker and Fowler 1992, Boltnev *et al.* 1998).

Bacula and testes are more variable than body size throughout life in the Cape fur seal and in the other species just discussed, and traits subject to sexual selection may be highly variable in general (Darwin 1871, Min 1997). Multiple proximate causes underlie such variation in male reproduction (Arata *et al.* 1965), with the overall consequence being variable mating behavior (Andersson 1994, Bradbury and Vehrencamp 1998). On the basis of current knowledge, we do not interpret the patterns of variation in pinnipeds as adaptations *per se* (*e.g.*, to variable or fluctuating environments and opportunities for mating; Simons and Johnston 1997).

Allometry—Growth-related allometry of the baculum in relation to body size in the Cape fur seal is strongly positive; for example, the slope of the allometric regression for bacular length *vs.* body length over all age classes is about 50% higher than isometry. Strikingly similar values characterize the subantarctic fur seal (slope = 1.4) and northern fur seal (slope = 1.5) (unpublished data[2]; EHM, unpublished data). In contrast, for the harp seal the slope of allometric regression for bacular length is 4.3 (EHM, unpublished data). More information is needed to determine whether this difference between otariids and phocids is general, but the large bacular size in most phocids suggests that it may be (Scheffer and Kenyon 1963).

Allometric relationships differ between pre- and postpubertal growth in the Cape fur seal, due mainly to patterns of testicular growth. After puberty, negatively allometric growth characterizes testicular length in relation to body length and bacular length in relation to testicular length. Similar trends occur in the subantarctic and northern fur seals (unpublished data[2]; EHM, unpublished data).

Size-related allometry of the baculum varies with age in the Cape fur seal, in a pattern similar to that noted for the harp seal (Miller *et al.* 1998). Comparative data on testicular size in other species are not available.

Scaling relationships among size of body, baculum, and testis—In breeding adult males of the Cape fur seal, bacular length averages 6.4%–6.8% and testicular length averages 3.4% of body length. Bacular length in the subantarctic fur seal averages 5.9% and testicular length averages 2.9% of body length in males >10 yr old.[2] Relative bacular and testicular length are substantially greater in breeding adult harp seals, averaging 9.9% and 5.7% of body length, respectively (Miller *et al.* 1998).

In otariids the baculum likely functions for mechanical support, as an aid to insertion in the vagina (particularly during forced copulations; Miller *et al.* 1996), and for vaginal and cervical stimulation (Eberhard 1985, 1996). Bacular differences between fur seals and the harp seal (taken as a representative aquatically mating phocid) may reflect different forms of sexual selection. In otariids females normally mate only once in a brief period, whereas female phocids copulate repeatedly over several days, often doing so with different males (Le Boeuf 1972, Atkinson 1997, Gentry 1998). Therefore, it may be selectively advantageous for male phocids to ejaculate far into the female's reproductive tract, to increase the likelihood of fertilizing the female or to minimize the risk that semen might flow back out; a large baculum (and penis) would be advantageous in this circumstance (Briskie and Montgomerie 1997). In contrast, otariids have shorter and more slender bacula that are more ornate terminally, which may be functionally important mainly in permitting repeated copulations with different females, or in stimulating the female reproductive tract (Miller 1974, Morejohn 1975). We presume that the likelihood of injury is a constraining factor to large bacular size in the extremely large terrestrially mating elephant seals (Scheffer and Kenyon 1963).

In general, testicular size is relatively large in species with high sperm production that copulate frequently or at brief intervals or that have long breeding seasons (Kenagy and Trombulak 1986, Jennions and Passmore 1993, Harcourt *et al.* 1995, Short 1997). The Cape fur seal is polygynous and has a long breeding season, yet its testes are small compared with those of the promiscuous harp seal, which has a very brief breeding season (Sergeant 1991). Morphology of the testis may clarify the functional and adaptive bases of these patterns (Gentry 1998).

Concluding remarks—Cape fur seals acquire large bacula (and presumably penes) and exhibit spermatogenesis years before they can compete for territories. Early spurts in body growth may be adaptively timed to occur when resources are abundant or mortality rates are low (Clinton 1994), but these factors seem less applicable to bacula and testes, and it also seems unlikely that the conspicuous spurts in growth of bacula and testes at an early age are simply in preparation for adulthood. We interpret these patterns as reflecting mating activities by young males away from colony sites, outside the season of pupping and territoriality, at low population density (*e.g.*, during colonization events), *etc.* (Otronen 1996, Wickens and York 1997). In the northern fur seal, young males mate with females late in the breeding season, after the main period of reproduction (Vladimirov 1987), and in both the Cape fur seal and Forster's fur seal (*Arctocephalus forsteri*) males may mate before the pupping season (Rand 1955, Stirling 1971). Physiological readiness for mating in young male otariids seems like a natural consequence of strong selective pressure on males to find alternative (and earlier) modes of reproduction to territoriality, because only a minority of males survives to successfully acquire territories and fertilize parturient females (Miller 1975, Warneke and Shaughnessy 1985, Vladimirov 1987, Wickens and York 1997). Information on reproductive activities of young males is badly needed to advance our understanding of social behavior and sexual selection in pinnipeds generally, and otariids in particular.

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