Growth and variation in the bacula of polar bears (*Ursus maritimus*) in the Canadian Arctic

Markus G. Dyck[1,*], Jackie M. Bourgeois[1] and Edward H. Miller [2]

[1] Department of Sustainable Development, Wildlife Division, Government of Nunavut, Box 1000, Stn. 1170, Iqaluit, NU X0A 0H0, Canada
[2] Biology Department, Memorial University, St. John's, NL A1B 3X9, Canada

Abstract

Structure and growth of the baculum (os penis) in arctoid carnivores have been well described for many species. This study presents the first extensive analysis of bacular growth and variation for bears (Ursidae), based on 871 bacula of polar bears *Ursus maritimus* (858 of known age) that were shot in the Canadian Arctic from 1994 to 1997. Bacular length, maximal diameter and mass increased from 109 mm, 5.93 mm and 2.68 g respectively in 1-year-old bears ($n = 34$) to 190 (maximum 222) mm, 18.7 (24.4) mm, and 20.4 (31.9) g respectively in bears ≥ 10 years of age ($n > 200$). Bacular length is $\sim 8\%$ of body length in adults. Bacula were moderately variable in size: coefficient of variation for length, diameter, and mass$^{1/3}$ were 5.2, 10.0 and 5.4% respectively (16.3% for mass). No geographic variation in size was apparent. Bacula reached asymptotic size at 8–9 years of age. At physiological sexual maturity (~ 6 years of age), bacula were at 89, 73 and 62% of asymptotic length, diameter and mass respectively (compared with body length at $\sim 95\%$). Interpretation of these findings must await behavioural and physiological information on courtship and copulation in the polar bear, and comparative data on other ursids.

Key words: *Ursus maritimus*, growth, morphometrics, baculum, sexual selection

INTRODUCTION

The baculum (os penis) is an anatomically diverse bone that occurs in five mammalian orders (Burt, 1960). It is large but structurally simple in some taxa (e.g. arctoid carnivores), large and complex in others (e.g. sciurid and arvicoline rodents) and small and simple in yet others (e.g. aleuroid carnivores, primates). Bacula function during intromission indirectly, for example through providing mechanical support or affecting penile shape. In some taxa, the complex bacula apex influences the shape of the glans directly (e.g. sciurid rodents); in other taxa the apex has articulating elements that may function dynamically during copulation (e.g. arvicoline rodents) (Anderson, 1960; Burt, 1960; Arata, Negus & Downs, 1965). Correspondingly, the baculum probably serves different functions across species: e.g. in mechanical support; protection of the urethra from compression; enabling protracted copulations; stimulation of the female reproductive tract; provision of information about male size or quality during intromission; reproductive isolation (Long & Frank, 1968; Patterson & Thaeler, 1982; Patterson, 1983;

Dixson, 1987, 1995, 1998; Larivière & Ferguson, 2002; Baryshnikov, Bininda-Emonds & Abramov, 2003). Multiple overlapping functions within species also seem likely.

Insights into bacular evolution and function can be obtained from comparative information about relative size, growth and variation (Dixson, 1987, 1995, 1998). For example, females of aquatically mating phocid seals mate repeatedly over several days with one or more males, and the male has a large simple baculum that may function to facilitate deep insertion or to prevent leakage of semen. It may also provide information about male quality (size) because it continues to grow throughout life (Mohr, 1963; Scheffer & Kenyon, 1963; Briskie & Montgomerie, 1997; Miller, Stewart & Stenson, 1998; Miller, Jones & Stenson, 1999; Morejohn, 2001; Miller, 2002). In contrast, females of the terrestrially mating otariid seals (fur seals and sea lions) usually mate only once on a single day, and the male possesses a much smaller baculum that is more complex apically, apical anatomy is interspecifically diverse, and apical growth continues into late life in at least some species (Mohr, 1963; Scheffer & Kenyon, 1963; Morejohn, 1975; Miller, Pitcher & Loughlin, 2000; Oosthuizen & Miller, 2000; Miller, 2002). Thus the roles played by the baculum during copulation probably differ between and within pinniped families.

Non-pinniped arctoids are also diverse in copulatory behaviour and bacula anatomy: e.g. some mustelids have

*All correspondence to present address: M. G. Dyck, Nanuq Consultants, Box 11016, Iqaluit, NU X0A 0H0, Canada.
E-mail: markus.dyck@nv.sympatico.ca
Order of the first two authors was determined by the flip of a coin.

multiple protracted copulations over several days; canids exhibit a coital lock in which the male and female face opposite directions (Ewer, 1968, 1973; Novak *et al*., 1987; King, 1989). Copulatory behaviour, bacula anatomy and bacula growth are well described for several arctoid families, but are poorly known for the Ursidae (eight species, excluding the red panda *Ailurus fulgens*; Wilson & Reeder, 1993; Flynn *et al*., 2000).

In this paper we present the first quantitative description and analysis of bacular growth and size for an ursid, the polar bear *Ursus maritimus* (illustrations and some measurements of the baculum of this species are in Didier (1950; republished in Miller, 2002) and Lønø (1970)). We first test for the presence of geographic variation in the sample, then describe growth, estimate asymptotic size and quantify variation (using the coefficient of variation, CV). It was not possible to relate baculum size to body size because bears were not measured and no other body parts were saved.

The polar bear evolved from within the brown bear *Ursus arctos* complex, rendering the latter paraphyletic (Shields *et al*., 2000; Barnes *et al*., 2002). Nevertheless, for simplicity, we refer to the brown bear as a single species below.

METHODS

Polar bears are shot in Nunavut Territory through legal or illegal hunting, or as problem bears (Taylor, DeMaster & Schweinsburg, 1987; Lee & Taylor, 1994). As part of the Nunavut polar bear hunt program, hunters are required to submit the baculum of males as proof of age and sex (Lee & Taylor, 1994).

We studied bacula from bears shot in the former Northwest Territories (now Northwest Territories plus Nunavut Territory) from 1994 to 1997. Bears were aged by counting cementum growth-layer groups in sectioned lower premolars (Stirling *et al*., 1977; Calvert & Ramsay, 1998). Bacula were frozen at $-20\,^{\circ}$C until further processing. Thawed bacula were boiled for 1–3 h, cleaned by hand, then air-dried at room temperature for several months before being measured. We measured greatest length and greatest diameter to 0.1 mm with digital callipers and mass to 0.1 g with a digital balance. For comparison with linear variables, we also computed mass$^{1/3}$.

Five specimens were excluded from analyses because they were malformed or appeared to be damaged; age estimates were judged to be incorrect for 13 other specimens (possibly through labelling error), based on visual inspection of growth curves, so those age estimates (but not the associated bacula measurements) were excluded from analyses. The final sample size was 871, including 858 bears of known age (1–27 years). Numbers for specimens of ages 1 through to 15 years and >15 years were 34, 109, 158, 95, 69, 63, 38, 46, 23, 31, 19, 23, 22, 13, 14 and 101 respectively. The sample included 857 bacula from known localities: Foxe Basin ($n = 207$), Lancaster Sound (158), western Hudson Bay (109), Baffin Bay (97), Gulf of Boothia (76), southern Hudson Bay (59),

M'Clintock Channel (59), Davis Strait (43), northern Beaufort Sea (24), southern Beaufort Sea (16), Norwegian Bay (6) and Kane Basin (3) (Taylor *et al*., 2001). Body measurements were not taken.

We investigated geographic variation with 1-way analysis of variance across localities within age classes 3 and ≥ 10, because those age classes had largest sample sizes. A *post hoc* test (MSE) was carried out to determine significant pair-wise differences between localities, with pair-wise *P*-estimates adjusted by Bonferroni correction. Based on the results of those tests (summarized below), geographic samples were combined for subsequent analyses.

We estimated asymptotes with a generalized von Bertalanffy function applied to all data. Growth curves were slightly sigmoidal in shape so we also fitted this function and the Gompertz equation to data on animals > 3 years of age. Asymptotic estimates were identical to those obtained in the first instance hence they are not reported (McLaren, 1993; Derocher & Stirling, 1998). The von Bertalanffy function used was:

$$L_x = L_\infty \left(1 - e^{\infty^k}\right)^b.$$

where L_x is size at age x, L_∞ is asymptotic size, ∞ reflects the rate of approach to the asymptote, b reflects the curvilinearity of that approach, $k = (x - x_0)$, and e is the base of the natural logarithm. We set $x_0 = 0$ (thus $k = x$ in our computations). The specific point at which prenatal growth begins has no effect on estimates of asymptotes.

RESULTS

Only two samples of 3-year-old bears differed significantly between localities: bacula were larger in Foxe Basin (FB) than Baffin Bay (BB) (e.g., length: $F_{[5,135]} = 3.09$, $P = 0.01$; Bonferroni-corrected P (FB–BB) $= 0.036$). No geographic variation occurred for males ≥ 10 years of age: length, $F_{[5,179]} = 0.59$, $P = 0.71$; diameter, $F_{[5,179]} = 1.62$, $P = 0.16$; mass, $F_{[5,179]} = 1.45$, $P = 0.21$.

Bacula increased in length, diameter and mass$^{1/3}$ by 74, 215 and 97%, respectively, between 1 year and ≥ 10 years of age (661% in mass; Fig. 1; Table 1). Growth was most rapid between 1 and 2 years of age: 18% in length, 25% in diameter and 17% in mass$^{1/3}$ (58% in mass), then declined substantially; a possible increased rate of growth at ~ 7 years of age is suggested by incremental growth curves (Fig. 2). Bacula attained 95% of asymptotic size at 8–9 years for length and 14–15 years for mass and diameter. Bacula variation was high during growth but modest in adults; for males ≥ 10 years of age, CVs for length, diameter and mass$^{1/3}$ were 5.2, 10.0 and 5.4%, respectively (16.3% for mass; Fig. 2).

DISCUSSION

The baculum of the polar bear is finer, more slender and less curved than that of the brown bear (Vereshchagin,
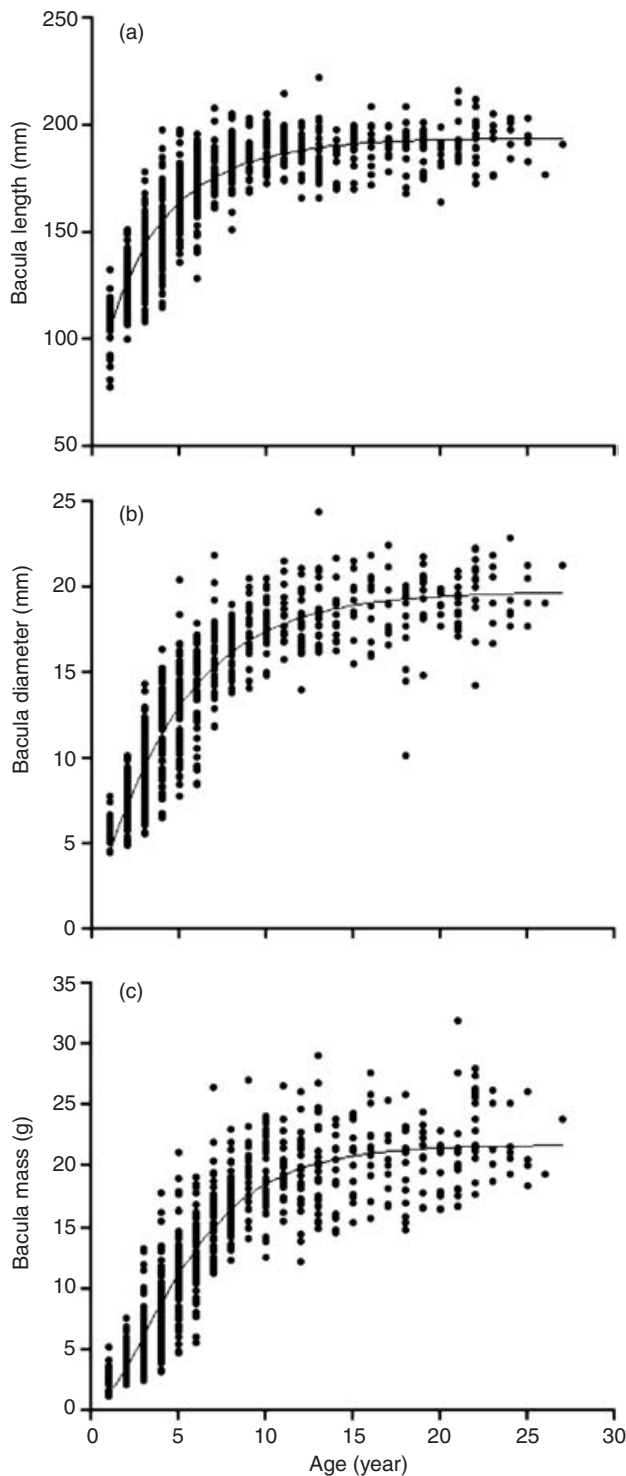
Fig. 1. The von Bertalanffy curve fitted to age and (a) bacular length $[L_x = 194(1\text{-}e\text{-}0.23x)0.51]$, (b) bacular diameter $[L_x = 19.7(1\text{-}e\text{-}0.22x)1.14]$, and (c) bacular mass $[L_x = 21.7(1\text{-}e\text{-}0.26x)2.50]$, of polar bears *Ursus maritimus* from the Canadian Arctic ($n = 858$).
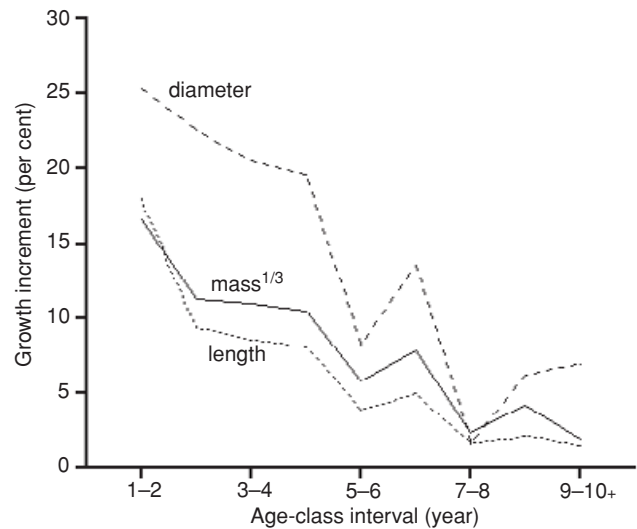
Fig. 2. Incremental growth curves for bacular length, mass and diameter *vs* age intervals of polar bears *Ursus maritimus* from the Canadian Arctic ($n = 858$).

reported for adults by Lønø (1970) fall within the range we observed. The small bacular size in bears 1 year of age at Svalbard agrees with the small size of bears in Svalbard, where Lønø's study took place (Derocher & Wiig, 2002). However, animals aged 2–6 years of age from Svalbard averaged slightly longer and heavier than in our study, perhaps due to the small sample sizes of Lønø (1970), or because of differences in sampling, ageing or specimen preparation. In any event, the polar bear exhibits considerable geographic and temporal variation in growth rate and body size, so it is unsurprising to find some differences across studies (Kurtén, 1964; Manning, 1971; Wilson, 1976; Atkinson, Stirling & Ramsay, 1996; Derocher & Stirling, 1998; Stirling & Lunn, 1998; Derocher & Wiig, 2002).

In keeping with the high environmental variation that polar bears encounter, and the high spatiotemporal variation in growth rates and body sizes that results, sexual maturation occurs over a range of ages (DeMaster & Stirling, 1981; Derocher & Stirling, 1992, 1995; Rosing-Asvid *et al*., 2002; Mauritzen *et al*., 2003; Wiig, Born & Pedersen, 2003). Males may mature physiologically at 3 years of age but usually do so later, and it is unlikely that many can mate (i.e. attain social maturity) before 6 years of age (DeMaster & Stirling, 1981; Rosing-Asvid *et al*., 2002). Adult males captured while they attended females during the spring breeding season (Lønø, 1970; Howell-Skalla *et al*., 2002) had a median age of 10.5 years (range: 5–24), in comparison with solitary males captured in the same period (median, 8.9 years; range: 5–25; Ramsay & Stirling, 1986). The weak growth spurt of bacula at ∼ 7 years of age is in agreement with this general picture.

Selection for large size in male polar bears reflects the intense and physical nature of intrasexual competition for access to and guarding of oestrous females, and has led to growth in body size being faster and lasting longer in males than females. Intersexual dietary differences

1969). Bacular length in adult (> 6 years of age) polar bears was reported as 168, 168–194 and 168 mm by Didier (1950; $n = 1$) and Lønø (1970; $n = 15$) respectively, compared with 151–222 mm (for bears > 6 years of age; 164–122 mm for ≥ 10 years) in our study. Bacular masses

Table 1. Summary of descriptive statistics for bacula of polar bears in our study and the study by Lønø (1970). Data in each column are summarized as: mean ± SE (range; N)

Age (years)	Baculum mass (g)		Baculum length (mm)		Baculum diameter (mm)
	This study	Lønø	This study	Lønø	This study
1	2.68 ± 0.760 (1.2−5.2; 34)	1.60 ± 0.141 (1.4−1.8; 5)	109 ± 11.7 (78−133; 34)	89.2 ± 3.96 (84−95; 5)	5.93 ± 0.709 (4.5−7.8; 34)
2	4.23 ± 1.103 (2.1−7.6; 109)	4.15 ± 0.926 (3.3−5.0; 4)	128 ± 11.2 (100−151; 109)	126 ± 7.7 (118−134; 4)	7.44 ± 1.112 (4.9−10.2; 109)
3	5.92 ± 2.031 (2.5−13.3; 158)	8.10 ± 0.872 (7.1−8.7; 3)	140 ± 13.5 (108−178; 158)	155 ± 11.0 (144−166; 3)	9.12 ± 1.844 (5.6−14.3; 158)
4	8.16 ± 2.937 (3.2−17.8; 95)	11.8 ± 1.56 (9.9−13.8; 7)	152 ± 16.6 (115−198; 95)	157 ± 19.5 (115−172; 7)	11.0 ± 2.42 (6.5−16.4; 95)
5	10.9 ± 3.18 (4.8−21.1; 69)	17.5 ± 0.98 (16.4−18.9; 6)	165 ± 14.0 (136−198; 69)	188 ± 10.2 (174−203; 6)	13.2 ± 2.33 (7.8−20.4; 69)
6	12.8 ± 3.17 (5.6−19.1; 62)	18.7 ± 0.44 (18.2−19.0; 3)	171 ± 14.2 (129−196; 63)	183 ± 11.8 (169−190; 3)	14.2 ± 2.17 (8.5−17.9; 63)
7	15.9 ± 3.16 (11.3−26.5; 38)	–	180 ± 10.2 (161−208; 38)	–	16.2 ± 1.99 (11.9−21.9; 38)
8	16.9 ± 2.50 (12.4−23.0; 46)	–	183 ± 10.5 (151−205; 46)	–	16.4 ± 1.15 (13.8−19.0; 46)
9	19.2 ± 2.98 (14.1−27.0; 22)	–	187 ± 9.6 (169−203; 23)	–	17.5 ± 1.68 (14.1−20.5; 31)
> 6	19.3 ± 3.59 (11.3−31.9; 325)	19.7 ± 1.92 (14.5−22.1; 15)	187 ± 10.6 (151−222; 330)	185 ± 6.3 (168−194; 15)	18.0 ± 2.05 (10.2−24.4; 330)
> 9	20.4 ± 3.32 (12.2−31.9; 219)	–	190 ± 9.9 (164−222; 223)	–	18.7 ± 1.86 (10.2−24.4; 223)

probably followed from the evolution of sexual dimorphism (Kingsley, 1979; Stirling, 1988; Atkinson *et al*., 1996; Derocher & Stirling, 1998; Badyaev, 2002; Derocher & Wiig, 2002). Males continue to grow in body size after they reach physiological sexual maturity, and bacula reach asymptotic size (especially in diameter and mass) later than when asymptotic body length is reached. Furthermore, at physiological sexual maturity (∼ 6 years of age), bacula are at 89, 73 and 62% of asymptotic length, diameter and mass respectively, but body length is ∼ 95% of asymptotic length (based on data in Derocher & Stirling, 1998). In polar bears from Greenland, testes also reach 95% of their asymptotic length at 5.8 years of age (Rosing-Asvid *et al*., 2002).

We lacked data on body size of polar bears whose bacula we measured. Asymptotic body length across six geographic sites in the Canadian Arctic averaged 231 cm (Derocher & Stirling, 1998). We estimated mean bacular length at 190 mm, or 8.2% of asymptotic body length. Using condylobasal length as a measure of body size, Baryshnikov *et al*. (2003) found that relative bacular size in the polar bear is about average for ursids (and for arctoids generally); among ursids, only the sloth bear *Melursus ursinus* has an unusually long bacular. In the American black bear *Ursus americanus*, bacular length averages 10.0% of body length (for 16 bacula lengths and 24 body lengths in males aged ≥ 4 years of age; Powell, Zimmerman & Seaman, 1997). Bacula of older male brown bears can attain 216 mm in length, about 8% of length of head plus body (Pasitschniak-Arts, 1993).

High variation in sexually-selected mensural traits such as baculum size is reported frequently, but comparison of variation across traits must consider whether the variation results from steep allometric slope or wide scatter about the slope of allometric regression (Eberhard *et al*., 1998; Miller & Burton, 2001). Therefore, measures and comparisons of variation need to consider allometric relationships of traits of interest. In this study we lacked information on body size so could not investigate allometric influences on variation in bacula size. Nevertheless, we note that bacula of adults were only moderately variable in size: CVs for length, diameter, and mass$^{1/3}$ were 5.2, 10.0 and 5.4% respectively. For comparison, Manning (1971) reported CVs of 3.3–6.5% (mean, 4.5) for 17 cranial variables on adult male polar bears. In contrast, bacular size is substantially more variable than body size in the harp seal and several mustelids (E. H. Miller, pers. obs.). In the context of mate choice under sexual selection, low variation for honest signals of quality is predicted (Pomiankowski & Iwasa, 1998) but information on baculum function and allometry is needed before such a prediction can be made for the polar bear. Finally, our knowledge of variation is strongly biased toward arctoids; comparative data on aeluroids (felids, hyaenids, viverrids, herpestids) – whose bacula are small, rudimentary or even lacking (Burt, 1960) – are badly needed to balance this picture.

Copulatory behaviour of the polar bear occurs in a ventro-dorsal position on land or ice, as in the American black bear and brown bear (Ludlow, 1976;

Craighead, Sumner & Mitchell, 1995). Meyer-Holzapfel (1957) includes a photograph of captive polar bears in copulation, and Lønø (1970:71) shows a photograph of a male apparently mounting a dead female. Malyov (1988) observed breeding polar bears in captivity where copulations were 25–30 min long and described as being 'rough'. Stirling (1988) reports brief copulations (3–10 min) in the wild but it seems unlikely that these are typical, judging by the aforementioned estimates plus information on other species. For example, copulations average 23 min long in the brown bear (range: 10–60 min; Pasitschniak-Arts, 1993; Craighead *et al.*, 1995). Rough copulations could explain the malformed or broken bacula we observed. Direct and indirect evidence from wild and captive polar bears indicates repeated copulation over several days with one or multiple males, as in the American black bear and brown bear (female brown bears in the wild copulate with 1–11 individual males in a single season; Meyer-Holzapfel, 1957; Ludlow, 1976; Ramsay & Stirling, 1986; Stirling, 1988; Pasitschniak-Arts, 1993; Craighead *et al.*, 1995; Schenk & Kovacs, 1995). Such a breeding system must be characterized by various forms of internal selection on sperm competition and penile form and function, both intra- and intersexually (Eberhard, 1985, 1996). Selection for choice of mates must be particularly important in the polar bear because of its low reproductive rate; furthermore, because females reproduce only every few years, available males out-number available females in any given year, increasing intermale competition and affording more choice to females. More information on reproduction and physiology are needed to elaborate on these possibilities.

REFERENCES

Anderson, S. (1960). The baculum in microtine rodents. *Univ. Kansas Publ. Mus. Nat. Hist.* **12**(3): 181–216.

Arata, A. A., Negus, N. C. & Downs, M. S. (1965). Histology, development, and individual variation of complex muroid bacula. *Tulane Studies Zool.* **12**: 51–64.

Atkinson, S. N., Stirling, I. & Ramsay, M. A. (1996). Growth in early life and relative body size among adult polar bears (*Ursus maritimus*). *J. Zool. (Lond.)* **239**: 225–234.

Badyaev, A. V. (2002). Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. *TREE* **17**: 369–378.

Barnes, I., Matheus, P., Shapiro, B., Jensen, D. & Cooper, A. (2002). Dynamics of Pleistocene population extinctions in Beringian brown bears. *Science* **295**: 2267–2270.

Baryshnikov, G. F., Bininda-Emonds, O. R. P. & Abramov, A. V. (2003). Morphological variability and evolution of the baculum (os penis) in Mustelidae (Carnivora). *J. Mammal.* **84**: 673–690.

Briskie, J. V. & Montgomerie, R. (1997). Sexual selection and the intromittent organ of birds. *J. Avian Biol.* **28**: 73–86.

Burt, W. H. (1960). Bacula of North American mammals. *Misc. Publs Mus. Zool. Univ. Mich.* No. **113**: 1–75.

Calvert, W. & Ramsay, M. A. (1998). Evaluation of age determination of polar bears by counts of cementum growth layer groups. *Ursus* **10**: 449–453.

Craighead, J. J., Sumner, J. S. & Mitchell, J. A. (1995). *The grizzly bears of Yellowstone: their ecology in the Yellowstone ecosystem, 1959–1992.* Washington, DC: Island Press.

DeMaster, D. P. & Stirling, I. (1981). *Ursus maritimus. Mammalian Spec.* **145**: 1–7.

Derocher, A. E. & Stirling, I. (1992). The population dynamics of polar bears in western Hudson Bay. In *Wildlife 2001 – populations*: 1150–1159. McCullough, D. R. & Barrett, R. H. (Eds). London: Elsevier Applied Science.

Derocher, A. E. & Stirling, I. (1995). Estimation of polar bear population size and survival in western Hudson Bay. *J. Wildlife Manage* **59**: 215–221.

Derocher, A. E. & Stirling, I. (1998). Geographic variation in growth of polar bears (*Ursus maritimus*). *J. Zool. (Lond.)* **245**: 65–72.

Derocher, A. E. & Wiig, Ø. (2002). Postnatal growth in body length and mass of polar bears (*Ursus maritimus*) at Svalbard. *J. Zool. (Lond.)* **256**: 343–349.

Didier, R. (1950). Etude systématique de l'os pénien des mammifères. Procyonidés. Ursidés. *Mammalia* **14**: 78–94.

Dixson, A. F. (1987). Baculum length and copulatory behavior in Primates. *Am. J. Primatology* **13**: 51–60.

Dixson, A. F. (1995). Baculum length and copulatory behaviour in carnivores and pinnipeds (Grand Order Ferae). *J. Zool. (Lond.)* **235**: 67–76.

Dixson, A. F. (1998). *Primate sexuality: comparative studies of the prosimians, monkeys, apes, and human beings.* Oxford: Oxford University Press.

Eberhard, W. G. (1985). *Sexual selection and animal genitalia.* Cambridge, MA: Harvard University Press.

Eberhard, W. G. (1996). *Female control: sexual selection by cryptic female choice.* Princeton, NJ: Princeton University Press.

Eberhard, W. G., Huber, B. A., Rodriguez, S. R. L., Briceño, R. D., Salas, I. & Rodriquez, V. (1998). One size fits all? Relationships between the size and degree of variation in genitalia and other body parts in twenty species of insects and spiders. *Evolution* **52**: 415–431.

Ewer, R. F. (1968). *Ethology of mammals.* New York: Plenum Press.

Ewer, R. F. (1973). *The carnivores.* Ithaca, NY: Cornell University Press.

Flynn, J. J., Nedbal, M. A., Dragoo, J. W. & Honeycutt, R. L. (2000). Whence the red panda? *Molec. Phylogen. Evol.* **17**: 190–199.

Howell-Skalla, L. A., Cattet, M. R. L., Ramsay, M. A. & Bahr, J. M. (2002). Seasonal changes in testicular size and serum LH, prolactin and testosterone concentrations in male polar bears (*Ursus maritimus*). *Reproduction (Cambridge)* **123**: 729–733.

King, C. (1989). *The natural history of weasels and stoats.* London: Christopher Helm.

Kingsley, M. S. C. (1979). Fitting the von Bertalanffy growth equation to polar bear age – weight data. *Can. J. Zool.* **57**: 1020–1025.

Kurtén, B. (1964). The evolution of the polar bear, *Ursus maritimus* Phipps. *Acta Zool. Fenn.* **108**: 1–30.

Larivière, S. & Ferguson, S. H. (2002). On the evolution of the mammalian baculum: vaginal friction, prolonged intromission or induced ovulation? *Mammal Rev.* **32**: 283–294.

Lee, J. & Taylor, M. (1994). Aspects of the polar bear harvest in the Northwest Territories, Canada. *Int. Conf. Bear Res. Manage.* **9**: 237–243.

Long, C. A. & Frank, T. (1968). Morphometric variation and function in the baculum with comments on correlation of parts. *J. Mammal.* **49**: 32–43.

Lønø, O. (1970). The polar bear (*Ursus maritimus* Phipps) in the Svalbard area. *Norsk Polarinstitutt Skrifter* **149**: 1–103 + 6 plates.

Ludlow, J. C. (1976). Observations on the breeding of captive black bears, *Ursus americanus.* In *Bears – their ecology and management*: 65–69. Pelton, M. R., Lentfer, J. W. & Folk, G. E. (Eds). Morges, Switzerland: IUCN.

Malyov, A. V. (1988). Reproduction and sexual behaviour of polar bears (*Ursus maritimus* Phipps) in the Kazan Zoobotanical Garden. In *Polar Bears – Proceedings of the Tenth Working Meeting of the IUCN/SSC Polar Bear Specialist Group*: 86–89. Amstrup, S. C. & Wiig, O. (Eds). Gland, Switzerland: IUCN.

Manning, T. H. (1971). Geographical variation in the polar bear *Ursus maritimus* Phipps. *Can. Wildlife Serv. Rep. Ser.* No. 13.

Mauritzen, M., Derocher, A. E., Pavlova, O. & Wiig, Ø. (2003). Female polar bears, *Ursus maritimus*, on the Barents Sea drift ice: walking the treadmill. *Anim. Behav.* **66**: 107–113.

McLaren, I. A. (1993). Growth in pinnipeds. *Biol. Rev.* **68**: 1–79.

Meyer-Holzapfel, M. (1957). Das Verhalten der Bären (Ursidae). *Hand. Zool.* **8** (Teil. 10, 17): 1–28.

Miller, E. H. (2002). Baculum. In *Encyclopedia of marine mammals*: 55–58. Perrin, W. F. & Thewissen, H. G. M. (Eds). San Diego: Academic Press.

Miller, E. H. & Burton, L. (2001). It's all relative: allometry and variation in the baculum (os penis) of the harp seal (Carnivora: Phocidae). *Biol. J. Linn. Soc.* **72**: 345–355.

Miller, E. H., Jones, I. L. & Stenson, G. B. (1999). Baculum and testes of the hooded seal (*Cystophora cristata*): Growth and size-scaling and their relationships to sexual selection. *Can. J. Zool.* **77**: 470–479.

Miller, E. H., Pitcher, K. W. & Loughlin, T. R. (2000). Bacula size, growth, and allometry in the largest extant Otariid, the Stellar sea lion (*Eumetopias jubatus*). *J. Mammal.* **81**: 134–144.

Miller, E. H., Stewart, A. R. J. & Stenson, G. B. (1998). Bacula and testicular growth, allometry, and variation in the harp seal (*Pagophilus groenlandicus*). *J. Mammal.* **79**: 502–513.

Mohr, E. (1963). Os penis und Os clitoridis der Pinnipedia. *Z. Säugetierkunde* **28**: 19–37.

Morejohn, G. V. (1975). A phylogeny of otariid seals based on morphology of the baculum. *Rapp. P. v. Réun. Cons. perm. lnt. Explor. Mer* **169**: 49–56.

Morejohn, G. V. (2001). A description of the baculum of the Weddell seal with comparisons to other phocid seals. *J. Mammal.* **82**: 877–881.

Novak, M., Baker, J. A., Obbard, M. E. & Malloch, B. (Eds) (1987). *Wild furbearer management and conservation in North America.* Toronto: Ontario Trappers' Association.

Oosthuizen, W. H. & Miller, E. H. (2000). Bacula and testicular growth and allometry in the Cape fur seal *Arctocephalus p.pusillus* (Ostariidae). *Mar. Mamm. Sci.* **16**: 124–140.

Pasitschniak-Arts, M. (1993). *Ursus arctos.* Mammalian Spec. **439**: 1–10.

Patterson, B. D. (1983). Baculum – body size relationships as evidence for a selective continuum on bacula morphology. *J. Mammal.* **64**: 496–499.

Patterson, B. D. & Thaeler, C. S. J. (1982). The mammalian baculum: hypotheses on the nature of bacula variability. *J. Mammal.* **63**: 1–15.

Pomiankowski, A. & Iwasa, Y. (1998). Runaway ornament diversity caused by Fisherian sexual selection. *Proc. Nat. Acad. Sci. USA* **95**: 5106–5111.

Powell, R. A., Zimmerman, J. W. & Seaman, D. A. (1997). *Ecology and behaviour of North American black bears: home ranges, habitat and social organization.* London: Chapman and Hall.

Ramsay, M. A. & Stirling, I. (1986). On the mating system of polar bears. *Can. J. Zool.* **64**: 2142–2151.

Rosing-Asvid, A., Born, E. W. & Kingsley, M. C. S. (2002). Age at sexual maturity of males and timing of the mating season of polar bears (*Ursus maritimus*) in Greenland. *Polar Biol.* **25**: 878–883.

Scheffer, V. B. & Kenyon, K. W. (1963). Baculum size in pinnipeds. *Z. Säugetierkunde* **28**: 38–41.

Schenk, A. & Kovacs, K. M. (1995). Multiple mating between black bears revealed by DNA fingerprinting. *Anim. Behav.* **50**: 1483–1490.

Shields, G. F., Adams, D., Garner, G., Labelle, M., Pietsch, J., Ramsay, M., Schwartz, C., Titus, K. & Williamson, S. (2000). Phylogeography of mitochondrial DNA variation in brown bears and polar bears. *Molec. Phylogen. Evol.* **15**: 319–326.

Stirling, I. (1988). *Polar bears.* Ann Arbor: Univerist of Michigan Press.

Stirling, I., Jonkel, C., Smith, P., Robertson, R. & Cross, D. (1977). The ecology of the polar bear (*Ursus maritimus*) along the western coast of Hudson Bay. *Can. Wildlife Serv. Occas. Pap.* **33**: 1–64.

Stirling, I. & Lunn, N. (1998). Environmental fluctuations in arctic marine ecosystems as reflected by variability in reproduction of polar bears and ringed seals. In *Ecology of arctic environments*: 167–181. Woodin, S. J. & Marquiss, M. (Eds). Oxford: Blackwell Science.

Taylor, M. K., DeMaster, D. & Schweinsburg, R. E. (1987). Modelling the sustainable harvest of female polar bears. *J. Wildlife Manage.* **51**: 811–820.

Taylor, M. K., Akeeagok, S., Andriashek, D., Barbour, W., Born, E. W., Calvert, W., Cluff, H. D., Ferguson, S., Laake, J., Rosing-Asvid, A., Stirling, I. & Messier, F. (2001). Delineating Canadian and Greenland polar bear (*Ursus maritimus*) populations by cluster analysis of movements. *Can. J. Zool.* **79**: 690–709.

Vereshchagin, N. K. (1969). Origin and evolution of the polar bear. In *The polar bear and its conservation in the Soviet arctic*: 22–50. Bannikov, A. G. (Ed.). (English translation on file at National Library of Canada, Ottawa, Ontario).

Wiig, Ø., Born, E. W. & Pedersen, L. T. (2003). Movements of female polar bears (*Ursus maritimus*) in the East Greenland pack ice. *Polar Biol.* **26**: 509–516.

Wilson, D. E. (1976). Cranial variation in polar bears. In *Bears – their ecology and management*: 447–453. Pelton, M. R., Lentfer, J. W. & Folk, G. E. (Eds). Morges, Switzerland: IUCN.

Wilson, D. E. & Reeder, D. M. (1993). *Mammal species of the world: a taxonomic and geographic reference.* Washington, DC: Smithsonian Institution Press.