Baculum and testes of the hooded seal (*Cystophora cristata*): growth and size-scaling and their relationships to sexual selection

Edward H. Miller, Ian L. Jones, and Garry B. Stenson

Abstract: Growth and size-scaling of the baculum and testes in the moderately polygynous hooded seal (*Cystophora cristata*) were studied using 107 specimens of known age (1 month to 28 years) from the northwestern Atlantic. Bacular growth was rapid between 2 and 5 years of age: length increased 150% and "density" (i.e., mass/length) increased 8-fold and mass 20-fold. Growth continued throughout life. In large, old (>14 years) males, the baculum averaged 20.7 cm in length, 2.1 g/cm in density, and 44.4 g in mass. Bacular length increased relative to body length until seals were about 5 years of age, after which it averaged 8.2%. Testicular growth continued until the seals were about 12 years of age. Testes from breeding males >12 years old averaged 11.2 cm in length, 4.6 cm in width, and 138 g in mass; length averaged 4.9% of body length. In males 2–5 years of age, bacular and testicular sizes were positively allometric relative to body length; in older males, bacular mass and density were positively allometric, and bacular length and testicular size isometric, relative to body length. Bacular size was mostly positively allometric relative to testicular size (bacular length exhibited some isometry). Compared with that of the related and ecologically similar harp seal (*Pagophilus groenlandicus*), which is presumed to have a promiscuous mating system, the baculum of the hooded seal was structurally simpler and grew more quickly but reached a relatively smaller size in adults (8.2 vs. 9.9% of body length). Relative testicular length was also smaller (4.9 vs. 5.7% of body length) and bacular density lower (2.1 vs. 2.8 g/cm) than in the harp seal. These observations suggest that intra- or inter-sexual competition via copulation is weaker in the hooded seal.

Résumé : La croissance et la taille relative du baculum et des testicules ont été étudiées chez le Phoque à capuchon (*Cystophora cristata*), un animal modérément polygyne, par examen de 107 spécimens d'âge connu (1 mois à 28 ans) de l'Atlantique du nord-ouest. La croissance du baculum est rapide de 2 à 5 ans et accuse une augmentation de longueur de 150%, une augmentation de la « densité » par un facteur de 8 (i.e., masse/longueur) et une augmentation de la masse par un facteur de 20. La croissance se poursuit durant toute la vie. Chez les vieux mâles (>14 ans), le baculum est en moyenne de 20,7 cm de longueur, de 2,1 g/cm de densité et de 44,4 g de masse. La longueur du baculum augmente relativement à la longueur du corps jusqu'à l'âge de 5 ans environ, après quoi elle fait 8,2% de la longueur du corps. La croissance des testicules se poursuit jusqu'à l'âge de 12 ans environ. Les testicules des mâles reproducteurs de plus de 12 ans ont en moyenne 11,2 cm de longueur, 4,6 cm de largeur et 138 g de masse; leur longueur est égale en moyenne à 4,9% de la longueur du corps. Chez les mâles de 2–5 ans, la taille du baculum et celle des testicules ont une relation allométrique positive avec la longueur du corps; chez les mâles âgés, la masse et la densité du baculum sont également en relation allométrique positive avec la longueur du corps, alors que la longueur du baculum et la taille des testicules sont en relation isométrique avec la longueur du corps. La taille du baculum est généralement en relation allométrique positive avec la taille des testicules (la longueur du baculum est parfois isométrique). Comparativement à la situation qui prévaut chez le Phoque commun (*Pagophilus groenlandicus*), un phoque apparenté et écologiquement semblable dont le système d'accouplement est présumément basé sur la promiscuité, le baculum du Phoque à capuchon est de structure plus simple et de croissance plus rapide, mais sa taille à l'âge adulte est relativement plus faible (8,2 vs. 9,9% de la longueur du corps); la longueur relative des testicules est également plus petite (4,9 vs. 5,7% de la longueur du corps) et la densité du baculum, plus faible (2,1 vs. 2,8 g/cm) chez le Phoque à capuchon. Ces observations indiquent que la compétition entre individus du même sexe et entre individus de sexes opposés via l'accouplement est plus faible chez le Phoque à capuchon.

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Introduction

The genitalic anatomy of male animals is typically complex and highly variable both within and across species (Slijper 1938; Ottow 1955; Burt 1960; Eberhard 1985). Such variation arises from natural and sexual selection and can provide insight into ecology and behaviour through comparative studies. Interspecific variation has long proved useful in mammalian systematics; both the penis (Lidicker 1968) and baculum (Anderson 1960; Hill and Harrison 1987; Thomas et al. 1994) have been studied extensively, yielding a wealth of comparative anatomical information. This information has aided interpretations of species' differences in copulatory behaviour, especially in rodents (Patterson and Thaeler 1982), and in recent years has also contributed to a general understanding of genitalic size and anatomy in relation to sexual selection and speciation (Patterson and Thaeler 1982; Patterson 1983; Eberhard 1985; Andersson 1994; Briskie and Montgomerie 1997; Harcourt 1997).

Male genitalic anatomy varies in relation to sexual selection and speciation because of interspecific differences in reproductive physiology and behaviour, female reproductive anatomy, life history, etc. (Eberhard 1985, 1996, 1998; Emerson 1997; Enomoto 1997). Therefore, comparative studies on related species are likely to be highly informative about mechanisms and patterns of evolutionary change. Pinnipeds offer an outstanding opportunity for comparative research because the 33 extant species are ecologically and socially diverse, vary greatly in body size and sexual differences in body size, and differ in copulatory behaviour and the medium in which copulation occurs (Bertram 1940; Scheffer and Kenyon 1963; Le Boeuf 1972, 1991; Stirling 1975, 1983; Trillmich 1990; Boness 1991; Miller 1991; McLaren 1993; Miller et al. 1996). In addition, phylogenetic relationships within pinnipeds are reasonably well known (Wozencraft 1993; Bininda-Emonds and Russell 1996). The opportunity for comparison is further enhanced by the fact that all male pinnipeds possess a large baculum that is easily preserved and measured.

Little information is available on the penile or testicular anatomy of pinnipeds, or on testicular size, but the bacula are reasonably well described (Pohl 1911; Chaine 1926; Didier 1953; Mohr 1963; Morejohn 1975). The bacula of pinnipeds vary in size, shape, and apical anatomy. Large bacula typify pinnipeds that copulate aquatically (Scheffer and Kenyon 1963) or that have long copulatory periods (Dixson 1995). The largest baculum of any species occurs in the walrus (*Odobenus rosmarus*), in which it can reach 62.4 cm in length and 1070 g in mass (Fay 1982; Piérard and Bisaillon 1983; Dixson 1995). Thus, genitalic anatomy and size in pinnipeds are diverse and provide the opportunity for comparative studies of genitalic form and function.

Bacular and testicular growth and allometry were quantified for a representative phocid, the harp seal, *Pagophilus groenlandicus* (Miller et al. 1998). A natural comparison is with the related hooded seal, *Cystophora cristata* (Mouchaty et al. 1995; Carr and Perry 1997; Kovacs et al. 1997). These species are similar in distribution, migration, annual cycle, association with ice for breeding and moult, and population biology (Reeves and Ling 1981; Kovacs and Lavigne 1986; Boyd 1991; Atkinson 1997). Hooded seals differ strikingly from harp seals, however, in exhibiting a large sexual difference in body size (Wiig 1985, 1986; McLaren 1993) and breeding behaviour: pups are weaned in about 4 days (vs. 12–14 days in harp seals; Bowen et al. 1985) and males compete with one another to attend parturient females until postweaning oestrus, doing so several times successively in each breeding season (serial polygyny; Miller and Boness 1979; Kovacs 1990). In contrast, harp seals have some form of promiscuous mating system (Lavigne and Kovacs 1988; Kovacs et al. 1996).

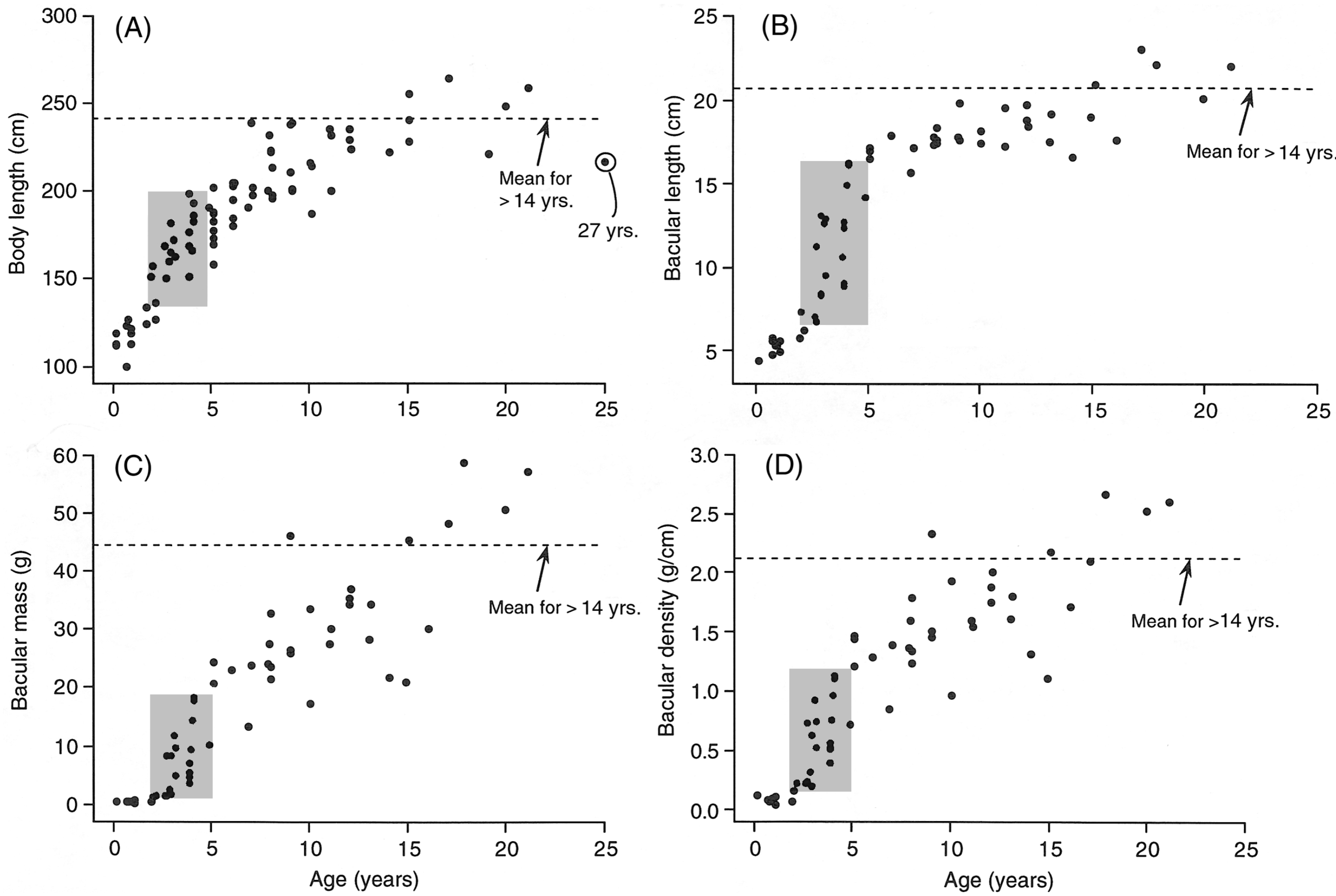
Our working hypotheses were based on the following considerations. First, high sperm competition in promiscuous species such as the harp seal can lead to the evolution of mechanisms for depositing sperm farther within the female reproductive tract (e.g., a large intromittent organ) or to the production of large quantities of sperm (e.g., large testes) (Smith 1984; Kenagy and Trombulak 1986; Møller 1988, 1990; Briskie and Montgomerie 1997; Harcourt 1997; Rose et al. 1997; Short 1997). We therefore hypothesized that the hooded seal would have a relatively smaller baculum and testes than the harp seal, a prediction that is not complicated by duration of the breeding season (this is similar between the species and may be less important than is widely believed; Kenagy and Trombulak 1986; Harcourt et al. 1995). Second, there is abundant evidence of variable or age-dependent changes in the mating behaviour of males (Bradbury and Vehrencamp 1998); in hooded seals, patchiness in breeding density and spatial segregation of animals of different ages (Øritsland and Benjaminsen 1975; Øritsland 1984; Bowen et al. 1987) should provide ample opportunities for variation in the mating behaviour of males. Therefore, our second hypothesis was that bacular and testicular sizes should be more variable than somatic traits. Finally, we investigated intraspecific allometry because although it is highly relevant to studies on reproductive ecology and sexual selection, very little information on the topic is available for mammals.

Methods

One hundred and seven specimens were collected from 1984 to 1995 in the northwestern Atlantic near Newfoundland. They ranged in age from 1 month to 28 years (mean 7.00 years, median 5.15 years). Sample sizes by month were as follows: 9 in January; 11 in February; 16 in March; 54 in April; 2 in May; 1 in June; 2 in October; 7 in November; and 5 in December. Animals were shot by personnel of the Department of Fisheries and Oceans or by commercial sealers. We chose standard length (American Society of Mammalogists 1967) as the best estimate of body size because body mass of pinnipeds is extremely variable, owing to seasonal and interannual fluctuations in blubber mass (Stewart and Lavigne 1984; Kovacs et al. 1991; Beck et al. 1993). Voucher specimens of bacula were deposited in the University of Alaska Museum, Fairbanks (catalogue Nos. 47311–47336).

Age was estimated by counting annuli of dentine or cementum in a cross-sectioned lower canine (Rasmussen 1960; Kapel 1975; Øritsland and Benjaminsen 1975; Popov 1982; Yakovenko 1983). Dentinal annuli were counted just below the enamel cap; annuli of cementum were counted in a section from about one-third of the height of the tooth above the root tip. Age was estimated to the nearest 0.1 years, assuming a birth date of 1 March.

Fig. 1. Growth in body length (A) and bacular length (B), mass (C), and density (D). Horizontal broken lines denote mean values for males >14 years of age and shaded rectangles denote samples from 2 to 5 years of age.



Penes were frozen in the field, then thawed and boiled for approximately 1 h in the laboratory, after which all flesh was removed. Bacula were air-dried at room temperature for several weeks, then measured (length to 1 mm; mass to 0.1 g). Bacular "density" was computed as bacular mass / bacular length. Testes and epididymides were removed in the field, trimmed of extraneous tissue, separated from one another, and placed in 10% formalin or frozen. Frozen specimens were subsequently placed in 10% formalin. After fixation, specimens were stored in 70% ethanol. In the laboratory, specimens were dried by being squeezed gently in a paper towel. Length and width of testes were measured to the nearest 0.1 mm; mass was measured to the nearest 0.1 g.

Reduced major axis regression is generally preferable to simple linear regression in allometric studies because there is no distinction between explanatory and response variables and because all variables are measured with error (Harvey and Harcourt 1984; McLaren 1993). These two kinds of regression are identical when $r = 1$, because in reduced major axis regression, slope = b/r, where b is the slope in simple linear regression (Ricker 1975). Because they are used so widely (Dawson 1994; Gould 1966), slopes from simple linear regression were also computed and are presented below for comparison. Estimates of slopes, intercepts, and confidence intervals are provided, as recommended by Peters (1983).

Analyses involving testicular size were restricted to seals collected from January 15 to March 31 because their testes were the largest in our sample. This covers the prewhelping, whelping, and mating periods (Kovacs and Lavigne 1986; Lavigne and Kovacs 1988).

Data and statistical results are reported to three decimal places for values <1, two decimal places for values <10, 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).

Statistical analyses were carried out with Kaleidagraph 3.0 (Abelbeck Software, 2457 Perkiomen Avenue, Reading, PA 19606, U.S.A.) and Statview 5.0 (SAS Institute Inc., SAS Campus Drive, Cary, NC 27513, U.S.A.).

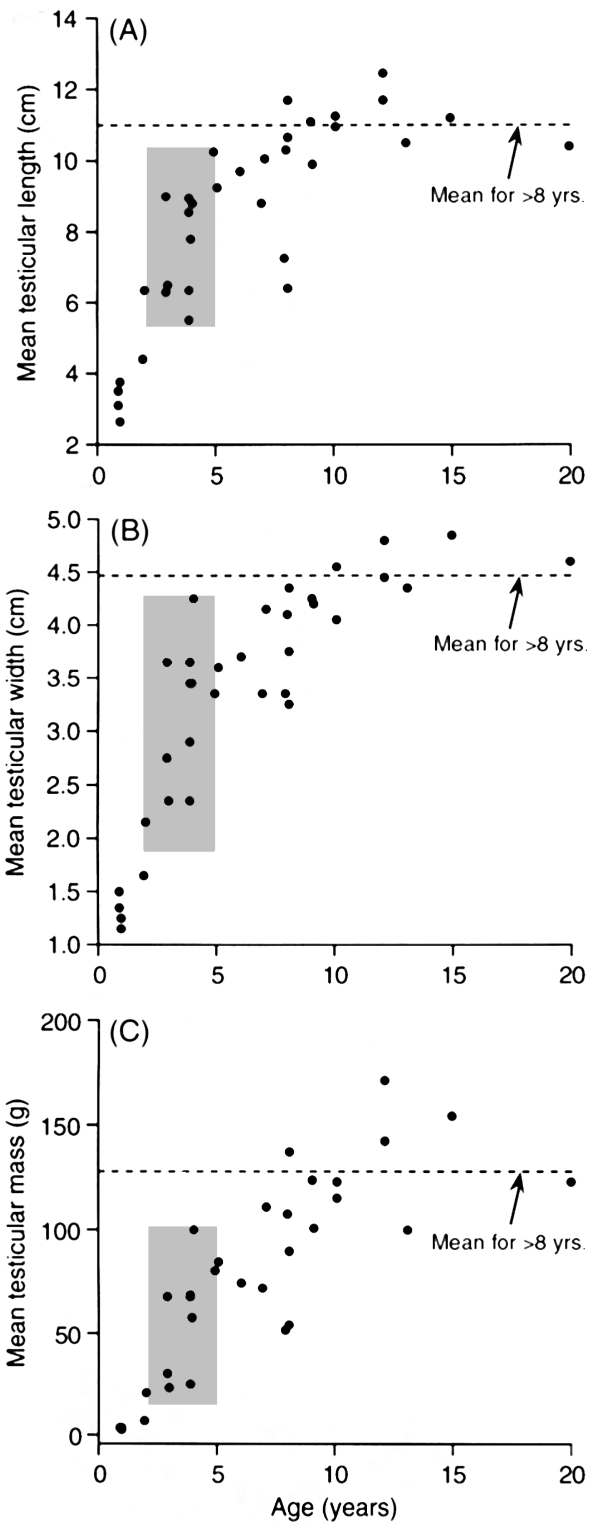
Results

Rates and patterns of growth

Growth in body size was rapid in early life, especially between 2 and 5 years of age, when body length increased by 31% (mean body length for 2- and 5-year-old seals was 138 and 181 cm, respectively; Fig. 1A). Body length of 5-year-old seals averaged 75% of adult length. Growth in body length continued until seals were 12–15 years of age; mean body length of males >14 years old was 242 ± 18.0 (SD) cm (range 217–164 cm, $N = 8$).

The baculum increased 152% in length in seals between 2 and 5 years of age (mean bacular length for 2- and 5-year-old seals was 6.43 and 16.2 cm, respectively; Fig. 1B); bacular length in 5-year-old seals averaged 78.3% of adult length (20.7 ± 1.90 cm, range 17.6–23.0 cm, $N = 7$). Bacular density increased about 8-fold in seals between 2 and 5 years of age (from 0.15 to 1.21 g), averaging 57% of adult density (2.12 ± 0.561 g/cm, range 1.10–2.66 g/cm, $N = 7$) at 5 years of age

Fig. 2. Growth in testicular length (A), width (B), and mass (C), based on data from seals collected between 15 January and 31 March. Horizontal broken lines denote mean values for males >8 years of age and shaded rectangles denote samples from 2 to 5 years of age.



(Figs. 1C, 1D). Finally, bacular mass increased nearly 20-fold in seals between 2 and 5 years of age (from 1.00 to 19.8 g), but at 5 years of age was only about 45% of adult mass (44.4 ± 13.98 g, range 21.0–58.7 g, N = 7).

In summary, prepubertal bacular growth was more rapid than growth in body size, but at 5 years of age bacular and body lengths were similar relative to those of mature adults. In contrast, bacular density and mass increased greatly between 5 years of age and adulthood.

Testicular size increased until seals were about 12 years of age (Fig. 2). In males >12 years old collected from mid-January through March (N = 5), mean estimates were as follows: length 11.2 ± 0.86 cm (range 10.4–12.4 cm), width 4.61 ± 0.216 cm (range 4.35–4.85 cm), and mass, 138 ± 27.8 g (range 99.8–172 g). The specimen with the largest testes was 17 years old and had testes that averaged 14.2 cm in length, 5.80 cm in width, and 246 g in mass (body length was not measured and the baculum was not collected, so these measurements were excluded from the analyses; collection date 18 May 1992).

In linear measurements, testes of 5-year-old seals averaged 89% (length) and 78% (width) of adult size; however, testicular mass of 5-year-olds was only 64% of adult size (Fig. 2).

Scaling of bacular and testicular sizes

Bacular size was positively allometric relative to body length among young males (2–5 years, when growth was most rapid) and also (except for bacular length, which exhibited isometry) among older specimens (6–21 years; Table 1). Testicular size was positively allometric relative to body length for young specimens and isometric for older ones collected from mid-January to March 31 (Table 2).

Bacular size increased relative to body size until seals were about 5 years of age (Fig. 3A). After that age, bacular length averaged 8.16% of body length (range 7.15–9.38%, N = 19). Growth in relative testicular size was more variable (Fig. 3B); testicular length averaged 4.49% of body length in seals >5 years old (range 2.88–5.30%, N = 11); when two males with unusually short testes were excluded, the mean was 4.76% (range 4.19–5.30%). In males >12 years old, testicular length averaged 4.87% of body length (range 4.19–5.30%, N = 5).

Positive allometry characterized most bacular growth relative to testicular growth in seals from mid-January to the end of March, but bacular length exhibited isometry (Table 3).

Relative bacular and testicular sizes at puberty

In 3- and 4-year-old seals, bacular and testicular sizes increased with body size but did not attain adult levels (Fig. 4). Some 3- and most 4-year-olds fell within the range of body sizes at which spermatogenesis occurs (Popov 1982; Yakovenko 1983).

Discussion

Bacular form and function

Compared with those of many mammals, the baculum of the hooded seal is simple (as in other phocids) and likely retains the ancestral function of mechanical support during insertion and copulation (Mohr 1963; Long and Frank 1968; Atkinson 1997). The baculum also serves for support in otariids but is relatively small (except in the walrus; Scheffer

Table 1. Allometric relationships of bacular size to body length.

	Slope	95% CI	SLR slope	Intercept	95% CI	r^2
Ages 2–5 years (*N* = 17)						
Bacular length	3.72	2.47, 4.97	2.94	–7.22	–10.0, –4.43	0.627 (*P* = 0.0002)
Bacular density	8.75	5.12, 12.4	5.75	–19.7	–27.8, –11.6	0.432 (*P* = 0.004)
Bacular mass	12.3	7.51, 17.1	8.69	–26.6	–37.3, –15.9	0.500 (*P* = 0.002)
Ages 6–21 years (*N* = 19)						
Bacular length	1.23	0.766, 1.69	0.834	–1.58	–2.67, –0.502	0.462 (*P* = 0.001)
Bacular density	3.83	2.36, 5.31	2.52	–8.69	–12.2, –5.20	0.434 (*P* = 0.002)
Bacular mass	4.85	3.06, 6.65	3.36	–9.80	–14.1, –5.54	0.479 (*P* = 0.001)

Note: The results of geometric mean regression are shown, using $\log_{10}$ transformations on all variables. CI, confidence interval; SLR, simple linear regression.

Table 2. Allometric relationships of testicular size to body length (using specimens collected from 15 January to 31 March only).

	Slope	95% CI	SLR slope	Intercept	95% CI	r^2
Ages 2–5 years (*N* = 11)						
Testicular length vs. body length	2.84	1.77, 3.90	2.46	–5.45	–7.82, –3.08	0.752 (*P* = 0.0005)
Testicular width vs. body length	3.11	1.27, 4.94	1.93	–6.45	–10.5, –2.36	0.386 (*P* = 0.04)
Testicular mass vs. body length	8.67	4.36, 13.0	6.51	–17.7	–27.4, –8.02	0.564 (*P* = 0.008)
Ages 6–20 years (*N* = 11)						
Testicular length vs. body length	2.66	0.928, 4.40	1.34	–5.26	–9.34, –1.18	0.251 (*P* = 0.116)
Testicular width vs. body length	1.72	0.890, 2.55	1.32	–3.43	–5.38, –1.48	0.590 (*P* = 0.006)
Testicular mass vs. body length	5.06	2.18, 7.94	3.32	–9.88	–16.7, –3.07	0.430 (*P* = 0.028)

Note: The results of geometric mean regression are shown, using $\log_{10}$ transformations on all variables. CI, confidence interval; SLR, simple linear regression.

1950; Scheffer and Kenyon 1963; Morejohn 1975; Dixson 1995; Oosthuizen and Miller 1999). Otariids also differ from phocids in having the bacular apex just beneath the glans, where it may function to stimulate the female reproductive tract (this is presumably why the bacular apex of otariids, sciurids, and some other taxa is of diverse shapes and sizes; Long and Frank 1968; Kim et al. 1975; Morejohn 1975; Patterson and Thaeler 1982; Patterson 1983; Dixson 1987). The bacular apex in phocids is farther from the glans and differs little interspecifically (Harrison et al. 1952; Harrison 1969; Green 1972; Tedman 1991; Laws and Sinha 1993). In the hooded seal, the apical cartilage of the baculum comes close to the glans and thus may directly stimulate the female reproductive tract, as also seems likely in the rodent genera *Neotoma* and *Peromyscus* (Arata et al. 1965; Long and Frank 1968; Patterson and Thaeler 1982). Further anatomical investigations of this structure in phocids are needed to determine its characteristics and differences among species. If it is prominent, the widely held assumption that there is a functional difference between the bacula of otariids and phocids may not hold.

The large size of the baculum in aquatically mating phocids and the walrus, and interspecific differences like those noted in this study, suggest that bacular length, massiveness, or shape may be important in aquatic copulatory behaviour by affecting penile size and shape directly (Patterson 1983) or indirectly, by interacting with cavernous tissues of the penis (Long and Frank 1968). Deep penetration may also afford protection of sperm from water damage (Briskie and Montgomerie 1997).

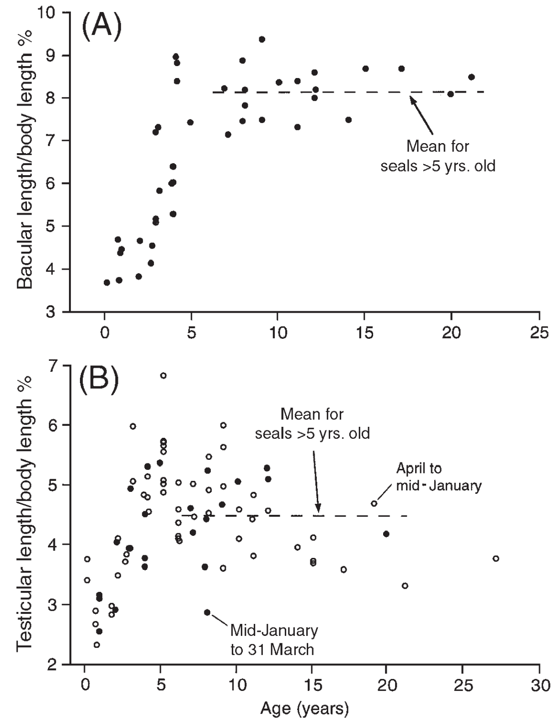
The baculum of the harp seal differs from that of the hooded seal in having a more massive base, a strongly developed dorsal keel (often with small projections), and a marked inflection in the dorsal surface (E.H. Miller, unpublished observation). These bacular features in the harp seal accord with that species' relatively greater testicular size and suggest an important role for the baculum in stimulating the female reproductive tract or displacing semen from other

Table 3. Allometric relationships of bacular size to testicular size (32 specimens from 15 January to 31 March only).

Testicular variable	Bacular length: Slope	Bacular length: Intercept	Bacular length: SLR slope	Bacular length: r^2	Bacular density: Slope	Bacular density: Intercept	Bacular density: SLR slope	Bacular density: r^2	Bacular mass: Slope	Bacular mass: Intercept	Bacular mass: SLR slope	Bacular mass: r^2
Testicular length	1.19 (0.999, 1.38)	0.067 (−0.109, 0.243)	(1.08)	0.817	2.85 (2.35, 3.34)	−2.66 (−3.12, −2.20)	(2.52)	0.783	4.01 (3.34, 4.67)	−2.57 (−3.19, −1.95)	(3.59)	0.803
Testicular width	1.17 (1.01, 1.32)	0.547 (0.461, 0.633)	(1.09)	0.869	2.79 (2.42, 3.16)	−1.51 (−1.71, −1.31)	(2.61)	0.874	3.94 (3.44, 4.44)	−0.957 (−1.24, −0.678)	(3.70)	0.882
Testicular mass	0.406 (0.356, 0.456)	0.445 (0.354, 0.536)	(0.383)	0.889	0.974 (0.843, 1.11)	−1.76 (−1.99, −1.53)	(0.908)	0.869	1.37 (1.20, 1.54)	−1.30 (−1.61, −0.994)	(1.29)	0.885

Note: The results of geometric mean regression are shown, using $\log_{10}$ transformations on all variables ($P < 0.0001$ for each regression). Values in parentheses show 95% confidence interval (CI). SLR, simple linear regression.

Fig. 3. Growth in length of the baculum (A) and testes (B) relative to body length.



males. The latter function must be important in the sperm competition that inevitably results if females mate with several males, as all phocids do (Boyd 1991; Atkinson 1997; Harcourt 1997).

To summarize, we interpret the differences in bacular size and shape between hooded and harp seals as being adaptive in the context of reproductive competition, the baculum of the harp seal being larger and more complex because of that species' promiscuous mating system.

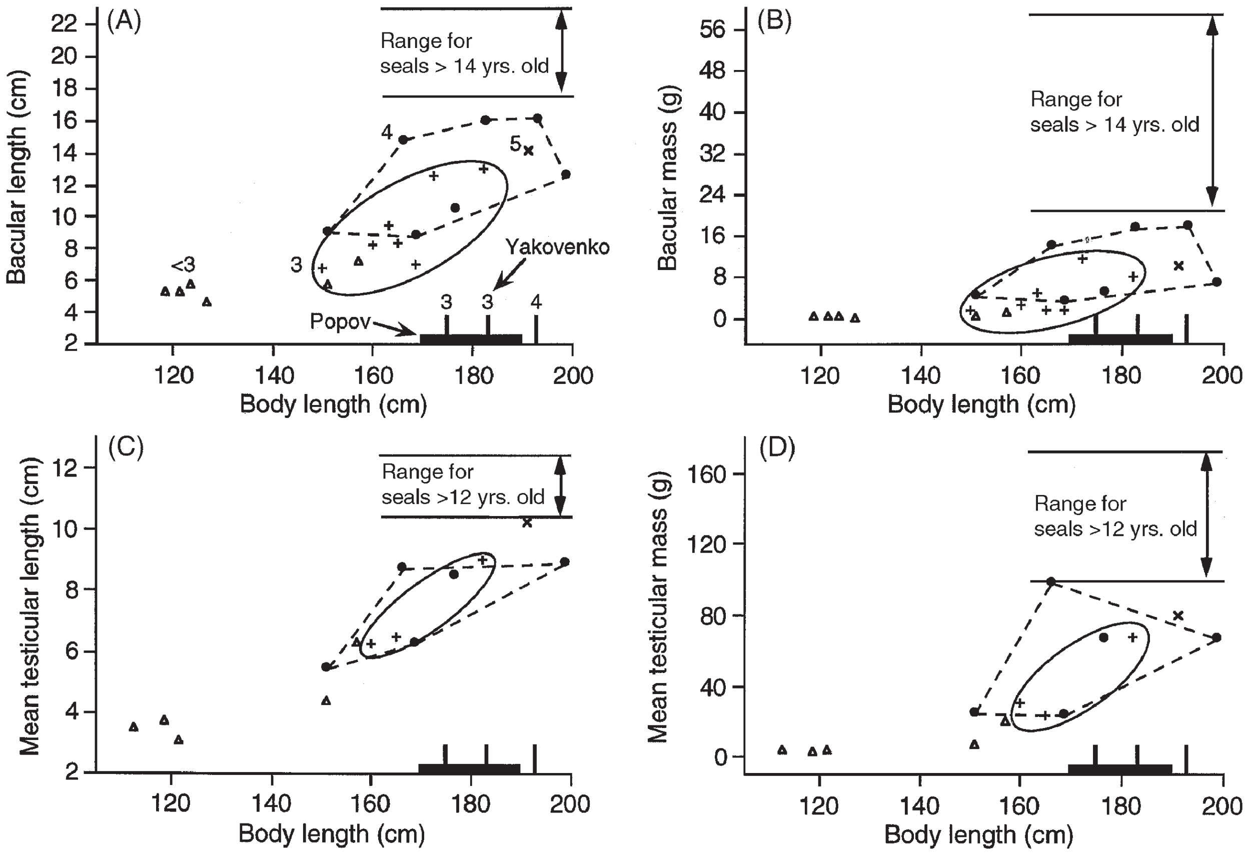
Rates and patterns of growth

Our small sample of old males included some large specimens, hence our estimate of asymptotic body length (242 cm) was higher than others (e.g., 229 and 228 cm, Wiig 1985; McLaren 1993). McLaren (1993) also provided estimates of 233 and 245 cm, based on the data of Rasmussen (1957, 1960).

Some data on bacular length and mass in captive hooded seals of known age were provided by Mohr (1963). Her measurement of bacular length (16.7 cm) in a 3- to 4-year-old animal is larger than those for specimens of similar age in our sample, but her other measurements are in keeping with ours.

Rapid bacular and testicular growth in the hooded seal occurs around the time of puberty (3–4 years), as in the harp seal (Miller et al. 1998). The two species are also similar in the pattern of rapid early growth in bacular length and lifelong growth in mass, so young males have relatively long thin bacula. This age-related difference has implications for the mechanics of copulation, assortative mating (by age?), sperm competition, and how internal mate choice by females is effected. The similarity in bacular and testicular growth between hooded and harp seals seems surprising, considering how different their social systems are. Comparative

Fig. 4. Relationship of bacular length (A), bacular mass (B), testicular length (C), and testicular mass (D) to body length around puberty. Data for 3- and 4-year-old seals are highlighted by ellipses (solid lines) and polygons (broken lines), respectively. The range of body lengths over which Popov (1982) observed sexual maturation is indicated by a black rectangle. Body lengths of two 3-year-old seals and one 4-year-old seal exhibiting active spermatogenesis are indicated by vertical lines above the rectangle (Yakovenko 1983).



behavioural data are needed to allow these findings to be placed in perspective.

Scaling of bacular and testicular sizes

Bacular length in the hooded seal was estimated to be 7.5% of body length by Scheffer and Kenyon (1963; a value that was used by Dixson 1995), based on a personal communication from E. Mohr, who subsequently published those and other data (Mohr 1963). Because body length has commonly been measured by means of different techniques (Fay 1982; McLaren 1993) and because Mohr's (1963) data yield an unusually high estimate of relative bacular length (11.2%), we reject both of her estimates of body length. The best estimate of relative bacular length in adult hooded seals is thus 8.16%.

Bacular growth and testicular growth are positively allometric in relation to growth in body size in young hooded seals and isometric thereafter. Relative growth between the bacula and testes is isometric in young animals. An exception is bacular mass, which exhibits some positive allometry, possibly because sexual activity stimulates continued bone deposition. Patterns of relative growth are identical in the harp seal (Miller et al. 1998).

Relative bacular and testicular sizes at puberty

Our data indicate that large-bodied 3- and 4-year-old hooded seals have large genital organs, hence rapid somatic growth early in life may accelerate sexual maturation. Some individuals of these ages exhibit spermatogenesis (Popov 1982; Yakovenko 1983).

The early sexual maturation of male hooded seals is notable considering the species' large size and the trend for old males to predominate in breeding patches (Rasmussen 1957, 1960; Kovacs et al. 1996). Nevertheless, some young males (5–6 years of age) occur, which supports the inference by Popov (1982, p. 7) that although "most males reach sexual maturity by the fifth year... they begin to take an active part in reproduction in the sixth year." However, spermatogenesis commonly occurs as early as 3 years of age in this species, and Yakovenko (1983) interpreted wounding of young males as evidence of breeding (or at least attempts to breed). The rapid increase in bacular and testicular sizes at 3–4 years of age supports this suggestion. Information on the distribution and behaviour of sexually immature and young sexually mature males during the breeding period is needed to clarify this matter.

Bacular and testicular variation in relation to mating strategies

Large variation in bacular and testicular sizes, even among individuals of the same age, is common in pinnipeds (Scheffer 1950; Tikhomirov 1971; Fay 1982; Miller et al. 1998; Oosthuizen and Miller 1999). Discrete mating strategies are commonly invoked to explain behavioural or reproductive variation in male animals, although strategies usually vary along a continuum (“continuous strategy sets”; Bradbury and Vehrencamp 1998). In our view, adaptive interpretations of intraspecific bacular and testicular variation are weakened by the widespread occurrence of large variation across pinnipeds, even in otariids, in which the baculum may be under fairly direct selection (Patterson and Thaeler 1982; Patterson 1983; Miller et al. 1998; Oosthuizen and Miller 1999). Large variation inevitably results from diverse genetic, endocrinological, and environmental differences among individuals, which lead incidentally to differences in behaviour or size at maturity (Arata et al. 1965; Hall 1998). Therefore, we feel that a non-adaptive view of the large intraspecific bacular and testicular variation in the hooded seal is most parsimonious and is in closest agreement with interspecific trends.

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