

## SEXUAL DIMORPHISM OF POLAR BEARS

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Sexual dimorphism in body mass, body length, head width, head length, and foreleg guard hair length of polar bears (*Ursus maritimus*) was examined from live-captured polar bears in Svalbard, Norway. Limited evidence of sexual dimorphism was apparent in cubs shortly after den emergence but was marked after the 1st year of life. Sexual dimorphism in adults resulted from both a higher growth rate and prolonged growth period in males. In mature animals, sexual dimorphism was greatest in mass, followed by foreleg guard hair length, head width, body length, and head length. Foreleg guard hair length was age related and hypothesized to be a form of ornamentation. Geographic variation in sexual dimorphism was evident for mass and body length for seven different populations but there was no evidence of a hyperallometric relationship in sexual dimorphism.

Key words: polar bear, sexual dimorphism, *Ursus maritimus*

Sexual dimorphism, the morphological differentiation between males and females, is common among vertebrates, with males usually larger than females (Andersson 1994; Eisenberg 1981; Ralls 1976; Schoener 1967; Selander 1966). The study of sexual dimorphism can give insights into the ecology and life history of a species although 3 main areas have been proposed for the occurrence of dimorphism in a species. Sexual dimorphism can arise, and be maintained, 1st, through sexual selection; 2nd, through separation of parental roles for males and females (e.g., greater maternal care of young); and 3rd, through intersexual competition for food (e.g., differences in prey species—Alexander et al. 1979; Darwin 1871; Ralls 1977; Schoener 1967). In many species, sexual selection is thought to be the ultimate cause for sexual dimorphism (Charnov 1992; Clutton-Brock et al. 1977; Cox and LeBoeuf 1977; Fairbairn 1997; Hoogland 2003; Selander 1972). Often, larger body size of males is correlated with higher reproductive success because of intermale competition for access to females (e.g., Andersson 1994; Clutton-Brock et al. 1982; LeBoeuf and Reiter 1988; Ralls 1976). Therefore, sexual selection is related to the mating system and in polygamous or promiscuous species tends to result in selection for larger males (Emlen and Oring 1977; Ralls 1977; Selander 1966).

Most studies of sexual dimorphism focus on sexually mature males and females. Even in the most dimorphic mammals, sexual dimorphism at birth is low, although often present.

Maternal factors can affect sexual dimorphism of offspring through differential investment after parturition (Boyd and McCann 1989; Lee and Moss 1986; Trivers 1972). Sexual dimorphism develops in most species through divergent growth patterns, that is, sex-specific differences in growth rate and growth duration (Badyaev 2002; Cheverud et al. 1992).

Another issue relevant to the examination of sexual dimorphism pertains to secondary sex differences. Exaggerated secondary sex differences are often referred to as ornamentation. Conspicuous examples in mammals are horns, antlers, tusks, and hair patterns (Andersson 1994). Ornamentation of males is presumed, and often demonstrated in empirical studies, to be preferred by females and can evolve even if female choice is costly (see review Mead and Arnold 2004). Showier males may be preferred by females if fertility is linked to phenotype (Blount et al. 2001; Sheldon 1994). Empirical and theoretical studies of ornamentation are a current issue in avian fauna (e.g., Evans 2004; Kraaijeveld et al. 2004; van Doorn and Weissing 2004) but recent studies of ornamentation in mammals are less common.

Sexual dimorphism tends to increase with size over a variety of taxa (Abouheif and Fairbairn 1997; Rensch 1950; Smith and Cheverud 2002). In species where males are larger than females, studies often find that sexual dimorphism increases with increasing body size (hyperallometry—Fairbairn and Preziosi 1994; Rensch 1959). Mammals commonly demonstrate geographic variation or trends in body size with latitude and longitude (Derocher and Stirling 1998a; Geist 1987; Langvatn and Albon 1986; McNab 1971) and, therefore, geographic variation in sexual dimorphism is likely to result. Conditions favorable for growth could result in increased sexual dimorphism, particularly if males and females are under different

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selective pressures. If sexual selection is a key factor explaining adult body size, then we would expect that an increase in adult size (i.e., favorable conditions during development) would be associated with an increase in sexual dimorphism (Fairbairn and Preziosi 1994; Mahoney et al. 2001).

Among mammals, the most commonly identified dimorphic taxa include primates, elephants, pinnipeds, ungulates, mustelids, and macropods (Ralls 1977; Weckerly 1998). Most carnivores have a polygamous or promiscuous mating system, and generally show distinct sexual dimorphism, with males being larger (Ewer 1973; Ralls 1977). In Ursidae, sexual dimorphism is poorly described but appears to be widespread (Stirling and Derocher 1990). Polar bears (*Ursus maritimus*) have been described as a sexually dimorphic species based on the comparison of body-mass growth curves, with adult males about twice the mass of adult females (Atkinson et al. 1996; Derocher and Wiig 2002; Kingsley 1979; Ramsay and Stirling 1986). The mating system of polar bears is poorly described and both a polygynous system (Berta and Sumich 1999) and a polyandrous system (Ramsay and Stirling 1986) have been suggested. Prolonged mother-offspring associations were postulated to result in a skewed operational sex ratio with 2 or 3 males available for every estrous female (Bunnell and Tait 1981; Ramsay and Stirling 1986) and these authors postulated that larger males may have preferential access to females. Evidence suggests that male polar bears compete intensely for access to estrous females and can suffer severe injuries while fighting (Ramsay and Stirling 1986).

In this paper, we examine sexual dimorphism and the ontogeny of sexual dimorphism in body length, body mass, head length, and head width in live-captured polar bears. Foreleg guard hairs, which are conspicuously long in adult males, were examined as a possible example of male ornamentation. We hypothesize that foreleg guard hair length is an age-related trait in male polar bears. We also examine geographic variation of sexual dimorphism to determine if size of males increases hyperallometrically with size of females.

## MATERIALS AND METHODS

Polar bears were captured as a part of a research program on the ecology of the Svalbard-Barents Sea population in Norway. Sampling occurred on the sea ice in the central Barents Sea (74–77°N, 37–43°E) and on the islands and the surrounding sea ice at Spitsbergen, Nordaustlandet, Edgeøya, Barentsøya, and Hopen Island, Svalbard, Norway (74–81°N, 15–45°E) from 4 March to 9 May 1987–2002. Bears in this area are part of the Barents Sea population that moves between Norway and Russia (Mauritzen et al. 2002). Yearlings and older bears were caught by remote injection of a dart (Cap-Chur Equipment, Douglasville, Georgia) containing the drug Zoletil (Virbac, Carros, France) fired from a helicopter (Stirling et al. 1989). Cubs were caught by hand injection of drug shortly after den emergence at about 4 months of age. Yearlings were approximately 16 months of age at capture. Offspring are normally independent of their mothers at about 2.5 years of age. Animal handling methods were approved by the National Animal Research Authority (Norwegian Animal Health Authority, Oslo, Norway) and were in accordance with guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

We attempted to sample all bears sighted and believe the sample is representative of the population. All bears were permanently marked for future identification by a tattoo (Ketchum Manufacturing Supply Inc., Brockville, Ontario) applied to the inner surface of the upper lip on each side, plastic tags placed in each ear (Edcan Industries, Edmonton, Alberta, Canada), and a transponder chip (Tiris, Texas Instruments, Dallas, Texas) placed subdermally behind the ear. A rudimentary premolar tooth was extracted from all bears more than 1 year old for age determination (Calvert and Ramsay 1998). The sex, reproductive status, and a series of standardized morphometric measure were collected from each bear. Body length (cm) was measured as the dorsal straight-line distance from the tip of the nose to the caudal end of the last tail vertebra. All bears were measured while lying sternally recumbent with the back legs straight behind and the forelegs flexed forward at the elbows parallel to the body. In the same position, axillary girth (cm) was measured as the circumference around the chest at the axilla with a rope (0.4-cm diameter) tightened with a tension of about 0.5 kg. Mass for bears > 1 year old was estimated from a regression model developed specifically for the study population that used axillary girth and body length (Derocher and Wiig 2002). A spring scale (Chatillon, Largo, Florida) was used to determine mass (to nearest 250 g) of cubs < 1 year old. Head measurements (mm) of captured bears were made with calipers. Head breadth was the maximum head width between the zygomatic arches. Head length was the straight-line length from between the upper middle incisors at the gum line to the most posterior dorsal skull process of the sagittal crest. Guard hair length (cm) on the back of the forelegs was measured at 5 evenly spaced locations on each leg from the top of the wrist to the elbow while the bear was lying on its side. We used the maximum guard hair length for analyses of age and sex variation.

To examine geographic variation in sexual dimorphism, we used published values of asymptotic body size from growth curves of polar bears. We examined the hypothesis that the relationship between the mass ( $\log_{10}$ ) of male and female polar bears would be hyperallometric with a regression slope > 1.0 (Leutenegger 1978; Lindenfors et al. 2002; Mahoney et al. 2001).

We used parametric statistics for all analyses by using SAS statistical software (SAS Institute Inc. 1989). Values are presented as means  $\pm$  1 SE. Some information was not available for all animals, resulting in varying samples sizes between analyses. Ages were  $\log_{10}$  transformed for statistical analyses. All estimates of sexual dimorphism were calculated as the ratio of males to females. Statistical significance was set to  $P \leq 0.05$ .

## RESULTS

*Ontogeny of sexual dimorphism.*—When combining litter sizes of 1, 2, and 3 cubs, mass of female ( $\bar{X} = 11.2 \text{ kg} \pm 0.4 \text{ SE}$ ,  $n = 86$ ) and male cubs ( $\bar{X} = 11.2 \pm 0.3 \text{ kg}$ ,  $n = 88$ ) in spring (about 4 months old) did not differ significantly ( $t$ -test,  $P = 0.97$ ). Similarly, no difference ( $t$ -test,  $P = 0.99$ ) was found in body length (females,  $\bar{X} = 75 \pm 1 \text{ cm}$ ,  $n = 86$ ; males,  $\bar{X} = 75 \pm 1 \text{ cm}$ ,  $n = 80$ ). Differences were evident in head length ( $t$ -test,  $P = 0.012$ ), with females ( $\bar{X} = 163 \pm 1 \text{ mm}$ ,  $n = 85$ ) slightly smaller than males ( $\bar{X} = 167 \pm 1 \text{ mm}$ ,  $n = 92$ ) resulting in a sexual dimorphism ratio of 1.02. Similar differences were found in head width ( $t$ -test,  $P = 0.003$ ), with females ( $\bar{X} = 100 \pm 1 \text{ mm}$ ,  $n = 85$ ) smaller than males ( $\bar{X} = 104 \pm 1 \text{ mm}$ ,  $n = 93$ ) resulting in a sexual dimorphism ratio of 1.04. To control for differences between mothers, we examined sexual

**TABLE 1.**—Comparison of sibling female and male polar bear cubs from litters of 2 for body mass, body length, head length, and head width. Bears were captured in the Svalbard–Barents Sea area, Norway.

	Sex <sup>a</sup>	n	$\bar{X} \pm SE$	P, paired t-test
Mass (kg)	f	36	10.8 ± 0.3	0.071
	m	36	11.2 ± 0.4	
Body length (cm)	f	35	75 ± 1	0.82
	m	35	75 ± 1	
Head length (mm)	f	34	162 ± 1	0.0001
	m	34	167 ± 2	
Head width (mm)	f	34	101 ± 1	0.012
	m	34	103 ± 1	

<sup>a</sup> f = female, m = male.

dimorphism within litters of mixed-sex twins but the patterns were similar to the pooled sample, with males larger than females in head length and width but not in mass or length (paired *t*-test; Table 1). Within twin litters of same-sex cubs, no differences were found in any of the 4 morphometric measurements (paired *t*-test, all *P* > 0.11, all *n* > 24).

Males were larger than females in all body measures after the 1st year of life. Examination of yearlings dependent upon their mother revealed differences in all 4 morphometric parameters (*t*-test; Table 2). When using mean values, the ratio for sexual dimorphism in mass was 1.30, in body length was 1.07, in head length was 1.07, and in head width was 1.08 for yearlings.

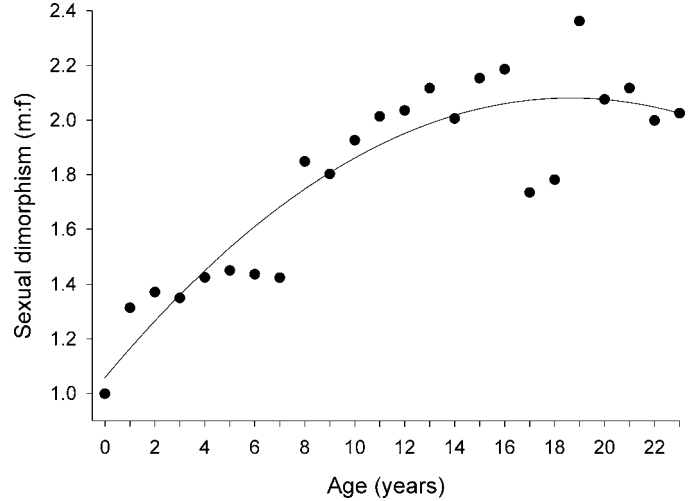
When using mean values for each age and sex, sexual dimorphism in mass increased with age, peaking at 18.7 years of age, and was described by a quadratic relationship (mass sexual dimorphism = 1.0574 + 0.1098age – 0.00294age<sup>2</sup>, *r*<sup>2</sup> = 0.83; *n* = 409 females and 364 males; Fig. 1). Similarly, head length (head length sexual dimorphism = 1.025 + 0.0233age – 0.000574age<sup>2</sup>, *r*<sup>2</sup> = 0.89; *n* = 492 females and 448 males), head width (head width sexual dimorphism = 1.043 + 0.0139age – 0.000433age<sup>2</sup>, *r*<sup>2</sup> = 0.76; *n* = 493 females and 448 males), and body length (body length sexual dimorphism = 1.031 + 0.0152age – 0.000409age<sup>2</sup>, *r*<sup>2</sup> = 0.84; *n* = 484 females and 434 males) increased in a quadratic manner peaking at roughly 16–20 years of age (Fig. 2).

*Foreleg guard hairs.*—Measurements were collected from 40 females and 74 males (≥1 year old). The maximum guard

**TABLE 2.**—Body mass, body length, head length, and head width for yearling female and male polar bears captured in the Svalbard–Barents Sea area, Norway (pooled for litters of 1 and 2 yearlings). The *t*-test results indicate the intersex comparison.

	Sex <sup>a</sup>	n	$\bar{X} \pm SE$	P, t-test
Mass (kg)	f	27	66 ± 3	0.0022
	m	24	86 ± 6	
Body length (cm)	f	27	141 ± 2	0.005
	m	24	151 ± 3	
Head length (mm)	f	28	269 ± 3	0.0009
	m	24	288 ± 5	
Head width (mm)	f	29	145 ± 2	0.0005
	m	24	156 ± 2	

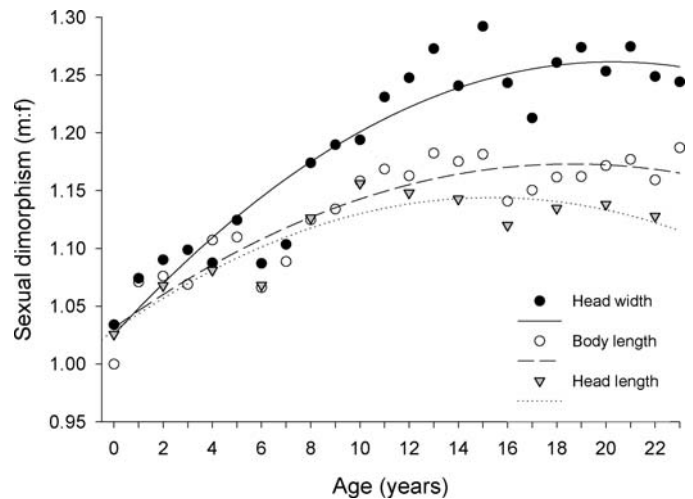
<sup>a</sup> f = female, m = male.



**FIG. 1.**—Sexual dimorphism in body mass of polar bears (males : females) captured in the Svalbard–Barents Sea area, Norway, based on age-specific mean size. Curve represents the quadratic regression (see text).

hair length ranged from 19 to 42 cm in males and from 17 to 28 cm in females. Mean maximum length of guard hairs in males (32 ± 0.6 cm) was longer (*t*-test, *P* < 0.0001) than in females (22 ± 0.4 cm), resulting in a sexual dimorphism ratio of 1.45. Guard hair length increased and then decreased with age in males (quadratic regression, guard hair = 20.2 + 2.068age – 0.0724age<sup>2</sup>, *r*<sup>2</sup> = 0.57) reaching a peak at 14.3 years (Fig. 3). No significant age-related pattern was found for females (linear regression, *P* = 0.48, quadratic regression *P* = 0.22; Fig. 3).

*Geographic variation and allometry.*—Comparison of 7 populations where growth curves were available revealed variation in sexual dimorphism between populations, with values between 1.93 and 2.31 in mass and between 1.16 and 1.20 in body length (Table 3). The most marked sexual dimorphism was noted in mass followed by that of head width, body



**FIG. 2.**—Sexual dimorphism in body length, head length, and head width of polar bears (males : females) captured in the Svalbard–Barents Sea area, Norway, based on age-specific mean size. Curves represent quadratic regressions (see text).

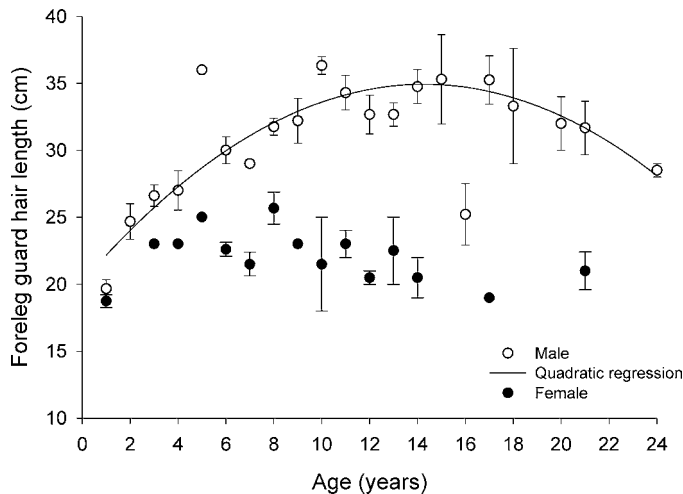


FIG. 3.—Maximum length ( $\pm$  SE) of foreleg guard hairs for female and male polar bears in the Svalbard-Barents Sea area, Norway. Curve represents the quadratic regression for data on males (see text).

length, and head length. Sexual dimorphism in head measurements appeared less variable than sexual dimorphism in mass or length but data were only available from 3 populations.

The allometric relationship between masses of males and females ( $\log_{10}$ ) for polar bears in 7 populations was not significantly different from 1 with a slope of  $1.13 (\pm 0.30)$  but was significantly  $> 0$  (linear regression,  $P = 0.013$ ,  $r^2 = 0.74$ ). The allometric relationship for body length ( $\log_{10}$ ) for males and females was not significant (linear regression,  $P = 0.071$ ).

## DISCUSSION

Measurement and description of sexual dimorphism is an area of active discussion, with issues pertaining to the appropriate morphometric parameters (e.g., body mass versus body length) and methods of analysis as central concerns (Lovich and Whitfield Gibbons 1992; Ranta et al. 1994; Schulte-Hostedde and Millar 2000; Weckerly 1998). In our study, we elected to examine several morphometrics to examine sexual dimorphism.

Some evidence of sexual dimorphism was present in head length and width in polar bear cubs shortly after they emerged from dens but prominent intersex differences were not apparent until the following year when they were yearlings. Similar to our findings, an earlier study examining body length and mass did not find sexual dimorphism in polar bear cubs at den emergence (Derocher and Stirling 1998b). The similar mass and length of female and male twins suggest that mothers invest equally in young of both sexes up to den emergence. The larger head size of male cubs reflected greater allocation of energy to head growth given the similar mass of both sexes. With increasing age, sexual dimorphism became more apparent in dependent young. One year after den emergence, as yearlings, males were larger than females in all 4 measured parameters. It is unknown how body size while dependent upon their mother affects adult size but given that size at den emergence is correlated with size at 1.5 years of age (Derocher and Stirling

TABLE 3.—Sexual dimorphism (males: females) in body mass, body length, head length, and head width based on asymptotic size from growth curves (Derocher 1991; Derocher and Stirling 1998a; Derocher and Wiig 2002).

Population	Sexual dimorphism			
	Body mass	Body length	Head length	Head width
Beaufort Sea	2.12	1.17	1.16	1.33
Central Arctic	2.07	1.20	—	—
High Arctic	1.94	1.18	—	—
Western Hudson Bay	1.93	1.18	1.17	1.30
Foxe Basin	2.27	1.20	—	—
Davis Strait	2.31	1.17	—	—
Svalbard	2.10	1.16	1.14	1.30
$\bar{X}$	2.11	1.18	1.16	1.31

1998b), it is possible that adult size is affected. However, countering this argument, the size of polar bears shortly after weaning was correlated with their adult size in females but not in males (Atkinson et al. 1996). These authors suggested that sex-based difference in body size during maternal care were unlikely to persist to adulthood. Female polar bears do not appear to differentially invest in male and female offspring upon den emergence, and the higher growth rates of dependent males may result from greater intake rates from prey.

Adult polar bears are highly dimorphic, with males 2.1 times the mass of females. This level of sexual dimorphism would place them between the 2 most dimorphic taxa of mammals; the Phocidae with a mean 1.81 for 17 species and Otariidae with a mean of 2.98 for 10 species (Weckerly 1998). In mature polar bears, sexual dimorphism was greatest in mass, followed by foreleg guard hair length, head width, body length, and head length, with the latter 2 similar.

Sexual dimorphism can result from sex-specific differences in growth rate and growth duration (Badyaev 2002). In polar bears, sexual dimorphism was produced by a combination of higher growth rates, evident in larger 1-year-old males, and from a prolonged growth period in males compared to females (Derocher and Stirling 1998a; Derocher and Wiig 2002; Kingsley 1979). The extended growth period of males was noted in Svalbard polar bears, where females reach 97% of their asymptotic body length by sexual maturity at 5 years of age whereas males took an additional 2.2 years to reach 97% of their asymptotic length (Derocher and Wiig 2002). Similarly, the same study revealed that females reached 97% of their asymptotic body mass at 7.3 years of age whereas males took 13.5 years. The prolonged growth period of males result in sexual dimorphism not reaching maximal levels until relatively late in life, roughly 16–20 years of age.

In general, pelage in carnivores is not sexually dichromatic (Ortolani and Caro 1996), so gender identification or intersexual display pelage is uncommon. Guard hair over most of the body in polar bears is 5–15 cm long depending on season (Obbard 1987; Uspenskii 1977), but the foreleg guard hairs of both females and males are noticeably longer than hairs on the rest of the body. Foreleg guard hair was sexually dimorphic in polar bears. In males, length of foreleg guard hair tended to

increase until 14 years of age, followed by a gradual decline. We hypothesize that foreleg guard hairs may act as a form of ornamentation in male polar bears and may be used by females as an indicator of male quality. Males with longer guard hairs may be more attractive to females. Ornamentation depends on both the phenotypic condition and overall genotype of animal (Andersson 1986). In African lions (*Panthera leo*), the mane is highly variable and reflects male condition (West and Packer 2002). This study also found that mane length was associated with fighting success and was associated with female choice. Although associated data on mating success in male polar bears is unavailable, foreleg guard hairs may indicate such qualities in polar bears and warrant further study.

Hair growth in other large mammals was suggested to increase apparent size of the animal (Andersson 1994). An alternative function of foreleg guard hair is that males with longer guard hairs may appear larger in intrasexual competitions. Polar bear males have been postulated to have a loose dominance hierarchy based on size (Derocher and Stirling 1990), which is assisted by social play outside of the breeding season (Latour 1981). Evidence from wounds, scars, and canine breakage in polar bear males suggest the risk of injury in intrasexual competitions is high (Ramsay and Stirling 1986). Therefore, accurately assessing potential opponents for mates would be advantageous (Clutton-Brock et al. 1979). However, additional data are required to assess foreleg guard hair length as an indicator of male quality. We were unable to determine the length of time that the guard hairs take to grow, so it is difficult to correlate length with the condition of males at capture. However, polar bears undergo a single annual molt, with gradual hair replacement from May to August (Kolenosky 1987). It is possible that the long guard hairs are maintained over more than 1 year so conclusions about the utility of it as a visual signal of condition at the time of capture are difficult to determine. Length of foreleg guard hairs was used as an indicator of age in adult females (Ovsyanikov 1998) but our results do not support its use as an age-related indicator in females.

Geographic variation in body size of mammals is common and often follows environmental gradients or varies with population density (e.g., Derocher and Wiig 2002; Fowler 1990; Kingsley et al. 1988; McNab 1971). Geographic variation in sexual dimorphism has been documented in some mammals (Levenson 1990; Ralls and Harvey 1985) and differences between the sexes in sensitivity to environmental conditions are thought to be a major cause of variation in sexual dimorphism between populations (Badyaev 2002). Mahoney et al. (2001) predicted hyperallometry in sexual dimorphism in black bears (*Ursus americanus*) between populations but found no such trend. Further, a recent study of pinnipeds found no evidence of hyperallometry and suggested that sexual dimorphism was not a consequence of an allometric relationship between sizes of males and females (Lindénfors et al. 2002). We found no evidence of hyperallometry of sexual dimorphism in polar bears but this could be revisited with data from additional populations.

We recognize that numerous factors may influence sexual dimorphism in polar bears. Differential niche use could be a

factor affecting sexual dimorphism in polar bears and males have been suggested to feed more often on the larger (about 400-kg) bearded seal (*Erignathus barbatus*), whereas females prefer the smaller (about 60-kg) ringed seals (*Phoca hispida*—Stirling and Derocher 1990). However, as Ralls (1976) noted, differences in the size of food eaten does not clarify the role of diet in sexual dimorphism because it cannot be separated from other selective pressures including sexual selection. Additional factors also can affect sexual dimorphism, and in bighorn sheep (*Ovis canadensis*) sexual dimorphism in mass was influenced by population density (LeBlanc et al. 2001). With the exception of the Svalbard population, all polar bear populations investigated here undergo a substantial harvest, and population densities may vary between populations and thus affect sexual dimorphism.

The ultimate cause of sexual dimorphism in polar bears and its implications for the ecology of the species are unknown. Study of a population over a longer period may yield insight into the dynamics of sexual dimorphism, which would allow some hypotheses to be examined. In addition, information on the mating success of individual males and the prey preferences of females and males could provide quantitative tests of sexual dimorphism hypotheses.

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