



It's all relative: allometry and variation in the baculum (os penis) of the harp seal, *Pagophilus groenlandicus* (Carnivora: Phocidae)

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We compared allometry and variation in the baculum (os penis), mandible, and humerus of the harp seal, *Pagophilus groenlandicus*. This species is presumed to have a promiscuous mating system in which choice of mate by females during intromission with different males is likely. The baculum is large and grows throughout life so may be an honest indicator of males' quality (size) or viability (age). We predicted that bacular size would exhibit stronger allometry relative to body size than mandibles or humeri. The baculum is less functionally (mechanically) constrained than mandibles or humeri so we also predicted it would be more variable, though less variable than sexually selected traits which do not function as honest indicators. Our sample ($N=67$ seals) represented broad ranges of size and age (0–35 yr) so we compared variation using residuals from allometric regressions of skeletal measurements on body length. Bacular size was isometric to body length until ~ 137 cm (when some seals enter puberty) in body length then was highly positively allometric; mandibular and humeral size were negatively allometric to body length throughout growth. Bacula were more variable than mandibles or humeri. Bacular size in large specimens (>137 cm in body length) was related strongly to body length and weakly to age. We interpret bacular size to be an uncheatable honest indicator of male quality and viability. High bacular variation conforms with theoretical predictions of females' asymmetrical choice of mate and choice of extremes, and may reflect corresponding anatomical variation among females. Some bacular variation may also result incidentally from positive allometry coupled with lifelong bacular growth, which can amplify early differences between reproductive and somatic growth, enabled by weak selection on bacular form in relation to function. © 2001 The Linnean Society of London

ADDITIONAL KEYWORDS: sexual selection – character variation – skeleton – baculum – reproduction – social system – growth.

INTRODUCTION

Females of many mammalian species select mates in part during intromission and evaluate attributes of the penis that are informative about a male's size or other characteristics (Patterson & Thaler, 1982; Patterson, 1983; Eberhard, 1985, 1996). Sexual selection acting in this way almost certainly explains much of the extraordinary interspecific anatomical diversity of the penis and supporting baculum (os penis) in mammals (Slijper, 1938; Ottow, 1955; Burt, 1960; Saban, 1967). Competition among males contributes to this diversity via selection for sperm displacement, deep insertion during intromission, etc. (Arnqvist, 1997).

It is difficult to make predictions about males' genitalic attributes or genitalic variation intraspecifically without some knowledge of social structure (e.g. anonymous large vs. stable small groups), or mating strategies of males and females. For example, if females can benefit by mating with large males and can estimate size of males by size of penis, then positive allometry of penile size relative to body size, and small residuals in allometric regression, may evolve (Eberhard *et al.*, 1998). In contrast, if choice of mate by females is independent of penile size, if males or females vary in their mating strategies, or if females vary in size or conformation of their reproductive tracts (Arnqvist & Danielsson, 1999), then isometry and wide scatter about allometric regression (of penile size to body size) might be expected. Some information about intraspecific mating patterns is therefore necessary

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for making biologically sensible predictions and interpretations about genitalic size, form, and allometry in male mammals (Arnqvist, 1997).

Information on bacular function during copulation is also valuable. In some species, bacula mainly provide mechanical support and in others they interact more directly with the female reproductive tract (Patterson & Thaeler, 1982; Patterson, 1983). Except for the walrus (*Odobenus rosmarus*), pinnipeds fall naturally into species with bacula that are: (1) relatively small and have a complex apex that lies close beneath the glans penis, so fairly direct interaction between the bacular apex and female reproductive tract must occur (fur seals and sea lions, Otariidae); or (2) large and serve primarily for mechanical support and to increase penile size (seals, Phocidae) (Harrison, Matthews & Roberts, 1952; Harrison, 1969; Green, 1972; Tedman, 1991; Laws & Sinha, 1993). The Weddell seal (*Leptonychotes weddellii*) may be an exception, as it develops a prominent dorsal bacular ridge along the distal part of the baculum following sexual maturity (Didier, 1953; Morejohn, 2001).

All Carnivora have a well developed baculum in males and a corresponding baubellum (os clitoridis) in females (Pohl, 1911; Scheffer, 1944; Mohr, 1963; Ewer, 1973; Fay, 1982). The baculum varies greatly in size across pinniped species (Mohr, 1963; Scheffer & Kenyon, 1963; Morejohn, 1975; Dixon, 1995; Miller, 2001), being relatively small in Otariidae and the large terrestrially mating elephant seals (*Mirounga species*), large in aquatically copulating species of Phocidae, and enormous (to 62 cm in length and 1040 g in mass) in the aquatically copulating walrus (Fay, 1982; Piérard & Bisailon, 1983). Several interpretations of interspecific variation have been offered, linking large bacula to aquatic copulation (Scheffer & Kenyon, 1963), copulatory duration or pattern (Dixon, 1987, 1995, 1998), risk of fracture (Miller, Pitcher & Loughlin, 2000), or mating strategies among males (Dixon, 1987, 1998; Miller, Stewart & Stenson, 1998). Recent evidence indicates that behavioural dominance and reproductive access to females may be only weakly correlated with reproductive success and paternity in pinnipeds, suggesting an important role for internal selection in this group (Slade *et al.*, 1998; Hoelzel *et al.*, 1999; Wilmer *et al.*, 1999, 2000).

The harp seal (*Pagophilus groenlandicus*) is a typical aquatically mating phocid in having a large baculum that averages about 10% of body length in mature males (maxima 22.3 cm in length, 91.7 g in mass) (Fisher, 1954; Mohr, 1963; Miller *et al.*, 1998). The baculum is large and variable in shape (Fig. 1), which must effect considerable individual variation in penile rigidity, size, and shape that is detectable by females. Mating by harp seals takes place in the water within vast 'whelping patches' that form annually on unstable

drift ice. Drift ice can vary greatly in location, size, and dispersion across years, and can change rapidly within years due to currents, sea conditions, or weather (Lavigne & Kovacs, 1988; Sergeant, 1991). Such an unstable and unpredictable environment precludes stable social structures like territoriality or harems that enable monopolization of individual females by males (Burns, 1970; Stirling, 1975, 1983; Boness, Bowen & Francis, 1993). This surmise is supported by observations of mature male harp seals associating with one another in mobile groups during the breeding season, swimming and periodically hauling out together on the ice (Merdsøy, Curtsinger & Renouf, 1978; Lavigne & Kovacs, 1988; Sergeant, 1991). Male harp seals can become physiologically mature at 3–4 years of age (Yakovenko & Nazarenko, 1967; L.-H. Ni *in litt.*) and can live to about 40 years of age, so reproduction by males occurs across a broad range of age and body size.

Taken together, these characteristics suggest that males compete for mates within physical and social environments that are unpredictable and dynamic over several scales. Furthermore, attributes of males related to mating (including bacular characteristics) are likely to be adaptively variable and opportunistic within and among age classes and over the lives of individuals (Andersson, 1994).

Female harp seals thus must encounter extensive behavioural and morphological variation among males that could be used as a basis for choice of mate. Female phocids are in oestrus for several days and copulate multiply in that period (Atkinson, 1997); this is true of captive harp seals (Miller, Sanvito & Jones, unpubl. data). For reasons given above, it seems likely that oestrous females copulate with different males, leading inevitably to intermale competition and to mechanisms for internal choice of mate by females (Eberhard, 1996; Ambs *et al.*, 1999). We conclude that there is ample variation among males to provide for choice of mate by females and ample opportunity for females to base their choice of mate partly on penile attributes during intromission. Females that do not make some choice of mate are evolutionary dead-ends (West-Eberhard, 1984); furthermore, monopolization of and aggressive behaviour toward females by males in some species should lead inevitably to the evolution of internal mechanisms for choice of mate by females (Gowaty, 1997; Birkhead, 1998; Gowaty & Buschhaus, 1998). It is unlikely that females would predicate a choice solely on bacular characteristics (Johnstone, 1995), but the baculum accounts for a large fraction of penile size so must be one source of biologically significant information that females appraise during copulation.

We investigated allometry and variation in the baculum of the harp seal and compared it with two skeletal elements not involved in reproduction: the

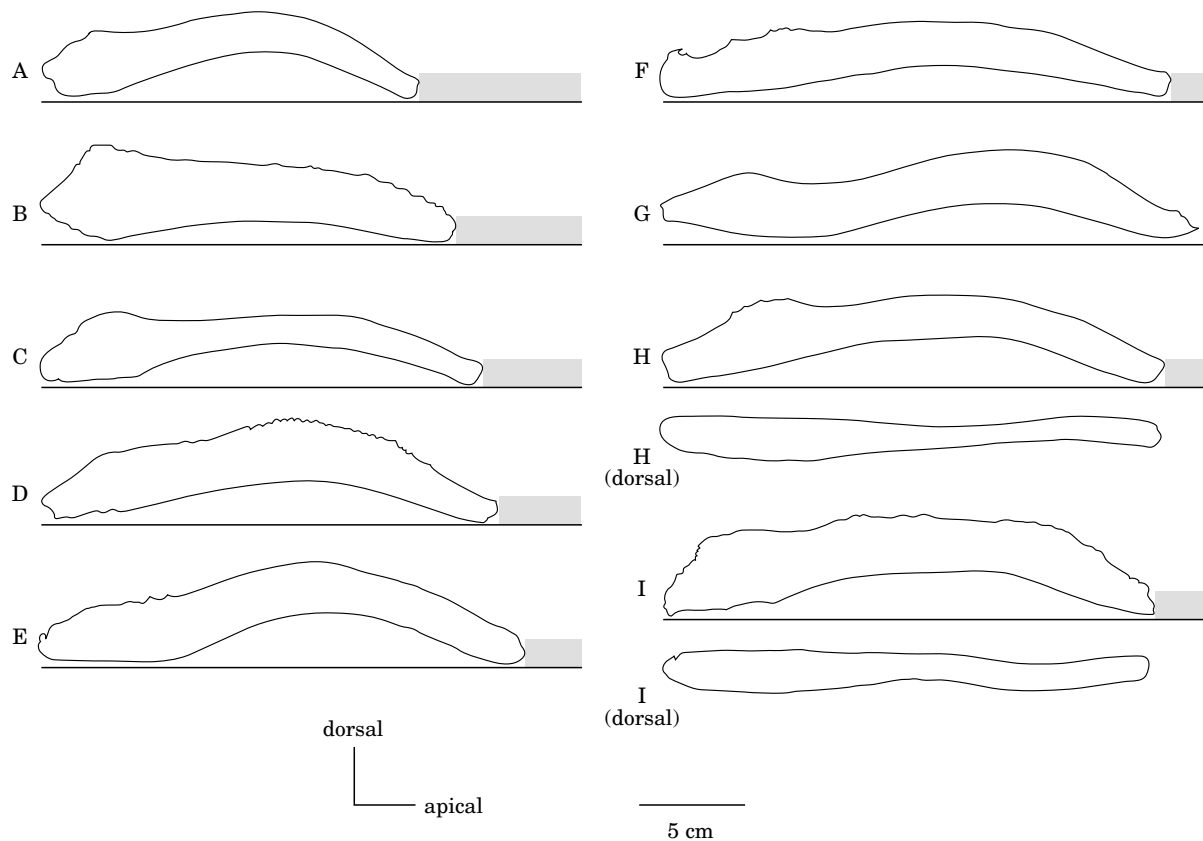


Figure 1. The baculum of the harp seal varies greatly in shape. Outlines of bacula from 10-year-old specimens are shown from right lateral (A–I) and dorsal (H, I) aspects. Note the bilateral asymmetry in specimens H and I. Shaded bars represent the difference in bacular length relative to the longest specimen (G).

mandible and humerus. Mandibles and humeri were chosen because they are bones of similar size to the baculum but are not shaped by sexual selection. We made three predictions. If bacular size is an honest indicator of body size, and if females favour large males during intromission, then (1) bacular size should have a steeper slope in allometric regression than mandibular or humeral size. However, (2) bacular size should exhibit higher variation about allometric regression than mandibular or humeral size because it is less constrained functionally (mechanically) than the latter. Finally, (3) bacular size should be less variable than sexually selected traits which do not function as honest indicators (e.g. Fisherian ornaments; our evidence on this point is indirect).

METHODS

Seals ($N=67$) were collected in May 1994 off north-eastern Newfoundland by personnel of the Department of Fisheries and Oceans (DFO), St. John's, Newfoundland. The seals were taken as part of DFO's annual scientific collecting program, not just for the

present study. The animals were killed by shooting through the head with a high-powered rifle. Standard length ('body length' hereafter) was measured to the nearest cm (American Society of Mammalogists, 1967). Body mass was measured but not included as a variable because it is affected greatly by seasonal and inter-annual fluctuations in blubber (Sivertsen, 1941; Bryden, 1969).

Lower mandibles, left forelimbs, and penes were removed and frozen in the field, and later thawed, rough cleaned and boiled in tap water for c. 1 h in the laboratory. After specimens were boiled, a lower canine was extracted for purposes of ageing, and flesh was removed using scrapers, knives, etc. Specimens were then air-dried at room temperature for several months before being measured.

Age was estimated by counting dentinal growth layers in the canine (Bowen, Sergeant & Øritsland, 1983). Age was estimated to the nearest 0.1 years, assuming a birth date of 1 March (Miller *et al.*, 1998).

Two measurements were taken on mandibles: maximal length from the anteriormost point on the mandible to the posteriormost point on or near the labial

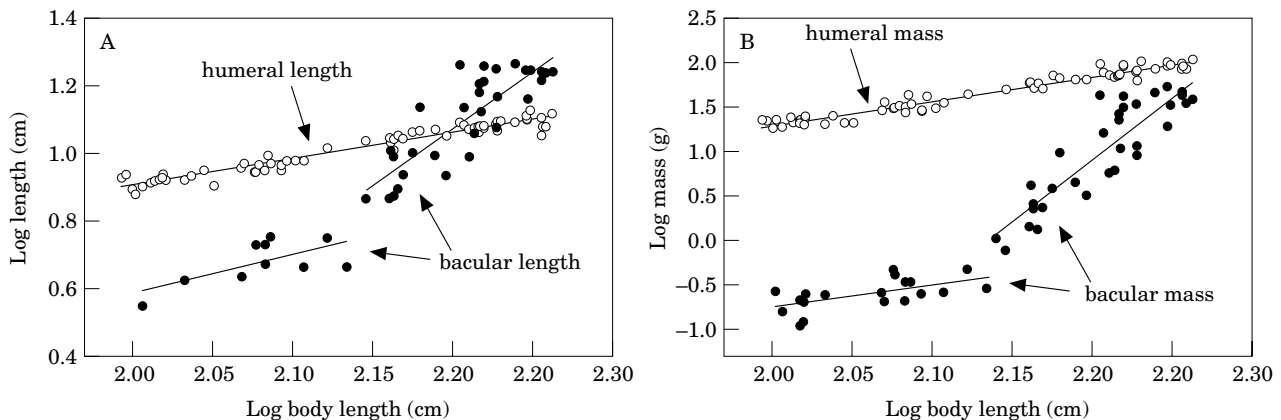


Figure 2. Allometric regressions on body length of (A) humeral and bacular length and (B) humeral and bacular mass. For details see Table 1.

end of the mandibular condyle; and length of post-canine (PC) toothrow, from the anterior margin of PC1 alveolus to the posterior margin of PC5 alveolus. Five humeral variables were used: mass; maximal length; maximal diameter of the proximal end; maximal breadth of the shaft across the deltoid crest; and length of the deltoid crest. Finally, four measurements were taken on bacula: mass; length; and height and breadth at the midpoint of the shaft. The latter two variables were closely correlated and provided identical analytical results so were combined as a measure of mean thickness of shaft [$=(\text{height} + \text{breadth})/2$]. Some bacula of young specimens were broken during cleaning so bacular length and mass could not be measured. Bacula of young specimens were very flexible; boiling caused some small bacula to become bent or twisted, so their length was not measured (12 of 28 bacula from specimens <2 yr of age were affected). Linear measurements were taken to 0.1 mm and mass to 0.1 g. Repeatability (Krebs, 1989) of measurements was high (the lowest was 96%, for length of deltoid crest) so we did not repeat measurements to correct for measurement error. Mandibular variables were excluded from some analyses because many mandibles were damaged when seals were shot.

Allometric (log–log) regressions were carried out for all mandibles and humeri together (except for analysis of residuals; see below), but bacular specimens were divided into two groups based on body length (above and below 137 cm; Fig. 1). The choice of 137 cm as a dividing point was based on visual inspection of allometric plots of bacular variables (e.g. Fig. 1), and knowledge that some young (3-year-old) seals show testicular growth above this length (asymptotic body length = 76 cm; Miller *et al.*, 1998). We acknowledge Gould's (1966: 599) caution about artificially imposing straight-line segments on curvilinear relationships, but think that the change shown in Figure 2 is pronounced enough to warrant this approach.

Simple linear regression (SLR) was used, although other methods are available (Harvey & Pagel, 1991; Green, 1999). We selected SLR because it is most widely used in allometric studies; mandibular, humeral, and bacular variables were closely correlated with body length; and measurement error was very small. Estimates of slopes, intercepts, and confidence intervals are given, as recommended by Peters (1983).

Age structures of the body-length classes were (rounded age in yr– N): <137 cm (0–1; 1–19; 2–9; 3–3; 4–1); and >137 cm (1–2; 2–3; 3–9; 4–2; 5–4; >5–14; the oldest specimen was 35 yr of age). Growth occurred over the age ranges represented in both body-length classes so residuals from allometric regression of the skeletal variables on body length were used to analyse variation. Differences in variation between bacular and non-bacular variables were tested for with one-tailed tests of F -ratios using the variances of the residuals. Two-tailed tests were used to compare variation between (1) non-bacular variables, (2) bacular variables, and (3) size classes, because we made no prediction about the direction of any differences. Residuals were computed for separate allometric regressions of each skeletal variable on body length, for each body-length class. The same procedures were followed to test for differences in variation between body-length classes. Bonferroni corrections were applied to multiple comparisons within body-length classes for (1) bacular vs. non-bacular ($k = 13$ comparisons) and (2) among non-bacular variables ($k = 15$), and (3) between body-length classes for each variable ($k = 8$). Comparisons involved multiple comparisons on the same specimens; however, patterns were statistically strong and interpretable.

To compare variation across species (see Discussion) we computed coefficients of variation (CV) corrected for bias (CV^*) with 95% confidence intervals, following Sokal & Rohlf (1995).

Humeral variables were strongly intercorrelated within each body-length class (all Bonferroni-adjusted

P -estimates <0.001 ; mandibles were excluded from this analysis for reasons given above). Therefore we conducted principal-components analyses (with varimax rotation) on humeral variables within each body-length class, and used scores on the first component as response variables in allometric regressions on body length. As expected, results were identical to those from separate univariate allometric analyses; to facilitate comparisons with our observations we report only upon the latter.

We used a simple regression model with interaction ($Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2$) to investigate the relationships of body size (β_1) and age (β_2) to bacular size (Y ; Neter *et al.*, 1996); data were log-transformed before computation because relationships were not linear. The analyses were carried out only for males >137 cm in body length, to exclude most young seals.

StatView 5.0 (SAS Institute Inc., SAS Campus Drive, Cary, North Carolina, USA) and Super ANOVA 1.11 (Abacus Concepts, Inc., Berkeley, California, USA) were used for statistical analyses. We follow Johnson (1999) and Nelder (1999) in taking guidance from P -estimates rather than accepting them blindly.

Mandibles, humeri, and bacula have been deposited in the University of Alaska Museum (Fairbanks, Alaska, USA) and the National Museum of Natural History (Smithsonian Institution, Washington, DC, USA).

RESULTS

Allometric regressions of mandibular, humeral, and bacular variables on body length were all statistically significant (Table 1). All mandibular and humeral variables exhibited negative allometry. Trends for the baculum differed strikingly: isometry characterized small specimens and positive allometry characterized large specimens (Table 1; Fig. 2).

Pairwise comparisons of variances of residuals in allometric regressions within each body-length class showed that: (1) bacular mass varied significantly more than humeral mass; and (2) linear bacular variables were significantly more variable than linear mandibular and humeral variables (Table 2). Variability did not differ significantly between bacular length and shaft thickness, or between linear mandibular and humeral variables except for two comparisons involving mandibular length: the latter varied less than two humeral variables (breadth of proximal end; length of deltoid crest) in body-length class <137 cm.

Only bacular mass differed significantly between the two body-length classes in variability; it was more variable in larger seals ($F = 3.73$; $df = 33, 20$; $P < 0.005$). Shaft thickness was also more variable in larger seals ($F = 2.73$; $df = 33, 24$; uncorrected $P < 0.01$ compared

with Bonferroni-corrected $P = 0.007$). For bacular length, $F = 2.37$, $df = 32, 10$, $P > 0.05$.

The regression model was highly significant ($P < 0.0001$) for each of the bacular variables, and patterns of significance were similar across variables (Table 3). All bacular variables were significantly affected by body length, and P -estimates were low ($c. 0.06$), suggesting a biologically meaningful relationship of bacular mass and shaft thickness to both age and (body length \times age) interaction. Estimates for β_3 were negative in all models, signifying an antagonistic relationship between age and body length: the effect of age declined as body length increased, and vice versa.

DISCUSSION

Our main predictions were met: bacular size had a steeper allometric slope and varied more than size of mandible or humerus. We also found that bacular mass and shaft thickness were more variable in large than in small harp seals. We discuss the latter finding first.

In other studies on pinnipeds the sizes of baculum, testis, and body were reportedly more variable in young than in old animals (Scheffer, 1950; Miller *et al.*, 1998; Oosthuizen & Miller, 2000). Variation within age classes often is overestimated due to growth within age classes, especially in young age classes in which rapid growth occurs (Yablokov, 1974). Nevertheless, young mammals are commonly more variable phenotypically than adults because phenotypic variation may decline with age through natural selection (Gould, 1966; Bell, 1997), and due to variation in neonatal mass, post-weaning growth, and sexual maturation within and across cohorts (Airoldi & Hoffmann, 1984). Preferential somatic growth occurs early in life because rapid early growth is important to fitness in drift-ice-breeding species, which have brief periods of lactation (Kovacs & Lavigne, 1986; Clutton-Brock, Albon & Guinness, 1988; Baker & Fowler, 1992; Trites & Bigg, 1992; Patterson-Buckendahl *et al.*, 1994; Boness & Bowen, 1996; Boltnev, York & Antonelis, 1998). High bacular variation around puberty is expected because individuals vary in the age at which they enter puberty and in levels of androgens that influence bacular growth. Selection favouring large bacula has led to positive growth-related allometry and lifelong bacular growth (especially in thickness and mass; Miller *et al.*, 1998), so intrinsic and developmentally open individual differences that begin before and are amplified during puberty (Arata, Negus & Downs, 1965) must continue over the species' long lifespan.

Many studies on intraspecific allometry have been made (Cock, 1966) but few have addressed sexually selected (SS) traits and very few have compared patterns between SS and non-SS traits. In several species

Table 1. Summary of allometric regressions of skeletal variables (cm of g) on body length (cm). Positive allometry is indicated by **bold** and negative by *italic* lettering

Dependent variable (log cm or g)	Body length (cm)	Intercept (95% C.I.)	Slope (95% C.I.)	<i>n</i>	<i>r</i> ²	<i>P</i>
Mandibular variables:						
Mandibular length	all	-0.060 (-0.225, 0.016)	<i>0.53 (0.45, 0.61)</i>	31	0.87	<0.0001
Tooththrow length	all	-0.24 (-0.47, -0.019)	<i>0.39 (0.28, 0.50)</i>	37	0.61	<0.0001
Humeral variables:						
Mass	all	-4.3 (-4.6, -4.0)	<i>2.8 (2.6, 2.9)</i>	66	0.96	<0.0001
Length	all	-0.68 (-0.78, -0.58)	<i>0.79 (0.74, 0.84)</i>	66	0.94	<0.0001
Breadth of proximal end	all	-0.57 (-0.69, -0.44)	<i>0.58 (0.52, 0.64)</i>	66	0.86	<0.0001
Breadth of shaft	all	-1.2 (-1.3, -1.1)	<i>0.82 (0.76, 0.88)</i>	66	0.92	<0.0001
Length of deltoid crest	all	-1.3 (-1.4, -1.1)	<i>0.95 (0.88, 1.0)</i>	66	0.92	<0.0001
Bacular variables:						
Mass	<137	-5.8 (-9.1, -2.4)	2.5 (0.89, 4.1)	20	0.37	0.004
Length	<137	-1.7 (-3.8, 0.47)	1.1 (0.10, 2.1)	10	0.45	0.035
Thickness at mid shaft	<137	-2.6 (-3.7, -1.4)	0.92 (0.36, 1.5)	24	0.34	<0.001
Mass	>137	-30.3 (-36.1, -24.5)	14.2 (11.6, 16.8)	33	0.80	<0.0001
Length	>137	-6.3 (-8.1, -4.6)	3.4 (2.6, 4.2)	32	0.71	<0.0001
Thickness at mid shaft	>137	-10.7 (-12.7, -8.7)	4.8 (3.9, 5.7)	33	0.80	<0.0001

Table 2. Summary of *F*-ratio tests to compare residuals from allometric regression for linear variables. Tests involving both bacular and non-bacular variables were 1-tailed; others were 2-tailed. Body-length class <137 in plain font; body-length class >137 in **bold** font. Cell entries are *F*-ratio (df)

	B2	M1	M2	H1	H2	H3	H4
Bacular variables (B-):							
B1: Length	1.25 (24, 10)	16.5 (10, 20) ¹	5.13 (10, 26) ¹	8.89 (10, 32) ¹	4.28 (10, 32) ¹	5.78 (10, 32) ¹	3.98 (10, 32) ²
	1.44 (33, 32)	24.9 (32, 11)¹	8.84 (32, 11)¹	20.3 (32, 34)	15.7 (32, 34)¹	12.2 (32, 34)¹	8.84 (32, 34)¹
B2: Thickness, mid shaft	20.6 (24, 20) ¹	35.8 (33, 11)¹	6.40 (24, 26) ¹	11.1 (24, 32) ¹	5.33 (24, 32) ¹	7.20 (24, 32) ¹	4.97 (24, 32) ¹
			12.7 (33, 11)¹	29.1 (33, 34)¹	22.5 (33, 34)¹	17.5 (33, 34)¹	12.7 (33, 34)¹
Mandibular variables (M-):							
M1: Length, Mandible			3.21 (26, 20)	1.86 (32, 20)	3.86 (32, 20) ³	2.86 (20, 32)	4.14 (32, 20) ³
			2.82 (11, 11)	1.23 (34, 11)	1.59 (34, 11)	2.05 (34, 11)	2.82 (34, 11)
M2: Length, Tooththrow				1.73 (26, 32)	1.20 (32, 26)	1.12 (26, 32)	1.29 (32, 26)
				2.30 (11, 34)	1.77 (11, 34)	1.38 (11, 34)	1.00 (11, 34)
Humeral variables (H-):							
H1: Length					2.08 (32, 32)	1.54 (32, 32)	2.23 (32, 32)
					1.30 (34, 34)	1.67 (34, 34)	2.30 (34, 34)
H2: Breadth, Proximal end						1.35 (32, 32)	1.07 (32, 32)
						1.29 (34, 34)	1.77 (34, 34)
H3: Breadth, Shaft							1.45 (32, 32)
							1.38 (34, 34)
H4: Length, deltoid crest							—

¹*P*<0.001; ²*P*<0.005; ³*P*<0.002.

of stalk-eyed flies (Diopsidae), eyespan in males is strongly positively allometric and thoracic breadth is negatively allometric to body length (Wilkinson,

Presgraves & Crymes, 1998; Wilkinson & Taper, 1999). Positive allometry also characterizes growth- or size-related allometry of bacula in other pinnipeds, antlers

Table 3. Summary of analyses of variance for multiple regression models with bacular variables as response variables, and body length plus age as predictor variables, for seals >137 cm in body length. The regression model used was $Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2$

Response variable: log bacular mass ($Y = -40.3 + 18.5X_1 + 21.4X_2 - 9.41X_1X_2$) ($F_s = 59.8$; $df = 3, 28$; $P = 0.0001$)					
Source of variation:	D.F.	Sum of squares	Mean square	F_s	P
Log body length (X_1)	1	1.13	1.13	22.9	0.0001
Log age (X_2)	1	0.193	0.193	3.91	0.058
Log body length \times log age (X_1X_2)	1	0.187	0.187	3.79	0.062
Residual	28	1.38	0.049		
Response variable: log bacular length ($Y = -8.29 + 4.22X_1 + 3.69X_2 - 1.63X_1X_2$) ($F_s = 30.0$; $df = 3, 27$; $P = 0.0001$)					
Source of variations:	D.F.	Sum of squares	Mean square	F_s	P
Log body length (X_1)	1	0.057	0.057	11.7	0.002
Log age (X_2)	1	0.006	0.006	1.17	0.288
Log body length \times log age	1	0.006	0.006	1.15	0.293
Residual	27	0.131	0.005		
Response variable: log bacular shaft thickness ($Y = -14.7 + 6.58X_1 + 7.71X_2 - 3.40X_1X_2$) ($F_s = 53.6$; $df = 3, 28$; $P = 0.0001$)					
Source of variation:	D.F.	Sum of squares	Mean square	F_s	P
Log body length (X_1)	1	0.144	0.144	22.5	0.0001
Log age (X_2)	1	0.025	0.025	3.92	0.058
Log body length \times log age (X_1X_2)	1	0.024	0.024	3.83	0.060
Residual	28	0.179	0.006		

in Cervidae, genitalia of male insects, etc. (Gould, 1974, 1977; Green, 1992; Katsikaros & Shine, 1997; Miller *et al.*, 1998; Miller, Jones & Stenson, 1999; Oosthuizen & Miller, 2000; Miller, 2001). Therefore positive allometry (growth- or size-related) of SS traits seems to be the norm, although patterns differ between traits under intra- vs. intersexual selection or with different social functions (Green, 1992; Petrie, 1992). For example, Eberhard *et al.* (1998, 1999) documented widespread *negative* allometry of genitalic size to body size in 20 species of insects and spiders, and concluded that genitalic size was not an indicator of good-viability genes in those species (negative allometry of male genitalic size may be an adaptation to ensure mechanical compatibility in copulation, in species where males vary greatly in size; Uhl & Vollrath, 2000).

The occurrence of positive intraspecific allometry in SS traits by itself is not informative about how sexual selection operates within a species. For example, SS traits whose expression depends on environmental conditions often exhibit positive allometry, but intra- or intersexual selection (or both) may be operating (Andersson, 1994; Emlen, 1994). Bacular size in harp seals (and most or all other phocids) cannot function as a flexible condition-dependent trait because bacular growth takes place over years (of course the meaning of 'condition-dependence' depends on the time scale over which structures develop; Markusson & Folstad, 1997; Dunn & Cockburn, 1999). Nevertheless, bacular size presumably reflects both intra- and intersexual selection because females likely copulate repeatedly over several days with different males, due to the

species' high breeding density and the indefensibility of females by males (high underwater mobility; dynamic and unstable drift-ice breeding environment; etc.; see Introduction). In summary, allometric analysis suggests that bacular size in harp seals is closely tied to body size so is an uncheatable honest indicator of male quality; bacular size also provides information about viability (age).

Intraspecific variation is generally high in ornamental SS traits (Rensch, 1959; Alatalo, Höglund & Lundberg, 1988; Barnard, 1991; Møller & Höglund, 1991; Evans & Barnard, 1995; Møller & Swaddle, 1997). High genetic variation underlying variable SS traits can result from asymmetric mating preferences, mutation bias, selection for modifier genes, and other factors (Williams, 1992; Pomiankowski & Møller, 1995). High variation can also characterize ornamental SS traits because they are less functionally (mechanically) constrained than non-SS traits (e.g. avian plumage ornamentation vs. body measurements). Variation in non-ornamental SS traits has been studied little, but low variation is predicted for honest signals of male quality [Pomiankowski & Iwasa (1998); 'low' in this sense is relative to SS traits that have evolved for other purposes, such as Fisherian ornaments, not skeletal elements like the mandible or humerus]. Patterns of variation in different characters provide some perspective.

Bacular variation in adult pinnipeds of asymptotic size is fairly high compared with other skeletal elements and measures of size. CV^* s (with lower and upper 95% confidence limits) for bacular length in

the harp seal and 8-year-old male Cape fur seals, *Arctocephalus p. pusillus*, are 8.4% (7.5–9.3) and 7.2% (6.0–8.5), respectively; in the northern fur seal, *Callorhinus ursinus*, $CV^* = 5.8\%$ (5.3–6.3; $N = 241$) (Miller *et al.*, 1998; Oosthuizen and Miller, 2000; E. H. Miller, unpubl. data). Body length is slightly less variable: CV^* s are 5.4% (5.0–5.8) in the harp seal and 5.9% (4.9–6.9) in 8-year-old male Cape fur seals. Post-cranial skeletal measurements of mammals exhibit very low variation, even lower than cranial measurements; CV s are generally 3–5% (Yablokov, 1974). Information on humeral variation in adult pinnipeds of asymptotic size is not available, but CV^* s (with lower and upper 95% confidence limits) for mandibular length in harp and ring seals (*Pusa hispida*) are 4.2% (3.5–4.9) and 5.2% (3.6–6.7), respectively ($N = 70$ and 25; E. H. Miller, unpubl. data). Linear measurements on soft tissues are more variable: for testicular length in breeding harp seals and 8-year-old Cape fur seals, CV^* s are 10.9% (9.2–12.7) and 8.8% (5.7–11.9), respectively; and for length of the small intestine in harp seals, $CV^* = 8.9\%$ (7.9–9.9) ($N = 156$; C. J. Hendry & E. H. Miller, unpubl. data).

Comparisons across species may be complicated by interspecific differences in body-size variation (McLaren, 1993) but variation in adult bacular length appears to be higher in harp seals than in other species of pinnipeds; it also is higher than in most other mammals. CV -estimates for adult bacular length are 4.4% for western pine marten (*Martes caurina*); 4.7% and 6.4% for river otter, *Lontra canadensis*; 5.8% for raccoon, *Procyon lotor*; 5.9% averaged for eight species and subspecies of *Thomomys* pocket gophers; and 6.8% averaged for four taxa of *Peromyscus* mice (we excluded a high estimate of $CV = 10.6\%$ for the Brazilian free-tailed bat, *Tadarida brasiliensis*, because the baculum is only variably present) (Long & Frank, 1968; Miller, Nagorsen & Stenson, 2001). Nevertheless, numerous 'functional' skeletal and dental attributes of mammals are similarly or more variable (Gingerich, 1974; Yablokov, 1974; Patterson, 1983), and even some behavioral characters are less variable (Wiley, 1973; Miller, 1986). We conclude that bacular size in harp seals is not surprisingly variable considering the species' long lifespan, and that the level of variation is consistent with bacular size being an honest indicator.

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