



The Polar Bear — *Ursus maritimus*

Biology, Management, and Conservation

by Steven C. Amstrup, Ph.D.

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Edited by George A. Feldhamer, Bruce C. Thompson, and Joseph A. Chapman

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Introduction

About the Author

Steven C. Amstrup is a Research Wildlife Biologist with the United States Geological Survey at the Alaska Science Center, Anchorage AK. He holds a B.S. in Forestry from the University of Washington (1972), a M.S. in Wildlife Management from the University of Idaho (1975), and a Ph.D. in Wildlife Management from the University of Alaska Fairbanks (1995).

Dr. Amstrup has been conducting research on all aspects of polar bear ecology in the Beaufort Sea for 24 years. His interests include distribution and movement patterns as well as population dynamics of wildlife, and how information on those topics can be used to assure wise stewardship. He is particularly interested in how science can help to reconcile the ever-enlarging human footprint on our environment with the needs of other species for that same environment.

Prior work experiences include studies of black bears in central Idaho, and pronghorns and grouse in Wyoming. On their honeymoon in New Zealand in 1999, Steven and his wife Virginia helped in a tagging study of little blue penguins. That experience gave Steve the honor of being one of the very few people ever to have been bitten by both polar bears and penguins.



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Polar Bear

Ursus maritimus

Steven C. Amstrup

NOMENCLATURE

C□□□□□N□□□□ Polar bear, nanook, nanuk, nanuk, ice bear, sea bear, eisbär, isbjørn, white bear

S□□□□□□□□N□□□ *Ursus maritimus*

Phipps (1774) first described the polar bear as a species distinct from other bears and gave the name *Ursus maritimus*. Subsequently, alternative generic names including *Thalassarctos*, *Thalarctos*, and *Thalatarctos* were suggested. Erdbrink (1953) and Thenius (1953) settled on *Ursus* (*Thalarctos*) *maritimus*, citing interbreeding between brown bears (*Ursus arctos*) and polar bears in zoos. Kurtén (1964) described the evolution of polar bears based on the fossil record and recommended the name *Ursus maritimus* as adopted by Phipps (1774). Harington (1966), Manning (1971), and Wilson (1976) subsequently promoted use of the name *Ursus maritimus*, and it has predominated ever since.

DISTRIBUTION

Polar bears occur only in the Northern Hemisphere. Their range is limited to areas in which the sea is ice covered for much of the year. Over most of their range, polar bears remain on the sea-ice year-round or visit land only for short periods. Polar bears are common in the Chukchi and Beaufort Seas north of Alaska. They occur throughout the East Siberian, Laptev, and Kara Seas of Russia and the Barent's Sea of northern Europe. They are found in the northern part of the Greenland Sea, and are common in Baffin Bay, which separates Canada and Greenland, as well as through most of the Canadian Arctic Archipelago (Fig. 27.1). Because their principal habitat is the sea-ice surface rather than adjacent land masses, they are classified as marine mammals. In most areas, pregnant females come ashore to create a den in which to give birth to young. Even then, however, they are quick to return to the sea ice as soon as cubs are able. In some areas, notably the Beaufort and Chukchi Seas of the polar basin, many females den and give birth to their young on drifting pack ice (Amstrup and Gardner 1994).

Polar bears are most abundant in shallow-water areas near shore and in other areas where currents and upwellings increase productivity and keep the ice cover from becoming too solidified in winter (Stirling and Smith 1975; Stirling et al. 1981; Amstrup and DeMaster 1988; Stirling 1990; Stirling and Øritsland 1995; Stirling and Lunn 1997; Amstrup et al. 2000). Despite apparent preferences for the more productive waters near shorelines and polynyas (areas of persistent open water), polar bears occur throughout the polar basin including latitudes $>88^{\circ}$ N (Stefansson 1921; Papanin 1939; Durner and Amstrup 1995).

Because they derive their sustenance from the sea, the distribution of polar bears in most areas changes with the seasonal extent of sea-ice



FIG. 27.1. Approximate worldwide winter distribution of polar bears (light gray). Polar bears are distributed throughout most ice-covered seas of the Northern Hemisphere. Hatched areas indicate known coastal regions preferred for maternal denning. Only in the Beaufort Sea adjacent to Alaska is denning in the pack-ice thought to be common.

Seas in summer, and polar bears occupying these areas may migrate as much as 1000 km to stay with the southern edge of the pack ice (Garner et al. 1990, 1994). Throughout the polar basin, polar bears spend their summers concentrated along the edge of the persistent pack ice. Significant northerly and southerly movements appear to be dependent on seasonal melting and refreezing of ice near shore (Amstrup et al. 2000). In other areas, for example, Hudson Bay, James Bay, and portions of the Canadian High Arctic, when the sea-ice melts, polar bears are forced onto land for up to several months while they wait for winter and new ice (Jonkel et al. 1976; Schweinsburg 1979; Pevett and Kolenosky 1982; Schweinsburg and Lee 1982; Ferguson et al. 1997; Lunn et al. 1997).

Until the 1960s, the prevalent belief was that polar bears wandered throughout the Arctic. Some naturalists felt that individual polar bears were carried passively with the predominant currents of the polar basin (Pedersen 1945). Researchers have known for some time that is not the

DESCRIPTION

Size and Weight. The polar bear is the largest of the extant bears (DeMaster and Stirling 1981). In Hudson Bay, the mean scale weight of 94 males >5 years of age was 489 kg. The largest bear in that group was a 13-year-old, which weighed 654 kg (Kolenosky et al. 1992). The heaviest bear we have weighed in Alaska was 610 kg, and several animals were heavy enough that we could not raise them with our helicopter or weighing tripod. Some animals too heavy to lift have been estimated to weigh 800 kg (DeMaster and Stirling 1981). Females are smaller, with peak weights usually not exceeding 400 kg. Total lengths of males in the Beaufort Sea of Alaska ranged up to 285 cm. Such an animal may reach nearly 4 m when standing on its hind legs and is 1.7 m shoulder height when standing on all four legs. Chest girth for large males is close to 200 cm. Although smaller, females in the Beaufort sea were as long as 247 cm with chest girths up to 175 cm. Only prehistoric polar bears and the giant short-faced bear (*Arctodus* spp.) of the Pleistocene were of greater stature than today's polar bears (Kurtén 1964; Stirling and Derocher 1990).

Manning (1971) suggested there is a cline in size of polar bears across the Arctic. Size increases, he suggested, with distance from east Greenland across the Nearctic to the Chukchi Sea between Alaska and Russia. Manning (1971) also suggested that polar bears from Svalbard may be larger than those from east Greenland. A cline in size across the Palearctic also might occur, but samples from the Russian Arctic are inadequate to confirm it (Manning 1971).

The hypothesized cline was based on measurements made from skulls housed in museums around the world. Unfortunately, the sources of skulls in the various collections were not similar. Of particular note was that many of the skulls originating in the Chukchi Sea may have been donated by trophy hunters. These hunters worked over the ice in teams of aircraft (Tovey and Scott 1957) and were quite effective in killing a great number of the largest polar bears (Amstrup et al. 1986). Another potential problem is that ages of bears in the sample were estimated only by class or life stage. Hence, older bears from one locale might have been compared to younger bears (of the same age class) in another.

Potentially nonstandardized collection methods prevent any meaningful conclusions about relative sizes of polar bears from different locales. Also, if there is a cline in skull sizes around the world, it appears that body sizes and weights of polar bears do not follow a similar cline. The largest bears for which actual scale weights are known have come from the Hudson and James Bay areas of Canada and from the Beaufort Sea of Alaska, not from the Chukchi Sea. That observation, too, may be subject to some bias, as the most prolonged and intensive polar bear studies have been conducted in Hudson Bay and the Beaufort Sea. Greater numbers of captures in those locations may have increased the probability that very large bears were included in the sample.

Despite their large adult sizes, the young of polar bears are among the most altricial (undeveloped) of eutherian mammals (Ramsay and Dunbrack 1986). Newborn polar bears weigh only 600–700 g. They are blind, only lightly furred, and totally helpless (Blix and Lentfer 1979). Mother polar bears when giving birth commonly weigh over 300 kg, and can weigh 400 kg (Ramsay 1986). If only a single cub is born, the ratio of maternal to neonate weights could be between 400 and 500 to 1. Even with the more common two-cub litter, the ratio of maternal to neonate mass is extraordinarily large (Ramsay and Dunbrack 1986). Cubs grow very fast after birth. In Alaska, they average 13 kg on emergence from the den in late March or early April, with maximum weights of 22 kg. Cubs continue to grow rapidly through their first summer on the sea-ice and some weigh over 100 kg as they approach 1 year of age.

Pelage. Polar bears are completely furred except for the tip of the nose. Pelage density is more even than in other ursids, which are often more sparsely furred ventrally and in axillary and groin areas. Even the pads



F□□□□27.2. In winter, polar bear foot pads may be densely furred. This may provide a better purchase on the slippery ice surface than naked pads. S□□□□□. Photo by Steven C. Amstrup.

fur, pads of the feet of polar bears are made up of the same cornified epidermis characteristic of the pads of other bears (Storer and Tevis 1955; Ewer 1973).

The skin of polar bears is uniformly black. Hence, if polar bears lose hair due to physical trauma or disease, they appear from a distance to have black patches on their bodies. Polar bear fur appears white when it is clean and in even sunlight. Because it actually is without pigment, however (Øritsland and Ronald 1978; Grojean et al. 1980), bears may take on the yellow-orange hues of the setting and rising sun and the blue of sunlight filtered through clouds and fog. They appear the whitest right after molting. In spring and late winter, however, many polar bears are “off-white” or yellowish because of oils from their prey and other impurities that have attached to and been incorporated into their hair.

The molt appears to be somewhat variable, but begins by late April and May. The molt appears to be complete by late summer, and bears captured in autumn have notably shorter coats than those captured in spring. The pelt is thick with a dense underfur and guard hairs of various lengths. Polar bear fur may have a high propensity to take on the colors of environmental impurities because the guard hairs have a hollow medulla (or core) where impurities may lodge. In zoo environments, some species of algae can enter the hollow cores of guard hairs and result in a pronounced “greening” of the fur (Lewin and Robinson 1979).

Lavigne and Oritsland (1974) noted that polar bears effectively absorb ultraviolet (UV) light, and suggested that could be useful in remote-sensing surveys to enumerate them. The discovery that polar bears appear to absorb UV light led to much speculation about their ability to capture the energy in that light. Popular and scientific reports claimed that the ability to absorb energy in the UV spectrum was an adaptation to help maintain body heat in the rigorous Arctic environment (Anonymous 1978; Grojean et al. 1980; Lopez 1986; Mirsky 1988). Suddenly, the hollow hairs of polar bears, adept at catching algae and other contaminants (Lewin and Robinson 1979) also were endowed with the powers of optic fibers to funnel UV light to the skin. According to this theory, the skin was black to better absorb such energy without damage. Capturing this high-frequency electromagnetic energy would be a great adaptation for polar bears. This ability has attained the status of an Arctic legend, and contributed to the mystique surrounding the great white bears of the north. Unfortunately, this supposed adaptation has no basis in fact. Lavigne (1988) and Koon (1998) established unequivocally that the hair of polar bears, although transparent in the

Claws. The claws of polar bears are shorter and more strongly curved than those of brown bears. They also are larger and heavier than those of black bears (*Ursus americanus*). They appear to be very well adapted to clambering over blocks of ice and snow and especially to securely gripping prey animals. The claws are normally black (Fig. 27.3), but rarely may, like polar bear fur, lack pigment (Fig. 27.4).

Skull and Dentition. Polar bears share the general ursid dental formula: I 3/3, C 1/1, P 4/4, M 2/3. The first premolars are vestigial and occur in a long diastema or gap between the functional canine and molariform teeth. That gap allows the powerful canines to penetrate deeply into the bodies of seals and other prey without interference from adjacent cheek teeth. Although polar bears apparently evolved from brown bears <250,000 years ago, their teeth have changed significantly from the brown bear form. The cheek teeth are greatly reduced in size and surface area, and the carnassials are more pronounced than in brown bears, reflecting the predatory lifestyle. The teeth of polar bears are well suited to the tasks of grabbing and holding prey and shearing meat and hide. They no longer are as suited to grinding grasses and other vegetation as are those of brown bears. The canine teeth of males are larger and heavier, relative to the size of the jaw, than those of females (Kurtén 1955), and the molar arcade of males is longer than in females (Larsen

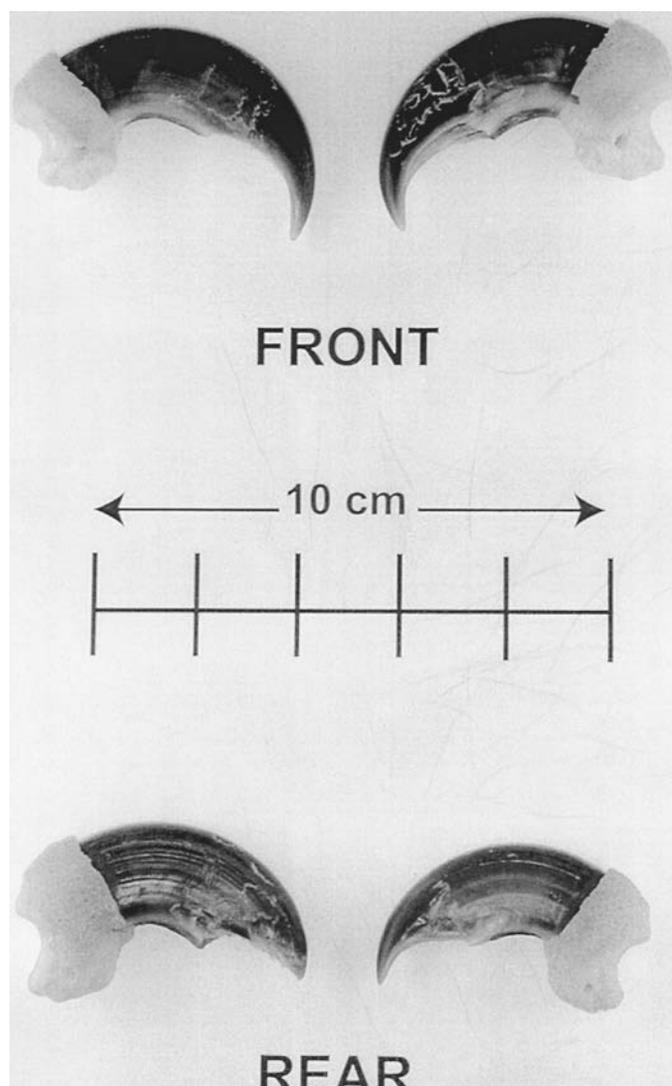


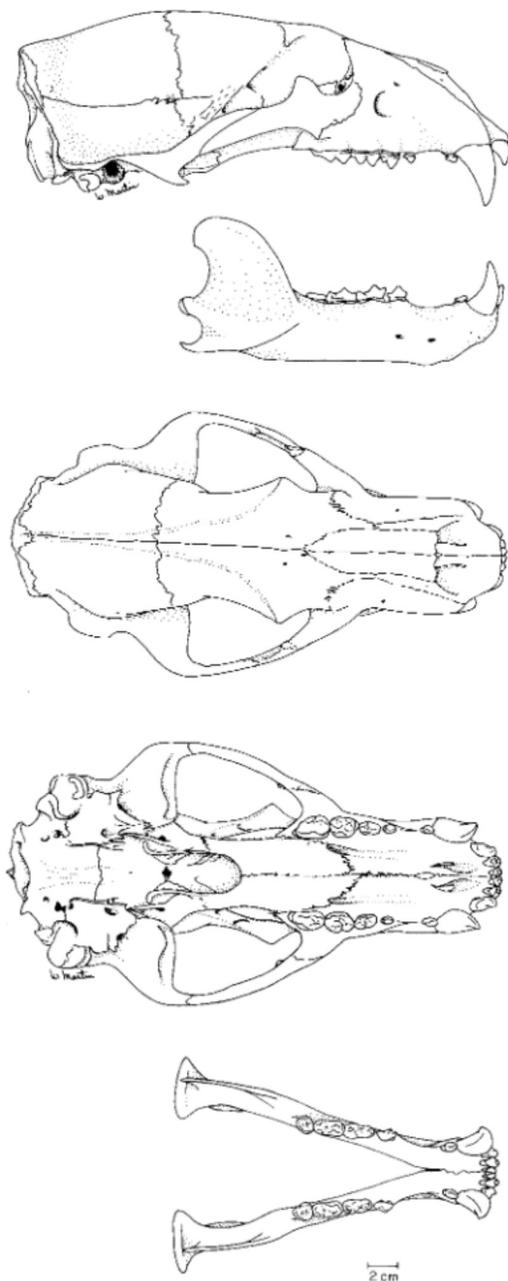
FIGURE 27.4. Rare unpigmented polar bear claws, on a polar bear captured in the southern Beaufort Sea. SOURCE: Photo by Steven C. Amstrup.

1971). The proportionately larger canines coincide with the pronounced sexual dimorphism which is more accentuated in polar bears than it is in any other ursid (Stirling and Derocher 1990).

The skull of the polar bear shares the principal characteristics of the skulls of other ursids. The largest brown bear skulls are larger than the largest polar bear skulls. Polar bear skulls are proportionately narrower across the palate between second molars than skulls of brown bears (Kurtén 1964). The ratio of condylobasal length to zygomatic width (L/W) also is larger in the polar bear, accentuating the narrower skull. The L/W for 279 brown bears taken by hunters was 1.59, whereas the L/W for 150 polar bears was 1.63 (calculated from Nesbitt and Parker 1977). The difference in actual measurements is not as pronounced as the visual impression suggests. This is because of the more strongly developed and overhanging occiput and significantly greater height in skulls of brown bears (Kurtén 1964). In lateral view, the lower height, combined with absence of the pronounced brow ridge that tends to give brown bears a “dish-faced” appearance, yields a smooth curve from canines across the maxillary bones to the cranium (Fig. 27.5). These features combine to give the polar bear a “Roman nose” appearance.

GENETICS

Despite the evidence of population segregation from marking, survey, and radiotelemetry data, initial evaluations using genetic techniques



F1111127.5. Skull of the polar bear (*Ursus maritimus*). From top to bottom: lateral view of cranium, lateral view of mandible, dorsal view of cranium, ventral view of cranium, dorsal view of mandible.

protein electrophoresis, Larsen et al. (1983b) found little variation in allozymes among polar bears. They concluded there was no reason to reject a hypothesis of one common polar bear population worldwide. Larsen et al. (1983b) assumed that high gene flow across the Arctic and strong common selective pressures reduced variation among polar bears. Supporting that concept, Durner and Amstrup (1995) recorded the movement of a radio-collared polar bear from near Prudhoe Bay, Alaska, to Greenland. That bear was only 1 of 106 equipped with platform transmitter terminals or satellite radio-collars between 1985 and 1992. Relatively few such movements, however, would be required to genetically homogenize polar bear populations worldwide (Paetkau et

al. 1999). Protein electrophoresis, however, may have a relatively low ability to resolve genetic variation among populations (Scribner et al. 1997). Therefore, the absence of differences in these markers may not be surprising.

More recent studies using highly variable nuclear genetic markers called microsatellites have resolved differences among polar bears living in different areas. Paetkau et al. (1995) found significant differences in genetic distances among members of four Canadian populations of polar bears. They concluded that the long-distance movements of polar bears have not resulted in complete genetic mixing of populations. Furthermore, Paetkau et al. (1999) reported significant correlations among movement data and genetic data from polar bear populations worldwide. They found greater differences among populations in the Canadian Arctic than among populations surrounding the polar basin. Such contrasts fit well with observed differences in movement patterns in these areas (Amstrup et al. 1986, 2000; Messier et al. 1992; Amstrup and Gardner 1994; Bethke et al. 1996; Scribner et al. 1997).

Genetic management units that correspond with boundaries defined by radiotelemetry have now been identified for most polar bear populations (Paetkau et al. 1999). The correspondence between movement data and recent genetic data allows managers to make better decisions about harvest or other human activities that could have population-level impacts.

Comparisons of the relative genetic variability among putative populations of different bear species are difficult because literature on brown, black, and polar bears has not presented easily comparable or consistent measures of interpopulation genetic variation. Nonetheless, microsatellite data that can be compared suggest there may be less genetic variation among populations of polar bears than among populations of black bears and brown bears (Paetkau et al. 1995, 1999). Paetkau et al. (1999) also found genetic distances among polar bear populations were at the lower extreme of the distances reported for the gray wolf (*Canis lupus*), another widely distributed carnivore.

Evidence from patterns in mtDNA also may hint at somewhat less genetic variation among polar bear populations than among populations of other bears. Cronin et al. (1991) reported only one basic polar bear mtDNA lineage, whereas black and brown bears each have two very divergent lineages. The older species (black and brown bears) appear to have more genetic variation across their ranges than the more recently derived polar bears.

Greater morphological variation among populations of brown bears (e.g., very large individuals, such as those living on Kodiak Island and coastal Alaska, vs. smaller interior or arctic bears) also appears to reflect more genetic variation than is present among polar bears (Stirling and Derocher 1990; Talbot and Shields 1996a, 1996b). Morphological variation among polar bears is minimal throughout their range. Paetkau et al. (1999) concluded from the relatively small genetic distances and absence of major discontinuities among polar bear populations that all polar bears belong to one evolutionary lineage at this time. Over long periods of geologic time there has been a considerable amount of genetic exchange across the range of polar bears, resulting in low levels of population differentiation.

Although polar bears show less genetic variation among populations than do other bears, genetic variation within populations of polar bears appears to be similar to that within populations of black and brown bears. Paetkau and Strobeck (1998) concluded that polar bear populations were less variable than brown bears, which were less variable than black bears. When levels were averaged over several putative populations of each species, however, microsatellite heterozygosity within populations was 0.68 for polar bears (Paetkau et al. 1999), 0.66 for brown bears, and 0.72 for black bears (Paetkau et al. 1997), suggesting little difference. This pattern was also observed when two functional genes were compared. Considerable allelic variation in

K-casein and the MHC are highly conserved because they influence milk quality and production and disease resistance. The functional importance of these genes may have led polar bears to retain their ancestral variability.

EVOLUTION

The polar bear appears to share a common ancestor with the present-day brown bear. It apparently branched off the brown bear lineage during the late Pleistocene. Kurtén (1964) suggested that ancestors of the modern polar bear were “gigantic.” Although still the largest of the extant bears, the polar bear, like many other mammals, has decreased in size since the Pleistocene. Also, significant morphological changes have continued within the last 20,000–40,000 years, perhaps through the present (Kurtén 1964). Stanley (1979) described the many recently derived traits of polar bears as an example of “quantum speciation.”

Evidence of polar bear evolution contained in the sparse samples of fossils has been strengthened recently by molecular genetics. Whereas traits of fossil teeth and bones from polar bears clearly indicate their brown bear origins, fossil remains include only a handful of specimens (Kurtén 1964). Genetic data from extant bears can provide phylogenetic information unavailable in the fossil record. Shields and Kocher (1991) first analyzed mtDNA sequences and showed a close relationship between brown bears and polar bears. Cronin et al. (1991) then discovered that mtDNA of brown bears is paraphyletic with respect to polar bears. That is, the mtDNA of brown bears of the Alexander Archipelago in southeastern Alaska is more closely related to the mtDNA of polar bears than it is to the mtDNA of other brown bears. Cronin et al. (1991) reported that mtDNA sequence divergence between Alexander Archipelago brown bears and polar bears is only about 1%, whereas a divergence of about 2.6% separates polar bears from brown bears occurring elsewhere. Cronin et al. (1991) and Cronin (1993) emphasized that mtDNA sequence divergence trees are not species trees and that mtDNA is not, by itself, a good measure of overall genetic differentiation. Nonetheless, these relationships provide a compelling argument regarding the origin and evolution of polar bears.

Following the discovery of Cronin et al. (1991), others corroborated the finding of paraphyletic mtDNA in brown bears and polar bears. Talbot and Shields (1996a, 1996b) suggested that the Alexander Archipelago brown bears represent descendants of ancestral stock that gave rise to polar bears. This stock may have survived Pleistocene glaciers in an ice-free refugium in southeastern Alaska, isolated from brown bears in other Pleistocene refugia (Heaton et al. 1996). This island-dwelling ancestral stock apparently has remained isolated from the more recent mainland bears by broad ocean passages.

Talbot and Shields (1996b) found mtDNA sequence divergence rates similar to those reported by Cronin et al. (1991), and proposed that ancestors of the Alexander Archipelago brown bears diverged from the other mtDNA lineages of brown bears 550,000–700,000 years ago. The mtDNA sequence divergences also suggested that polar bears branched from the Alexander Archipelago ancestral stock of brown bears about 200,000–250,000 years ago, a date closely corresponding with that suggested in the fossil record (Thenius 1953; Kurtén 1964). Shields and Kocher (1991) and Cronin et al. (1991) reported that the mtDNA nucleotide sequence divergence between brown and polar bears (grouped together) and black bears was 7–9%. Applying the substitution rate (6%/million years) for mtDNA genes reported by Talbot and Shields (1996a) to the sequence divergence reported by Cronin et al. (1991) suggests that brown bear ancestral stock diverged from that of black bears approximately 1.2–1.5 million years ago. This “molecular clock” estimate may be low. The fossil record suggests black bears diverged from the brown bear lineage 1.5–2.5 million years ago.

Cronin (1993) cautioned that mutation rates vary among genes as well as among taxa, and that conclusions based on “molecular clocks”



F□□□□27.6. Ringed seal (*Phoca hispida*), named for the ringlike pattern in the fur. Ringed seals, which weigh < 100 kg, make up the greatest portion of the polar bear diet worldwide. S□□□□: Photo by Steven C. Amstrup.

S. Amstrup, unpublished data). That is, the DNA sequences do not resolve the relationships among the species. These functional genes are presumably under strong selection and do not diverge as rapidly as mtDNA. Nonetheless, the mtDNA analyses indicate that Alexander Archipelago brown bears derive from more ancient stocks and are more closely related to polar bears than are other members of the brown bear clan. These conclusions also corroborate the recent appearance of the polar bear in the fossil record and the more ancient roots of the black bear (Thenius 1953; Kurtén 1964). All DNA evidence, regardless of some areas of uncertainty, corroborate conclusions from the fossil record that the polar bear is a recently derived species and is undergoing rapid evolution. The extreme arctic marine environment is undoubtedly exerting strong selection pressures for rapid adaptation.

FEEDING HABITS

The polar bear is more predatory than other bears and is the apical predator of the arctic marine ecosystem. Polar bears prey heavily throughout their range on ringed seals (*Phoca hispida*) (Fig. 27.6) and, to a lesser extent, bearded seals (*Erignathus barbatus*) (Fig. 27.7). Ringed seals



apparently have been a principal food of polar bears for a significant portion of their coevolutionary history and ringed seal behaviors appear to be oriented around avoidance of polar bear predation. Stirling (1977) contrasted the behavioral ecology of ringed seals and Weddell seals (*Leptonychotes weddelli*). Steady predation pressure from polar bears may have led ringed seals to use subnival birthing lairs and to interrupt spring and summer basking with frequent periods of scanning their surroundings for predators. Weddell seals, on the other hand, evolved in the Antarctic system, where surface predators are absent. They give birth unsheltered on the surface of the sea ice, and they are so ambivalent about activities on the ice surface that human researchers often can walk right up to them for study purposes (Stirling 1977).

Although seals are their primary prey, polar bears also have been known to kill much larger animals such as walrus (*Odobenus rosmarus*) and belugas (*Delphinapterus leucas*) (Stirling and Archibald 1977; Kiliaan et al. 1978; Smith 1980, 1985; Lowry et al. 1987; Calvert and Stirling 1990). The heaviest prey may be taken mainly by large male polar bears (Stirling and Derocher 1990), and unusual circumstances may be required. Nonetheless, in some areas and under some conditions, alternate prey may be quite important to polar bear sustenance. Stirling and Øritsland (1995) suggested that in areas where the estimated numbers of ringed seals are proportionately reduced relative to numbers of polar bears, other prey species were being substituted.

Overall, polar bears are most effective predators of young ringed seals, perhaps because they are naive with regard to predator avoidance. In spring, polar bears may concentrate their predatory efforts on capture of new-born ringed seal pups (Smith and Stirling 1975; Smith 1980). In some areas, predation on pups is extensive. Hammill and Smith (1991) estimated that polar bears annually kill up to 44% of new born seal pups if conditions are right. Throughout the rest of the year, polar bears take seals predominantly from the first two year classes (Stirling et al. 1977a; Smith 1980). Whereas abundance of ringed seals may regulate density of polar bears in some areas, polar bear predation may regulate density and reproductive success of ringed seals in other areas (Hammill and Smith 1991; Stirling and Øritsland 1995).

Polar bears apparently digest fat more easily than protein (Best 1984). They seem to prefer the fatty portions of seals (and presumably other animals) to muscle and other tissues. Stirling (1974) reported that polar bears often remove the fat layer from beneath the skin of freshly killed seals and consume it immediately. Because over half of the calories in a whole seal carcass may be located in the layer of fat between the skin and underlying muscle (Stirling and McEwan 1975), a bear that quickly consumes most of the fat available has maximized its caloric return in the minimal amount of time possible. This may be important to all but the largest polar bears because there is considerable competition for kills. Younger and smaller bears often are driven away from their kills by larger bears.

A high-fat and low-protein diet apparently serves polar bears physiologically as well. They are very efficient at recycling nitrogenous products of catabolism, and can use metabolic water released from fat metabolism (Nelson et al. 1983). Digestion of protein requires water, whereas digestion of fat releases water. In a cold environment, free water is available only at the energetic cost of melting ice and snow. The lipophilic habits of the polar bear minimize energy expended to obtain water in winter (Nelson 1981).

Polar bears tend not to cache prey animals they have killed like grizzly bears do (Stirling 1974; DeMaster and Stirling 1981; Stirling and Derocher 1990). This may be another reason why they consume the highest reward portion of their prey first. Although they have not been observed to cache, polar bears are surplus killers. Stirling and Derocher (1990) reported seeing a polar bear kill two seals within an hour of feeding extensively on another seal. Neither of the latter two seals killed was eaten. Stirling and Øritsland (1995) also have reported surplus killing in polar bears. I once observed a young male polar bear still-hunting at a

still-hunting site, ran to the pile of dead seals, and covered them with his body as if to protect his stash. This bear apparently had eaten his fill from the first seal but was continuing to hunt, catch, and stack seals despite a low probability that he would consume much of them.

An interesting adaptation to the carnivorous diet, and a difference between polar bears and other temperate and arctic bears, is that only the pregnant females enter dens for the entire winter. Other members of the population continue to hunt seals on the sea-ice throughout the winter. The year-around availability of seals allows denning in polar bears to be strictly a reproductive strategy (affording an acceptable environment for neonates), whereas in most bears it is largely a foraging strategy (avoiding the winter period of food unavailability).

Like other ursids, polar bears will eat human refuse (Lunn and Stirling 1985), and when trapped on land for long periods they will consume coastal marine and terrestrial plants and other terrestrial foods (Derocher et al. 1993). The significance of other foods to polar bears may be limited, however (Lunn and Stirling 1985; Derocher et al. 1993). Over most of their range, polar bears have little opportunity to take foods of shoreline or terrestrial origin. Derocher et al. (1993) found that 31% of pregnant polar bears in the Hudson Bay area fed on berries before denning in autumn. The significance of this to their productivity was not known. Ramsay and Hobson (1991) and Hobson and Stirling (1997) differed in opinions of the value of supplemental terrestrial food. In general, the significance of terrestrial foraging to polar bears is poorly understood.

Clearly the value of alternate foods for polar bears depends on their richness and digestibility. Polar bears are poorly equipped to consume and digest most plant parts (Bunnell and Hamilton 1983), and it seems likely that except for fruiting bodies, plants will contribute little to their energy balance. Lunn and Stirling (1985) found that polar bears using human refuse at a dump maintained their weight or lost less weight than bears not using anthropogenic foods. Some bears using the dump even gained weight, but the supplemental food did not appear to confer a reproductive advantage (Lunn and Stirling 1985). Derocher et al. (2000) reported that some polar bears in Svalbard have become adept at catching reindeer (*Rangifer tarandus*). Considering the high digestibility of meat, it seems plausible that if readily available, reindeer could be an important alternate food of polar bears. Likewise, in the Beaufort Sea, dozens of polar bears each year have developed a habit of gathering at the butchering sites of bowhead whales (*Balaena mysticetus*) that are killed by local Native people. The value of this alternate food is apparently great, as nearly every bear seen near whale carcasses in autumn is obese.

MOVEMENTS

Data collected from radio-collared polar bears have confirmed their close ties to the ice. For example, between May 1985 and April 2001, we obtained 34,034 high-quality satellite radio-locations of polar bears in the Chukchi and Beaufort Sea areas of Alaska and northwestern Canada. Some collars had duty cycles that allowed them to transmit more frequently than other collars. When duty cycles were standardized so that each bear contributed one relocation per week, only 975 (7%) of 14,622 weekly locations were on land (Amstrup et al. 2000; Amstrup unpubl. data). Most of those were bears occupying maternal dens for the winter. In the polar basin area, polar bears truly are pelagic organisms (Garner et al. 1994)!

Telemetry data also have proven that polar bears do not wander aimlessly on the ice, nor are they carried passively with the ocean currents as previously thought (Pedersen 1945). Rather, they occupy multiannual activity areas outside of which they seldom venture. Annual activity areas of female polar bears monitored by radiotelemetry for multiyear periods varied among years. Collared animals, however, seemed to use seasonally preferred or "core" regions every year despite

as well as geographically (Stirling and Smith 1975; Ferguson et al. 1997, 1998, 2000a, 2000b; DeMaster et al. 1980; Amstrup et al. 2000). In areas of volatile ice, a large multiannual home range of which only a portion is used in any one season or year is an important part of the polar bear life history strategy.

Linear movements and activity areas are very large compared to those of most terrestrial mammals, and they vary in different regions of the globe, presumably because of variation in patterns of productivity and other sea-ice characteristics. In the Beaufort Sea, where polar bears have been followed by radiotelemetry for 20 years (Amstrup et al. 2000), total annual movements, calculated as the sum of straight-line distances separating consecutive weekly relocations, averaged 3415 km and ranged up to 6200 km. Movement rates of >4 km/hr were sometimes sustained for long periods, and movements of >50 km/day were observed. Annual activity areas of 75 radio-collared female polar bears in the Beaufort Sea region averaged 149,000 km². The smallest annual activity area was nearly 13,000 km², whereas the largest was 597,000 km² (Amstrup et al. 2000).

Whereas movements of polar bears in the Beaufort Sea are impressive in their magnitude, movements of bears in areas of more dynamic ice may be even greater. The mean activity area size for six bears followed by satellite telemetry in the Chukchi Sea was 244,463 km² (Garner et al. 1990). The mean annual distance moved by those bears was 5542 km. The potential mobility of polar bears in regions of volatile ice was illustrated by a mean rate of northerly spring movement of 14.1 km/day at a time when ice was moving as much as 15.5 km/day in the opposite direction (Garner et al. 1990).

In contrast, Schweinsburg and Lee (1982) reported maximum activity areas of $<23,000$ km² in the Canadian Arctic Archipelago. Ferguson et al. (1999) also reported very large-scale movements for polar bears in the volatile sea-ice conditions of Davis Strait and Baffin Bay, and much smaller movements for bears in the interior of the Canadian Arctic Archipelago. The sea-ice of the Chukchi and Beaufort Seas and Baffin Bay is more dynamic and unpredictable than the ice in much of the Canadian Arctic Archipelago. The mobility of polar bears appears to be directly related to that variability (Garner et al. 1990, 1994; Gloersen et al. 1992; Messier et al. 1992; Ferguson et al. 2001).

Seasonal movement patterns of polar bears serve to emphasize the role of sea-ice in their life cycle. In the Beaufort Sea, the largest monthly activity areas were in June–July and November–December. These also were the months of highest movement rate. This matches the patterns of ice ablation and formation observed in the area (Gloersen et al. 1992). Polar bears catch seals mainly by still-hunting (Stirling and LaTour 1978). The volatile summer and autumn ice must minimize predictability of seal hunting opportunity. That unpredictability could require longer movements and larger activity areas during seasons of freeze-up and break-up. From May through August, measured net monthly movements of polar bears in the Beaufort Sea were significantly to the north for all bears. In October bears moved back to the south (Stirling 1990; Amstrup et al. 2000). Those movements appeared to be correlated with general patterns of ice formation and ablation. Between May and August, the ice of the southern Beaufort Sea is degrading (Gloersen et al. 1992). October is usually the month of freeze-up in the southern Beaufort Sea and may be the first time in months when ice is available over the shallow water near-shore. Polar bears summering on the persistent pack ice quickly move into shallow-water areas as soon as new annual ice forms in autumn, and they disperse easterly and westerly as ice solidifies through winter.

In contrast to polar bears of the Beaufort Sea region, Messier et al. (1992) reported that peak movement rates of instrumented polar bears in Viscount Melville Sound within the Canadian High Arctic Archipelago occurred from May to July. Movements, although increasing after January, were less from October through March. Ferguson et al. (2001) reported high movement rates in spring and summer in

northern Beaufort Sea areas, movement rates remained high in November and December and low in May. The lower level of winter movement among polar bears of Viscount Melville Sound may be a consequence of the year-round abundance of multiyear ice (Gloersen et al. 1992; Messier et al. 1992; Ferguson et al. 2001). The density of ringed seals is lower there than in most other areas of polar bear habitat from Alaska through to West Greenland (Stirling and Øristsland 1995), and seals that are present in Viscount Melville Sound tend to be more concentrated along tidal cracks and pressure ridges that parallel the island coastlines (Kingsley et al. 1985). By comparison, the annual ice that predominates in most of the southern Beaufort Sea is more dynamic, and allows a greater amount of sunlight into the water column to support primary productivity. This facilitates easier access to air for seals to breathe, and supports higher densities and numbers of ringed seals and polar bears (Stirling et al. 1982; Kingsley et al. 1985; Stirling and Øristsland 1995).

Polar bears in the Beaufort Sea may spend more time in winter actively foraging, and those in the Viscount Melville Sound area may spend more time resting and conserving energy. Messier et al. (1992) reported that long periods of “sheltering” were common among bears wintering in Viscount Melville Sound, and attributed this behavior to the poor foraging conditions there. Another factor may be the greater predictability of the foraging conditions in the stable ice of the High Arctic. With less change in the character of the sea-ice after freeze-up, polar bears may be able to determine the profitable hunting areas in early winter. Predictable sea-ice conditions could help bears minimize midwinter searching for good hunting areas and maximize benefits of sheltering. The constantly changing sea-ice in places like the Beaufort Sea or Baffin Bay, however, may require major modifications of foraging strategy from month to month or even day to day during break-up, freeze-up, or periods of strong winds. Polar bears are adaptable enough to modify their foraging patterns for the extreme range of sea-ice scenarios (Ferguson et al. 2001).

Just as the labile nature of the sea-ice results in annual variability in the distribution of suitable habitat for polar bears, it also eliminates any benefit to polar bears of defending territories. The location of resources is less predictable than resources on which terrestrial predators depend. Seals tend to be distributed over very large areas at low densities (Bunnell and Hamilton 1983). Furthermore, their distribution, density, and productivity are extremely variable among years (DeMaster et al. 1980; Stirling et al. 1982; Stirling and Øristsland 1995). As radiotelemetry studies have shown, female polar bears show only general fidelity to seasonal feeding areas (Ferguson et al. 1997; Amstrup et al. 2000). Absence of strict fidelity, especially during breeding and denning seasons (Garner et al. 1994; Amstrup and Gardner 1994), essentially prohibits defendable territories. Males similarly must be free of the need to defend territories if they are to maximize their potential for finding mates each year (Ramsay and Stirling 1986b).

Although there may be limited spatial segregation among individual polar bears, telemetry studies have demonstrated spatial segregation among groups or stocks of polar bears in different regions (Schweinsburg and Lee 1982; Amstrup et al. 1986, 2000; Garner et al. 1990, 1994; Messier et al. 1992; Amstrup and Gardner 1994; Bethke et al. 1996; Ferguson et al. 1999). Patterns in spatial segregation suggested by telemetry data, survey and reconnaissance, marking and tagging studies, and traditional knowledge resulted in recognition of 19 partially discrete polar bear groups (Lunn et al. 2002:21–35). There is considerable overlap in areas occupied by members of these groups, and boundaries separating the groups have been adjusted as new data were collected. Nonetheless, these boundaries are thought to be ecologically meaningful, and the units they describe are managed as populations.

A 20th polar bear population may occur in the central polar basin (Table 27.1). It is unclear whether bears that occur in this region are simply visitors from populations nearer to islands and continental shore-

1. Summary of polar bear population status as determined by both historical harvest (1995-96 to 1999-00) levels and current management practices. Abundance estimates are the best available data for each population, which ranges from little or no information to detailed inventory studies. The percent females statistic excludes bears of unknown sex, and deaths are not included

Population	Abundance Estimate	Certainty of Estimate	Monitoring of Harvest and Other Removals	% Females in Kill	Sustainable Kill ^a	Mean Annual Kill	Environmental Concerns ^b	Status ^c
Barrow	2000	poor (1997)	fair	38	unknown	80	P, W	?
Beluga	2000-5000	poor (1982)	Norway - good Russia - poor		na	Norway - 2 Russia - ?	P, W	?
Chukotka	unknown	unknown	poor		na	unknown	P, I	?
East Siberian	800-1200	poor (1993)	poor		na	unknown	P	?
East Siberian	2000+	poor (1997)	US - good Russia - poor	US - 35 Russia - ?	86+	US - 76 Russia - ?	W, I	S?
East Siberian	1800	good (2001)	good	33	81	50	W, I	I
East Siberian	1200	good (1987)	good	33	54	32	W	I
East Siberian	200	poor (1995)	good		9?	0	P	S?
East Siberian	230	fair (1992)	good	25	4	4	S	S
East Siberian	100	fair (1979)	good	32	4	4	W	S ^a
East Siberian	1700	fair (1996)	good	25	77	76	W	S ^a
East Siberian	350	fair (2001)	good	26	11	24	W	S?
East Siberian	900	poor (1986)	good	40	34	37	W	S ^a
East Siberian	2300	good (1996)	good	36	97	90	W	S ^a
East Siberian	1200	good (1997)	good	35	52	49	W	S ^a
East Siberian	1000	fair (1986)	good	36	41	45	S	S
East Siberian	200	fair (1996)	fair	32	9	10	S	S
East Siberian	2200	fair (1996)	fair	36	93	139		D
East Siberian	1400	fair (1996)	fair	38	56	63	W	D?
East Siberian	unknown	unknown	none		na			?
Estimated for world abundance:	21,500-25,000							

^a Lunn et al. 2002:22.

^b Data for Viscount Melville Sound, sustainable harvest is based on population estimate (N), estimated rates of birth and death, and harvest sex ratio (Taylor et al. 1987):

$$\text{Sustainable harvest} = \frac{N \times 0.015}{\text{Proportion of harvest that was female}}$$

of harvest that was female is the greater of the actual value or 0.33. Unpublished modeling indicates a sex ratio of 2 males: 1 female is sustainable, although mean age and abundance of males will be maximum sustainable yield. Harvest data (Lee and Taylor, 1994) indicate that selection of males can be achieved
 industrial development current or proposed; P - evidence of pollutants in bear tissues; W - evidence global warming effects on sea ice or populations
 decreasing; I - increasing; S - stationary; S^a - stationary, population managed with a flexible quota system in which any over-harvest in one year results in a fully compensatory reduction to the following
 ; ? - indicated trend uncertain

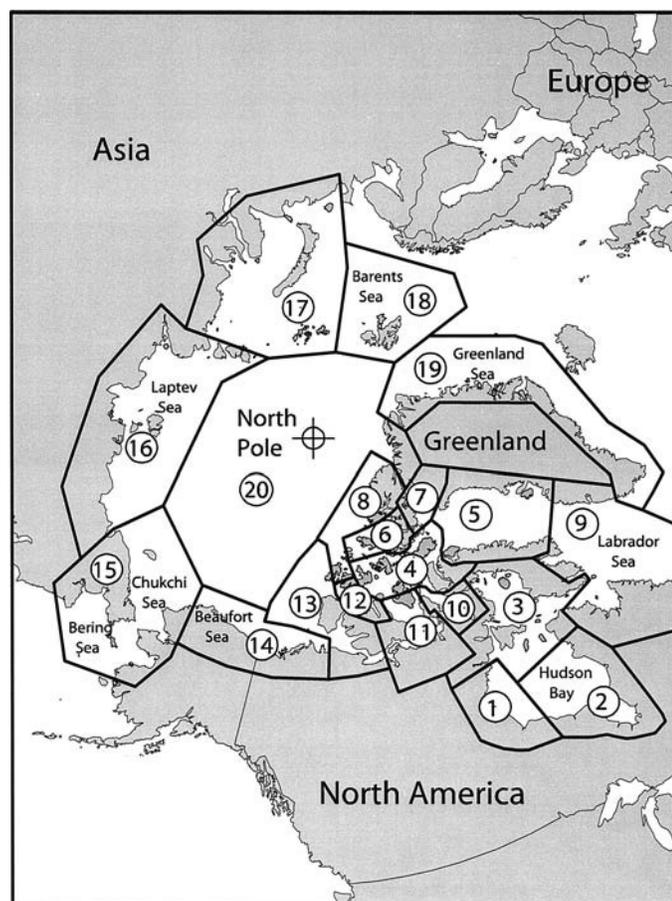


FIG. 27.8. The circumpolar range of polar bears is subdivided, according to observed movement patterns, into 20 hypothesized populations or stocks. 1, Western Hudson Bay; 2, southern Hudson Bay; 3, Foxe Basin; 4, Lancaster Sound; 5, Baffin Bay; 6, Norwegian Bay; 7, Kane Basin; 8, Queen Elizabeth Islands; 9, Davis Strait; 10, Gulf of Boothia; 11, M'Clintock Channel; 12, Viscount Melville Sound; 13, northern Beaufort Sea; 14, southern Beaufort Sea; 15, Chukchi Sea; 16, Laptev Sea; 17, Novaya Zemlya; 18, Svalbard; 19, East Greenland; 20, Arctic basin. Boundaries are constantly being adjusted as new data and ecological insights are obtained. S. Adapted from Lunn et al. (2003:23).

DENNING

Across most of their range, pregnant female polar bears excavate dens in snow and ice in early winter (Harington 1968; Lentfer and Hensel 1980; Ramsay and Stirling 1990; Amstrup and Gardner 1994). They give birth in those dens during midwinter (Kostyan 1954; Harington 1968; Ramsay and Dunbrack 1986) (see section on reproduction), and emerge from dens when cubs are approximately 3 months old. Because neonates are so altricial, the period of denning is essential to their early survival. Recognizing it as a critical phase in the polar bear life cycle, scientists have devoted much attention to aspects of maternal denning.

Distribution of Denning. Historically, polar bear dens were thought to represent the "core areas" of their ranges (Harington 1968). In those core areas, large numbers of polar bears repeatedly and predictably concentrated their denning within relatively small geographic regions (see Fig. 27.1). Examples of concentrated denning areas include particular islands of the Svalbard Archipelago north of Norway (Lønø 1970; Larsen 1985); Franz Josef Land, Novaya Zemlya, and Wrangel Island

Concentration or core areas were easily detected by aerial or ground surveys, and often had been known from reports of early explorers or Native people residing in the area. Early knowledge of concentrated denning led to the view that all polar bears must use such core areas, and that areas without them did not significantly contribute to polar bear reproduction. Harington (1968:8) implied as much when he stated, "No major denning areas seem to exist in Alaska." It was assumed geographic regions without such areas mainly were populated by visiting polar bears. That concept led Native people of northern Canada to believe that harvests in Alaska were being sustained by polar bears produced in Canada (Stirling and Andriashek 1992). Over much of their range, we now know, polar bears den in a more diffuse pattern where individual dens are scattered over broad reaches of habitat at low density (Lentfer and Hensel 1980; Stirling and Andriashek 1992; Amstrup 1993; Amstrup and Gardner 1994; Messier et al. 1994; Ferguson et al. 2000a; Durner et al. 2001, 2003).

Successful denning by polar bears requires accumulation of sufficient snow that a pregnant female can create a snow cave early in winter and subsequently be covered over. A variety of weather and topographic conditions meet that requirement. Bears denning in the concentration areas of the Svalbard Islands or the large islands north of the Russian coast meet their needs in rugged mountains and fjordlands (Uspenski and Chernyavski 1965; Lønø 1970; Uspenski and Kistchinski 1972; Larsen 1985). One famous concentration area, however, is in the relatively flat tundra along the west coast of Hudson Bay in Canada (Ramsay and Andriashek 1986; Ramsay and Stirling 1990). There, dens are concentrated along relatively low banks and ridges supporting small trees. In the regions where denning is dispersed, the topography ranges from mountainous to essentially flat (Harington 1968; Lentfer and Hensel 1980; Stirling and Andriashek 1992; Amstrup 1993; Amstrup and Gardner 1994; Messier et al. 1994; Ferguson et al. 2000a; Durner et al. 2001, 2003).

Research on Wrangel Island (Belikov 1976) and Hudson Bay (Kolenosky and Prevett 1983) suggested that polar bears select den sites based on specific topography and habitat. Whether the habitats are scattered or concentrated, however, all denning areas have micro- or macrohabitats that predictably catch snow in the autumn and early winter (Durner et al. 2003). In the mountains, snow-catching features are obvious. The snow-catching ability of the very flat terrain in coastal Alaska, where until recently denning was presumed to be insignificant, is not so obvious. There, the most frequently used denning habitats are along coastal and river banks. Although the mean bank height where female bears den is 5.4 m (SD = 7.4 m), banks as low as 1.3 m provided sufficient snow depth for successful denning (Durner et al. 2001). The Alaskan northern coast gets relatively little snow. However, the landscape is so flat that what snow there is, is blown incessantly across the plain throughout the winter. Any areas of relief in the otherwise flat terrain are filled solidly with snow from the very early winter. Banks used for denning in Alaska most commonly had water or level ground below the slope and relatively level ground above, enhancing the chance for sufficient snow build-up for denning (Durner et al. 2001).

Across the range of polar bears, most denning, whether in concentration areas or dispersed, occurs relatively near the coast. In early visual surveys, Harington (1968) found that 61% of dens located over broad regions of the Canadian Arctic were within 8 km and 81% were within 16 km of the coast. All dens seen by Stirling and Andriashek (1992) in the Canadian Beaufort Sea were along the coast. Likewise, Stishov (1991) reported that 83% of dens found during surveys of northern Russia were in snow banks formed under shore slopes and precipices. Most polar bear dens were within 3 km of the coast of Svalbard (Larsen 1985). Even on Wrangel Island, where bears move inland to den in high mountains, most are located within 8 km of the coast. The main exception to coastal denning appears to be the Hudson Bay area, where

investigators to locate dens anywhere bears establish them. More than 80% of maternal dens found on land by radiotelemetry in the Alaskan Beaufort Sea were within 10 km of the coast and over 60% are right on the coast or on coastal barrier islands (S. C. Amstrup, unpublished data). Messier et al. (1994) used satellite telemetry to learn that maternal dens in the Canadian High Arctic were widely scattered in coastal areas, and averaged 8.6 km from the coast. Ferguson et al. (2000a) reported that most dens found using telemetry in the Canadian High Arctic and Baffin Bay areas were within 20 km of the coast.

Denning on the Pack Ice. Although most maternal denning appears to occur on coastlines of mainlands and islands, Amstrup and Gardner (1994) discovered that 53% of the dens of polar bears radio-collared between 1981 and 1991 were on drifting pack ice. They also found that 4% were on land-fast ice adjacent to shore. Lentfer and Hensel (1980) recognized the occurrence of dens on pack ice, but suggested that it was limited to bears that could not make it to shore to den. Harington (1968) concluded that denning on ice was not preferred, and Messier et al. (1994) reported no maternal denning on pack ice, although some "shelter denning" on pack ice was observed. The discovery that half of the bears in the Beaufort Sea may den on drifting sea ice, therefore, was not expected.

Bears that den on pack ice potentially are subject to a number of disruptions that could not affect bears denning on land. First, the sea-ice changes throughout the year. It shifts, breaks up, and refreezes. Ice floes can turn over or have other floes rafted onto them. Therefore, a maternal den could be overturned, buried, or otherwise compromised any time in the denning cycle. Amstrup and Gardner (1994) reported observations of six polar bears in pack-ice dens that were swept past Point Barrow and southwest into the Chukchi Sea due to unusually unstable ice. Two of those females were observed after their dens had been destroyed by rafting action of sea-ice in mid-February. The females carried tiny cubs in their mouths, probably in desperate attempts to relocate to a new den site. When observed later that spring, however, neither of these bears was accompanied by young. Only one of six females swept into the Chukchi Sea that year had cubs when reobserved later. Hence, there are risks involved in denning on sea-ice.

On emergence of the female and her new cubs, the predictability of available resources may be limited even if a pack-ice den remains intact. Bears that den on pack ice may drift up to 1000 km during the winter (Amstrup and Gardner 1994). Despite observed and hypothetical risks, production of cubs from dens at sea was not significantly different than that from dens on land (Amstrup and Gardner 1994), and sea-ice denning has obviously been maintained as a successful reproductive strategy in the Beaufort Sea region.

Despite the absence of conclusive reports, sea-ice denning probably occurs at some level in other areas. When engaged in polar bear aerial surveys on the high pack ice northeast of Greenland and north of Svalbard, Larsen et al. (1983a) observed numerous tracks of females with cubs of the year near 84° N latitude. These animals were moving predominantly in a southeasterly direction, toward Svalbard. The distance of these sightings from land and the time of the year in which they were recorded suggested those cubs were born on the pack ice. Little significance was attached to those footprints at that time. However, that observation takes on a greater significance in light of the confirmed frequency of sea-ice denning in the Beaufort Sea (Amstrup and Gardner 1994; Amstrup et al. 2000) and the recent recognition of a possible polar basin stock of polar bears. Because other recent studies using satellite radiotelemetry have not revealed significant amounts of sea-ice denning, it seems reasonable to assume that its overall frequency is low. The linear coastline of central Arctic Russia may be more similar to the Beaufort Sea than other areas, and hence may be another area where sea-ice denning is common. Satellite data from that region, however, are too few to test that hypothesis.

used areas after long distances of passive transport. How polar bears accomplish this is unknown.

Fidelity to Denning Locales. Although there are no historical data regarding denning fidelity, it has logically been assumed that concentrated denning areas are maintained by fidelity of individual females to those sites (Uspenski and Chernyavski 1965; Lønø 1970; Uspenski and Kistchinski 1972; Larsen 1985). Pregnant females return, it is assumed, to areas where they have successfully denned in the past.

The greatest number of records of den-site fidelity derives from the Beaufort Sea. There, 27 polar bears were followed to more than one suspected or confirmed maternity den (Amstrup and Gardner 1994). One radio-collared polar bear was followed to four maternal denning sites, 7 were followed to three dens each, and 19 to two dens. Confirmed sequential dens were separated from their precursors by a mean of 308 km (SD = 262, n = 30), and the minimum distance was 23 km. Distances separating sequential land dens were not different from those separating sequential pack-ice dens. Bears that denned once on pack ice were more likely to den on pack ice than on land in subsequent years, and vice versa. Similarly, bears were faithful to general geographic areas. Those that denned once those that denned once in the eastern half of the Alaskan coast were more likely to den there than to the west in subsequent years. When all years were considered, denning polar bears preferred some areas, but no areas were used by collared bears in all years. Weather, ice conditions, and prey availability, all of which varied annually, probably determined where bears denned. Those annual variations and the long-distance movements of polar bears (Amstrup et al. 1986, 2000; Garner et al. 1990) make seasonal recurrence at exactly the same location unlikely.

Although Beaufort Sea polar bears were not faithful to particular denning sites, data on den distribution and fidelity of females to denning areas indicated there are both "pack-ice" and "land-denning" bears. Den substrate switching appeared to be limited. This segregation may have begun when some females were prevented from reaching land in the fall.

The only other region where data are available on fidelity to denning areas is Hudson Bay. There, pregnant females initiate their over-winter denning period in earthen dens they occupy in summer. During winter, they burrow into adjacent snow drifts (Watts and Hansen 1987). The presence of hundreds of earthen dens in the region suggests a long tradition of use. In three instances, cavities were reused by different bears, but no observations of reuse of a cavity by the same bear were reported (Ramsay and Stirling 1990). On average, bears followed to second dens chose locations 27 km (4–52 km) from previous attempts (Ramsay and Stirling 1990). Hence, there was greater fidelity to local areas than in the Beaufort Sea, but site-specific philopatry was not apparent.

Despite general fidelity to local areas, the overall distribution of denning along the west coast of Hudson Bay shifted markedly over a 20-year period (Ramsay and Stirling 1990). Because bears have the navigational skills to return to the same area, the reason for the shift is not clear. A similar shift appears to be occurring in the Beaufort Sea region as well, however. During the 1990s, more females appeared to choose den locations in the central and western portions of the northern Alaska shore than during the 1980s (S. C. Amstrup, unpublished data). Such shifts must reflect changing ice formation and ablation patterns, food availability, or other unidentified ecological factors. Harington (1968), Larsen (1985), and Lønø (1970) concluded that variation in the local pattern of sea-ice movements during the preceding summer and autumn accounts for annual changes in the distribution of winter dens. Multiple-year trends in sea-ice patterns could clearly alter denning and other behavioral patterns.

Denning Chronology. Pregnant female polar bears enter their dens in the autumn after drifts large enough to excavate a snow cave are formed.

known about the chronology of denning. Larsen (1985) reported that most dens on Svalbard were opened in late March and vacated by mid-April. Lentfer and Hensel (1980) reported Alaskan polar bears came ashore to den in late October and early November and left their dens in late March and early April. Lønø (1970) concluded dens on Svalbard were entered in November and December and abandoned between 10 and 25 April. At the far north of Svalbard, he speculated that bears entered dens as early as late October. Observations in other High Arctic areas suggest abandonment between mid-March and mid-April (Uspenski and Chernyavski 1965; Kistchinski 1969; Belikov et al. 1977). Hansson and Thomassen (1983) suggested the first dens were opened in the first week of March and most were abandoned by mid-April. Kolenosky and Prevett (1983) and Ramsay and Andriashek (1986) reported emergence from dens in the Hudson Bay area in late February and early March. Polar bears are largely food deprived while on land in the ice-free period. During this time, they survive by mobilizing stored fat. Pregnant females that spend the late summer on land and then go right into dens may not feed for 8 months (Watts and Hansen 1987; Ramsay and Stirling 1988). This may be the longest period of food deprivation of any mammal, and it occurs at a time when the female must give birth and nourishment to her new cubs.

Satellite telemetry has now confirmed that the chronology of denning varies somewhat around the world. In the Beaufort Sea, mean dates of den entry were 11 and 22 November for land ($n = 20$) and pack-ice ($n = 16$) dens, respectively (Amstrup and Gardner 1994). Female bears continued foraging right up to the time of den entry. Then they denned near where they happened to be foraging. On average, Beaufort Sea polar bears emerged from their dens with new cubs on 26 March if they were on the pack ice ($n = 10$) and 5 April if they were on land ($n = 18$). Dates of entry and exit varied somewhat among years depending on sea-ice, snow, and weather conditions.

Messier et al. (1994) reported the mean entry into maternal dens in the Canadian Arctic was 17 September (SE = 3 days; range 27 August–12 October) and mean emergence was 21 March (SE = 3 days; range 4 March–7 April). Females and their cubs remained near dens for a mean 13 (SE = 3) days in the spring before leaving the denning area. Those data may indicate an earlier and more protracted denning period at higher latitudes than in the Beaufort Sea. Ferguson et al. (2000a), on the other hand, observed that bears denning at higher latitudes entered their dens a bit later than those to the south, but that exit times did not differ by latitude. They reported a mean den entry of 15 September (1 September–7 October), a mean exit of 20 March (15–28 March), and a mean 180 days in dens (163–200 days).

As noted, initiation of denning depends on sufficient snow accumulation to allow excavation of a den cavity. For bears denning on sea-ice or moving from sea-ice to land denning habitat, timing of sea-ice consolidation can alter the onset of denning. Sea-ice dens must be in ice stable enough to stay intact for up to 164 days while being pushed by currents for hundreds of kilometers.

Whereas only pregnant female polar bears enter dens for the entire winter, any bear may enter shelters for shorter periods to avoid storms, extreme cold or heat, or periods of poor hunting. Sheltering is best known along the west coast of Hudson Bay. Because the ice in Hudson and James Bays disappears entirely, the whole population there is forced onto land in summer. Feeding opportunities are minimal, and many animals take shelter in earthen dens, where it is cooler and they minimize insect harassment. When the ice forms in fall, most of the bears in earthen shelters go out on the new ice to hunt. Pregnant females, however, remain in the dens and eventually move into snow that drifts over their earthen structures (Stirling et al. 1977b; Derocher and Stirling 1990).

Use of shelter dens also occurs at higher latitudes. Messier et al. (1992) reported that long periods of “sheltering” were common among all classes of female bears (except those in maternal dens) wintering in

Canadian High Arctic, Ferguson et al. (2000a) reported a bimodal incidence of sheltering. Autumn sheltering occurred from mid-September to early November, whereas winter shelters were occupied mainly from late December to March. Autumn shelters were occupied for a mean 56 days (range = 50–70), whereas winter shelters were occupied for a mean 65 days (range = 35–86). At higher latitudes, the frequency of winter sheltering increased and the frequency of autumn sheltering decreased.

Although more female polar bears have been followed for longer periods there than anywhere, sheltering for protracted periods has not commonly been observed in the Beaufort Sea region (Amstrup and Gardner 1994; S. C. Amstrup, unpublished data). Yet, the latitude of the Beaufort Sea is in the middle of the range reported by Ferguson et al. (2000a). Clearly, use of sheltering in the eastern Canadian High Arctic and Baffin Bay is not so much a function of latitude as of sea-ice and other ecological conditions. Sea-ice formation and ablation, weather, and prey availability, although influenced by latitude, are as much controlled by the shapes of coastlines, presence of islands, water depths, currents and other factors. In areas of Baffin Bay and Davis Strait, seasonal absence of sea-ice forces polar bears onto land in autumn as it does in Hudson Bay. While on land, the best strategy is to conserve energy (Nelson et al. 1973; Guppy 1986). Conversely, ice is available in the High Arctic year-round, and autumn sheltering is less necessary. The winter increase in sheltering at higher latitudes is probably an adaptation to avoid the harshest of winter weather and heavy ice. In the Beaufort Sea, the sea-ice substrate is available year-round, but winter ice conditions may not be as harsh as in the eastern High Arctic. Those realities may ameliorate the need for sheltering. Messier et al. (1994) also concluded that variations in the availability of satisfactory hunting conditions may encourage a facultative approach to use of shelters.

Human Influences on Denning. The time spent in maternal dens is the only period in their life cycle during which polar bears are unable to simply move away from a potential disturbance. Premature exposure of altricial neonates to the outside arctic environment can be fatal (Amstrup and Gardner 1994). Therefore, disturbance of denning bears could result in reproductive failures. The only quantitative data on sensitivity of denning polar bears to human disturbances are from the Beaufort Sea region. Amstrup (1993) reported considerable tolerance of human activities near dens. Subsequent observations (S. C. Amstrup, unpublished data) corroborate those early records. Polar bears seem secure in their dens, and appear very tolerant of aerial and ground traffic very near maternal dens in winter and spring. These observations corroborate the results of Blix and Lentfer (1992), who observed that only seismic testing <100 m from a den and a helicopter taking off at a distance of 3 m produced noises inside the dens that were notably above background levels. They also concluded that a polar bear in its den is unlikely to feel vibrations unless the source is very close. Preliminary analyses of more recent work (MacGillivray et al. 2002) confirm that sound penetration into dens is greatly ameliorated. They also suggested, however, that helicopters and some ground vehicles may be detectable in dens at much greater distances than suggested by Blix and Lentfer (1992).

Observations of grizzly bears also suggested substantial tolerance of such activities. McLellan and Shackleton (1989) found that grizzly bears in summer were not displaced from the immediate vicinity of seismic testing supported by helicopters. Reynolds et al. (1986) reported some movements and possible increased heart rates when denned grizzly bears were exposed to seismic testing activities. However, they also observed that similar movements and heart rate patterns sometimes occurred in absence of human activities, and they concluded that “effects on the bears were probably minimal” (Reynolds et al. 1986:174). Although the observations appear compelling, the sample sizes reported by Amstrup (1993) are small. The tests of Blix and Lentfer (1992) also were relatively limited in scope, and the degree to which information

using the best available information, can prevent most potentially disruptive activities from overlapping with polar bear denning.

Delayed implantation and birth of altricial young mean that early in pregnancy, parental investment is low. Female polar bears have less to lose by leaving a den in the fall than they do by leaving after parturition. Perhaps that explains why polar bears appear to be more willing to abandon dens in fall than later in the denning period (Amstrup 1993; S. C. Amstrup, unpublished data). Belikov (1976) also reported that polar bears were more easily displaced from their dens in the fall. Five Alaskan polar bears thought to abandon dens because of human interference in the autumn were successful in re-denning elsewhere (Amstrup 1993, S. C. Amstrup, unpublished data). Likewise, three bears disturbed from dens near Hudson Bay relocated to other den sites (Ramsay and Stirling 1986a). The relative resilience of denning bears to disruptions in spring and their plasticity regarding den selection in autumn have significant management ramifications.

In the Beaufort Sea, individual polar bears have strong ties only to general denning areas and substrata. Denning habitat there is widely scattered across broad areas and is not limiting. Where such circumstances prevail, temporal and spatial management of human activities should eliminate most conflicts between those activities and maternal denning (Amstrup 1993; Amstrup and Gardner 1994). For example, proposed human activities can be directed around most of the narrow bands of habitat that are suitable for denning (Durner et al. 2001). Furthermore, initiation of intense human activities in autumn would give bears enroute to land dens the opportunity to den in less disturbed areas. If a bear encountered activities it didn't like, it could move up or down the coast to a place where it is comfortable. Also, bears already in dens could relocate more easily in autumn than after parental investment increases.

Much relocation of denning appears to occur naturally in autumn before bears finally settle down for the winter. Natural fluctuations in areas used for denning (Uspenski and Chernyavski 1965; Uspenski and Kistchinski 1972; Ramsay and Stirling 1986a, 1990) suggest that, even in some concentrated or core denning areas, alternate den sites may be available to bears if they are disturbed. However, data regarding fidelity to denning locales and responses to disturbances of dens are largely unavailable outside of the Beaufort Sea. More importantly, a human activity with potential to disturb denning bears will affect more individuals where dens are geographically clustered than where they are widely scattered. In the Beaufort Sea region for example, even expansive human activities, such as some related to oil exploration, would likely overlap with only a very small number of dens in any given year. In the concentrated denning areas of the world, a similar activity could overlap with dozens of dens. The risks that human activities could have population level effects are greater where dens are geographically clustered. Clearly, human activities around all maternal denning areas must be managed with utmost caution. Each development scenario must be approached with full understanding of the ecological and behavioral situation, and wherever human activities proceed, outcomes must be carefully monitored so that management can be adjusted as needed.

PHYSIOLOGY

Liver Toxicity. Polar bear liver can contain very high levels of vitamin A (Rodahl and Moore 1943; Lewis and Lentfer 1967; Russell 1967). The concentration varies greatly among individuals, but does not seem to be age dependent. The liver is toxic to humans if eaten. Rodahl and Moore (1943) summarized the variety of human health effects reported by Arctic explorers who had eaten polar bear liver. Effects ranged from drowsiness, headache, and general irritability to large-scale peeling of the skin. Peeling was often localized, but sometimes covered victims from head to foot. Variation in the quantity of liver consumed and the vitamin A concentrations within each liver probably accounted for the

reported relatively high thermal conductivity for polar bear fur in both air and water. Likewise, Øritsland (1970) concluded that polar bears depend on a combination of fur, fat, and subdermal vascularization to maintain their body temperature. Øritsland (1970) and Best (1982) showed that polar bears can increase effective peripheral insulation with vasomotor controls. Such controls could be most effective during water immersion. All adaptations, however, were inadequate to contend with either exceptionally cold or hot air temperatures; polar bears may depend on postural and behavioral mechanisms during extremes of air temperature.

Newborn cubs have short, thin hair and no subcutaneous fat (Blix and Lentfer 1979). Therefore, they are poorly equipped for survival outside of the maternal dens in which they are born. On emergence from the den, however, cubs are much better equipped for outside exposure. Blix and Lentfer (1979) reported a lower critical temperature for a 12.5-kg cub of -30°C . At -45°C , the cub's oxygen consumption increased only 33%, and there was no decrease in core temperature. Immersion of this cub into ice water resulted in a precipitous and immediate drop of body temperature. Despite the small size and minimal subcutaneous fat, it appears that cubs are ready to face the outside world at the time of den departure. They are, however, not ready for immersion.

Locomotion. Øritsland et al. (1976), Hurst et al. (1982a, 1982b), and Best (1982) concluded that polar bears are relatively inefficient walkers. Measurements were made from two polar bears walking on treadmills. Oxygen consumption and heat storage were higher than might have been predicted for other mammals of comparable size. Inefficient walking was attributed to aspects of polar bear morphology, specifically the massive forelimbs evolved for capture of prey (Øritsland et al. 1976; Hurst et al. 1982a, 1982b). Economy of transport, they suggested, was compromised by considerations of thermoregulation and hunting strategy. Nonetheless, the typical daily, seasonal, and annual movements of polar bears place them among the most mobile of all quadrupeds (Amstrup et al. 2000). Locomotion in polar bears is clearly an area where additional research is in order.

Hibernation. Like other ursids, polar bears have evolved a very specialized winter dormancy. Females occupy maternal dens of ice and snow for periods of 4–8 months. During that time, they neither eat nor drink and they do not urinate or defecate (Nelson et al. 1973; Folk and Nelson 1981; Nelson 1987; Watts and Hansen 1987; Ramsay and Stirling 1988). In hibernating bears, normal mineral levels are maintained, lean body mass is constant, blood electrolyte balance is preserved, and levels of blood metabolites are largely unchanged despite loss of nearly half of their total body mass after den entry (Nelson et al. 1973; Folk and Nelson 1981; Guppy 1986; Nelson 1987; Atkinson and Ramsay 1995). They appear able to maintain constant fluid levels by using metabolic water produced from fat catabolism (Guppy 1986; Nelson 1987).

Polar bears may be even more highly evolved with regard to their ability to survive food deprivation than the other ursids. Behavior and physiology of polar bears are well adapted to a feast-and-famine feeding regimen (Lunn and Stirling 1985; Watts and Hansen 1987; Ramsay and Stirling 1988; Derocher and Stirling 1990; Derocher et al. 1990). It now appears that they can alter their metabolism during periods of food deprivation at any time of the year (Nelson et al. 1983). Atkinson and Ramsay (1995) and Derocher et al. (1990) demonstrated that polar bears, unlike other bears, can shift as needed into a hibernation-like metabolic pattern when confronted by a period of food shortage. Facultative changes into and out of a hibernation-like state would magnify the value of summer and winter shelter denning described by Messier et al. (1994) and Ferguson et al. (2000a). This ability could make polar bears the most advanced of all mammals when it comes to dealing with food and water deprivation (Nelson 1987).

basin, the peak of estrus as evidenced by turgidity of the vulva and vaginal discharge seems to be in late April and early May. Ovulation is thought to be induced by coitus (Wimsatt 1963; Ramsay and Dunbrack 1986; Derocher and Stirling 1992). Implantation is delayed until autumn, and total gestation is 195–265 days (Uspenski 1977), although during most of this time, active development of the conceptus is arrested. Young are born by early January (see below), but stay within the shelter of the den until March or early April (Amstrup and Gardner 1994). Litters of two cubs are most common over most of the polar bear range. Litters of three cubs are seen sporadically across the Arctic, and were most commonly reported in the Hudson Bay region (Stirling et al. 1977b; Ramsay and Stirling 1988; Derocher and Stirling 1992). Young bears will stay with their mothers until weaning most commonly in early spring when the cubs are 2.3 years of age. Female polar bears undergo a lactational anestrus and are available to breed again after weaning. Therefore, in most areas, the minimum successful reproductive interval for polar bears is 3 years (see below).

Newborn polar bears have hair, but are blind and weigh only 0.6 kg (Blix and Lentfer 1979). The growth of cubs is very rapid, and they may weigh 10–12 kg by the time they emerge from the den in the spring. After leaving the den, the rapid growth continues, and cubs may increase their weight by an order of magnitude between den exit and their first birthday (S. C. Amstrup, unpublished data). Cubs can double their weight between their first and second birthdays. Cubs receive an especially rich milk from their mothers. The milk of polar bears typically has a higher fat content than that of other bears, and in general the milk of bears is richer in fat and protein than the milk of other carnivores (Jenness et al. 1972). Polar bear milk is more similar to that of pinnipeds than it is to milk of most terrestrial mammals (Jenness et al. 1972; Ramsay and Dunbrack 1986). Although polar bears may nurse cubs through their second birthday, some females apparently stop allowing cubs to suckle sometime after their first birthday. The contribution to growth from milk during the second year of life is much lower than during the first year (Arnould and Ramsay 1994). Arnould and Ramsay (1994) noted that fat content begins to decline fairly early in lactation, but the biggest differences are between the first and the second year of the cubs' lives. Mean fat content of milk provided to cubs of the year was $31.2 \pm 1.6\%$, whereas the fat content of milk fed to yearlings was $18.3 \pm 2.4\%$. The energy contribution from milk is a significant contributor to the observed rapid growth of cubs and comes at a significant cost to mother bears (Arnould and Ramsay 1994).

The exact timing of birth may vary across the range of polar bears. Harington (1968) reported births as early as 30 November with a median date of 2 December. Derocher et al. (1992), reported, based on progesterone spikes in the blood of pregnant bears and the implied date of implantation, that births of Hudson Bay bears probably occur from mid-November through mid-December. Messier et al. (1994) suggested that polar bears give birth by 15 December. In contrast, many pregnant female polar bears in the Beaufort Sea did not enter dens until late November or early December (Amstrup and Gardner 1994; S. C. Amstrup, unpublished data). Unless those bears were giving birth immediately on den entry, a later date of birth can be assumed. One captive female in Barrow, Alaska gave birth on 27 December, corroborating that assumption (Blix and Lentfer 1979). Similarly, Lønø (1972) reported that implantation of the conceptus into the uterus of the polar bear began in November, around the peak of den entry in the Beaufort Sea. The timing of implantation, and hence that of birth, is likely dependent on body condition of the female. Condition of the female, in turn, depends on a variety of environmental factors. The interaction between environmental and physiological factors that control births is clearly an area in need of further research.

Testes of male polar bears reside in the abdomen for most of the year. They descend into the scrotum in late winter, and remain there through May. Descent of the testes permits spermatogenesis, which

(1970) further concluded breeding could last into July. Deteriorating ice conditions preclude scientific observations in most polar bear habitats by June, so the frequency of summer breeding cannot be easily documented.

Lentfer and Miller (1969) concluded, from presence of mature spermatozoa in epididymides, that male polar bears in Alaska may be able to breed as early as 3 years of age. Presence of sperm also guaranteed reproductive capability until at least age 19 years (Lentfer and Miller 1969). A recent study in Greenland found that 2 of 7 two-year-old males, 5 of 10 three-year-olds, and 4 of 9 four-year-olds had some spermatazoa in epididymides (Rosing-Asvid et al. 2002). Although spermatazoa occurred at low density in the younger bears, all bears ≥ 5 years old, except for one very thin individual, had produced abundant spermatazoa and appeared capable of breeding. Lentfer et al. (1980) observed males 3–11 years old in consort with estrous females, confirming at least the age of earliest breeding ability for male polar bears. It should be noted, however, that excessive hunting in Alaska just before and during the time those observations were made had all but eliminated prime males (aged >10 years) from the population (Amstrup et al. 1986). Subsequently, few male bears that young have been observed with females. Since 1980, the proportion of prime males in Alaskan waters has been high (Amstrup 1995). Presently, large males weighing 400–500+ kg are abundant in this region. Three- and 4-year-old bears typically weigh ≤ 250 kg, and would not be able to compete successfully for mates with the now-abundant large males. Currently, young males must have very low reproductive output despite their apparent reproductive potential.

Productivity of polar bear populations appears to be largely dependent on numbers and productivity of ringed seals. For example, in the Beaufort Sea, ringed seal densities are lower than in some areas of the Canadian High Arctic or Hudson Bay. As a possible consequence, female polar bears in the Beaufort Sea usually do not breed for the first time until they are 5 years of age (Stirling et al. 1976; Lentfer and Hensel 1980). This means they give birth for the first time at age 6. In contrast, across many areas of Canada, females reach maturity at age 4 and produce their first young at age 5 (Stirling et al. 1977b, 1980, 1984; Ramsay and Stirling 1982, 1988; Furnell and Schweinsburg 1984).

Craighead and Mitchell (1982:527) reported that in grizzly bears “reproductive longevity approximates physical longevity.” Female polar bears, on the other hand, may show a reproductive senescence long before the end of their lives. Derocher et al. (1992) calculated an average age of first breeding in the Hudson Bay area of 4.1 years. Productivity, assessed by estimated pregnancy rates, remained high between 5 and 20 years of age and declined thereafter (Derocher et al. 1992). Unfortunately, long-term monitoring of individual polar bears is uncommon and data addressing senescence are few. One 32-year-old female in the Beaufort Sea was monitored for the last 25 years of her life and seen annually during her last 10 years. This bear was in extraordinary condition nearly every autumn. Although she was not recaptured during the autumn of her 30th year, she was observed standing next to a 400-kg female that was captured that season. The 30-year-old female appeared larger, but still did not enter a den that autumn. Despite her apparent excellent physical condition, she last produced cubs at age 22, suggesting a prolonged reproductive senescence. Some contrary evidence also is available. One 29-year-old female in the Beaufort Sea was clearly in estrus (based on turgidity of the vulva) and traveling with an adult male in the spring of 2001. Derocher et al. (1992) also indicated that some females retained reproductive competency throughout life. The reproductive longevity of brown bears and polar bears appears to be fertile ground for further research.

Derocher and Stirling (1994) noted that litter size varied with maternal age, increasing until age 14 years, after which it declined. Heavy hunting reduces numbers of prime-age and older polar bears of both sexes (Amstrup et al. 1986). If such changes occurred without

heavily harvested into the 1970s, but numbers there appear to have increased since then (Prevett and Kolenosky 1982; Derocher et al. 1997). Litter size, litter production rate, and other reproductive factors can be expected to change with population size relative to carrying capacity. It also changes in a response to hunting pressure and other population perturbations. Hence, comparisons among populations or within populations over time must take into account the status of the population relative to natural and anthropogenic features of the environment.

In most parts of the Arctic, female polar bears cannot complete a reproductive cycle more frequently than every 3 years. The inter-birth interval is determined by the length of time cubs are attended by their mothers, which most commonly is 2.3 years (Stirling et al. 1976, 1980; Lentfer et al. 1980; Amstrup et al. 1986; Amstrup and Durner 1995) (Fig. 27.9). Lønø (1970) concluded that in the Svalbard area, most cubs were weaned by about 17 months of age. Likewise, Ramsay and Stirling (1988) reported that during the 1970s and early 1980s, a significant proportion of female polar bears in the Hudson Bay region weaned their cubs at about 1.3 years of age. After weaning her cubs in the spring of their second year (at age 1.3 years), a female bear could breed again that same spring and achieve a 2-year reproductive interval.

The historically shorter reproductive interval of polar bears living in Hudson Bay (Stirling et al. 1977b) meant that they were more prolific than most other populations of polar bears. Captures of many hundreds of female polar bears and their young in Alaska, Canada, and Svalbard have suggested geographic differences in litter size, litter production, onset of maturity, and reproductive interval. For example, mean litter sizes of cubs and yearlings in Alaska were 1.63 and 1.49, respectively (Amstrup 1995). In Svalbard, these values were 1.81 and 1.32, respectively, whereas litter sizes of polar bears in Hudson Bay during the early 1980s were 1.9 and 1.7 for cubs and yearlings, respectively (Ramsay and Stirling 1988, Derocher and Stirling 1992). Annual litter production rates as high as 0.45 litters/female have been reported for polar bears in the Hudson Bay area (Derocher and Stirling 1992). Nearly half

of the females in that population were annually producing a litter of cubs at that time. By comparison, only one fourth of the female polar bears in the Beaufort Sea produce a litter of cubs each year (a litter production rate of 0.25) (Amstrup 1995). That is, in Hudson Bay, each female had a litter nearly every other year, but in the Beaufort Sea, each female produced a litter only every fourth year. Because polar bears in Hudson Bay also produced larger litter sizes, these differences in litter production rates translated into a much higher overall reproductive rate there than in the Beaufort Sea. Female polar bears in the Beaufort Sea produced only ~0.40 cub/year, whereas in the Hudson Bay area they produced up to 0.90 cub/year at the time those studies were conducted (Derocher and Stirling 1992). Reproductive rates in most other areas appear to be more similar to those in the Beaufort Sea than in Hudson Bay.

In assessing reproductive intervals, it is critical to confirm weaning, as opposed to mortality of cubs. Many polar bear cubs die in their first year of life (Amstrup and Durner 1995). Those females can breed again in the year of the loss (if it occurs early enough in the spring) or the next year. The breeding frequency, by itself, might suggest a short reproductive interval when it is actually prolonged by poor cub survival. In addition to documenting that tagged females were no longer accompanied by yearling cubs in the spring, Ramsay and Stirling (1988) also captured many weaned yearlings in the autumn of their second year (approximately 1.8 years of age), confirming that many females in the Hudson Bay region actually did have a 2-year reproductive interval.

Lønø (1970), Stirling et al. (1977b), and Ramsay and Stirling (1988) reported on populations that may have been well below carrying capacity due to unregulated hunting (Stirling et al. 1977b; Larsen 1986; Derocher and Stirling 1992, 1995a). Likewise, breeding intervals in the Hudson Bay area have increased, possibly in response to increased relative density of bears in the area (Derocher and Stirling 1992, 1995b). Annual litter production rate in the Hudson Bay region declined from 0.45 litter/female in the period from 1965–1979 to 0.35 during 1985–1990 (Derocher and Stirling 1992). A higher proportion produced cubs every 3 years in the latter period. The inverse of the litter production rate is the interbirth interval. That increased from 2.22 years in 1965–1979 to 2.86 years in 1985–1990. Simultaneously, cub mortality from spring to autumn was significantly higher in the latter period (Derocher and Stirling 1992). The proximate factor associated with all of these trends was the declining weight of adult females during this 25-year period (Derocher and Stirling 1992). Age of first successful reproductive effort increased, although pregnancy rates did not change noticeably. An increasing age of maturation may indicate that a population is approaching carrying capacity. Age of maturation in mammals is often associated with attainment of a threshold body mass (Sadleir 1969) which could be more difficult to attain as competition for resources increases.

A delay in reaching that threshold mass may signal density-dependent influences on the population. Such influences, however, also could result from environmental changes that reduce carrying capacity rather than from increases in polar bear numbers. The documented declines in body weights of females, declines in numbers of independent yearlings, and protracted reproductive intervals appear to be closely related to earlier deterioration of the sea-ice of Hudson Bay (Stirling et al. 1999). The sea-ice extent in the Arctic has been declining throughout the past two decades (Gloersen and Campbell 1991; Vinnikov et al. 1999). Declining Arctic sea-ice cover by itself is difficult to link with polar bear reproductive performance. The timing of melt of the sea-ice in Hudson Bay, however, is more easily connected. Polar bears there, especially pregnant females, depend heavily on the spring and early summer foraging for seals to carry them through the ice-free period (late summer to autumn). Pregnant females, unlike other polar bears in Hudson Bay, remain ashore in autumn when ice returns, and may be

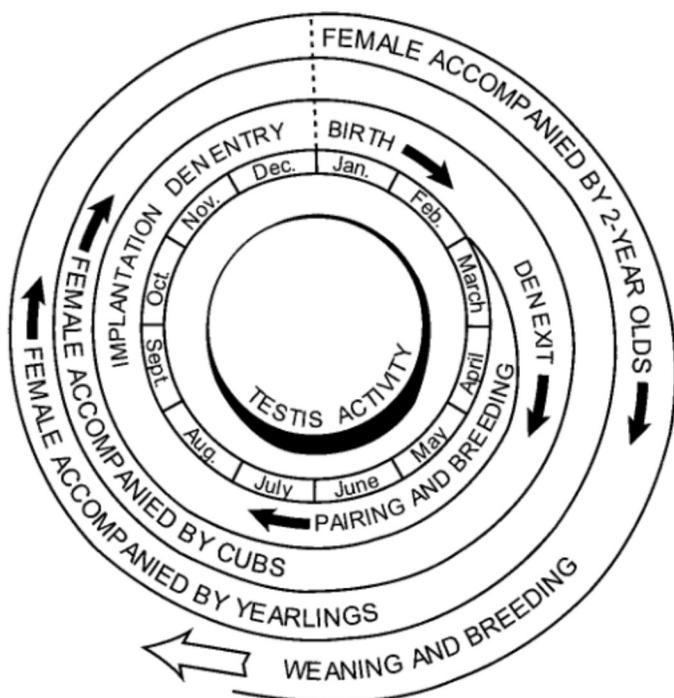


FIG. 27.9. The 3-year reproductive cycle typical of polar bears throughout

earlier than it was in the 1970s and early 1980s (Stirling et al. 1999). Earlier break-up and the shortened foraging period accompanying it may mean a significant reduction in the fat stores female polar bears can accumulate before denning. This hypothesis is strengthened by the observation of a transient increase in condition of females coming ashore during the early 1990s when cooler than normal temperatures resulted in later break-ups (Stirling et al. 1999).

Evidence of the critical link between availability of seal prey and reproduction in polar bears is also available in more northerly parts of the range. Weights of females and their reproductive output in the Beaufort Sea decreased markedly in the mid-1970s following a decline in ringed and bearded seal populations (Stirling et al. 1976, 1977b; Kingsley 1979; DeMaster et al. 1980; Stirling et al. 1982; Amstrup et al. 1986). The strength and longevity of declines in reproductive parameters varied both geographically and temporally with the severity of ice conditions that reduced numbers and productivity of seals (Amstrup et al. 1986).

SURVIVAL

The very low reproductive rate of polar bears means that there must be a high rate of survival to maintain population levels. In fact, polar bears "defer" reproduction in favor of survival when foraging conditions are difficult (Derocher et al. 1992). A complete reproductive effort is energetically expensive for polar bears. So, when energetically stressed, female polar bears will forgo reproduction rather than increase risks by incurring the energetic costs of the reproductive process. The reproductive cycle lends itself to convenient early termination if that is appropriate (Ramsay and Dunbrack 1986; Derocher and Stirling 1992). Many radio-collared female polar bears in the Beaufort Sea region entered dens and then abandoned them early without cubs (Amstrup and Gardner 1994). Others lost cubs shortly after emerging from their den and bred again that same spring. Bears leaving dens early may have resorbed their fetuses or may have experienced a pseudopregnancy (Derocher et al. 1992). In any event, they did not complete a full reproductive cycle.

Breeding takes place in the early spring, long before the female can assess whether she will secure sufficient resources to bring her pregnancy to fruition. After fertilization, if she has been able to secure sufficient reserves, birth and rearing can follow pregnancy with some reasonable probability of success. Polar bears, however, also are equipped to abandon a reproductive effort if reserves are insufficient. Because implantation is delayed many months (Wimsatt 1963), and because neonates are so undeveloped (Blix and Lentfer 1979; Ramsay and Dunbrack 1986), early stages of reproduction are relatively inexpensive. Termination of the reproductive process, through abortion or resorption of the fetus or failure to nurse after birth, costs a female relatively little (Derocher et al. 1992). The biggest maternal investment begins with postpartum lactation (Ramsay and Dunbrack 1986). Even after emergence from the den, however, it is not unusual for females in poor condition to lose their cubs (Amstrup and Gardner 1994; Amstrup and Durner 1995). Polar bears that terminate a pregnancy and leave their dens early or lose their cubs in early spring usually breed again, preparing them for an opportunity to successfully rear cubs the following year if conditions improve.

In the Hudson Bay region during the 1980s, the survival rate of more than 200 cubs from spring through the ice-free period of autumn was 44% (Derocher and Stirling 1996). Although less mortality was thought to occur after the ice returned in autumn, first-year survival clearly was lower than the 48% reported by Larsen (1985). The body mass of cubs was a significant determinant of survival during early life that included the ice-free period of food deprivation. The mass of cubs, of course, is at least partly dependent on the mass of their mother. Survival of Hudson Bay cubs ($N > 400$) from

Because many in that age class were independent of their radio-collared mothers, they were not recaptured or reobserved, and their fate was not known. Hence, these must be considered minimum survival values, and likely are below the actual values.

In the Beaufort Sea, survival of cubs was approximately 65% from den exit to the end of their first year of life. Yearlings fared much better, with 86% surviving to weaning (Amstrup and Durner 1995). Observations of the young of radio-collared females substantiate the observation from Hudson Bay that most cub mortality comes early in the period after emergence from the den (Amstrup and Durner 1995; Derocher and Stirling 1996), but depart radically from the very minimal yearling survivals observed there. Derocher and Stirling (1996) suggested that a heavy harvest accounted for much of the yearling mortality in Hudson Bay. Nonetheless, only 15% ($44\% \times 35\%$) of the cubs produced were confirmed to survive through their second autumn. This contrasts with the survival of 56% ($65\% \times 86\%$) of Beaufort Sea bears surviving until weaning, 5 months beyond their second autumn. If actual values are close to the minimums reported there, the differences in survival could more than compensate for the apparent reproductive differences between bears in the Beaufort Sea and Hudson Bay.

Tait (1980) hypothesized that brown bear females may choose to abandon a single cub on the chance that they might enhance fitness by breeding again and giving birth to twin or larger litters. That concept has resulted in much discussion and debate about parental care and investment in young. Whether or not it makes sense mathematically, such a strategy apparently does not prevail among polar bears. In the Hudson Bay area, single cubs may actually survive at a somewhat higher rate than cubs from larger litters (Derocher and Stirling 1996). Furthermore, deaths of dependent young in the Beaufort Sea were independent of litter size, and cubs were lost at similar rates whether as whole litters or portions of litters (Amstrup and Durner 1995). Parental investment in single polar bear cubs is not different from investment in litters of two or more. Single cubs are often much heavier than twin cubs (S. C. Amstrup, unpublished data), and survival of cubs appears to be heavily dependent on their weight (Derocher and Stirling 1992).

Estimating survival rates of independent polar bears has been an even greater challenge than estimating survival of dependent young. Eberhardt (1985) argued that survival of adult marine mammals must be in the high 90% range for their populations to be sustaining. However, early estimates of survival in polar bears derived by mark and recapture methods were much lower (Amstrup et al. 1986). More recent estimates derived from Hudson Bay, where the intensity of marking exceeds all other study areas, still have ranged between 0.86 and 0.90 (Derocher and Stirling 1995a; Lunn et al. 1997). Only by relying on radiotelemetry monitoring of individual animals have estimates in line with Eberhardt's (1985) theory been developed. Amstrup and Durner (1995) estimated that survival of adult females in the prime age groups may exceed 96%. Although that estimate fits well with population dynamics theory, the fact that it is much higher than estimates derived by other methods suggests added work on polar bear survival is necessary.

Causes of natural mortalities among polar bears are largely unknown. Because polar bears spend most of their time on drifting sea-ice, dead animals are likely to go undiscovered and cause of death for animals that are discovered is seldom discernible. Therefore, we are forced to extrapolate from a very few observations to understand natural mortality patterns and causes. Accidents involving unskilled young must be a common cause of natural death in the harsh arctic environment (Derocher and Stirling 1996). Starvation of independent young as well as very old animals must account for much of the natural mortality among polar bears. Age-specific differences in hunting success rates have been reported by Stirling and Latour (1978) for polar bears of the central Canadian High Arctic. Cubs of any age spent little time hunting, and were not effective at taking seals in the spring of the year. During summer, the success rate of 2-year-olds was similar to that of

observations of independent bears <2 years old in all populations except Hudson Bay. Also, age structure data show that subadults aged 2–5 years survive at lower rates than adults (Amstrup 1995), probably because they are still learning hunting and survival skills. I once observed a 3-year-old subadult that weighed only 70 kg in November. This was near the end of the autumn period in which Beaufort Sea bears reach their peak weights (Durner and Amstrup 1996), and his cohorts at that time weighed in excess of 200 kg. This young animal apparently had not learned the skills needed to survive and was starving to death. As they age, polar bears that avoid serious injury must simply get too old and feeble to catch food, and thus literally die of old age. Local and widespread climatic phenomena that make seals less abundant or less available also can significantly affect polar bear populations (Stirling et al. 1976; Kingsley 1979; DeMaster et al. 1980; Amstrup et al. 1986).

Injuries sustained in fights over mates or in predation attempts also may lead to natural mortalities of polar bears. Some injuries are immediately fatal. I have seen three instances where a bear has killed another and consumed it. Broken teeth and even broken jaws may frequently result from fighting and failed predation attempts. In brown and black bears, such injuries commonly are not life-threatening. L. Aumiller (Alaska Department of Fish and Game, pers. commun.) has observed several brown bears at Alaska's McNeil River Sanctuary with jaws that had broken and healed in a variety of distorted conformations. D. Garshelis (Minnesota Department of Natural Resources, pers. commun.) captured a 2-year-old black bear with a missing lower jaw. The jaw and all lower teeth were destroyed by gunshot wounds that had largely healed when Garshelis examined the bear in its winter den. The bear was radio-tracked through the following spring and summer and killed by a hunter the following autumn as a normal-size 3-year-old. Brown bears and black bears often survive on a diet including plant parts, fish, insects, small animals, and carrion. A videotape made by the hunter revealed how ingenious the young Minnesota black bear was in feeding without a lower jaw. These and other observations of injured brown and black bears (D. Moody, Wyoming Game and Fish Department, Pers. Commun.; M. Haroldson, USGS Interagency Grizzly Bear Study Team, pers. commun.) suggest they regularly survive with severely damaged mouth-parts, perhaps because of their great adaptability and the small particle size of most of their foods.

Injuries to polar bear's mouth parts also may not be immediately fatal, but they probably are deadly in the long run. Despite capture of thousands of polar bears worldwide, confirmed observations of mended jaws or survival of polar bears with broken jaws are rare or lacking. The long penetrating canine teeth are the polar bear's most important trophic appendage and are critical to holding and killing large prey. Polar bears usually cannot switch to a diet of smaller food particles, and a broken jaw may simply reduce hunting efficiency below the survival threshold. I captured an emaciated but very large male polar bear one autumn when he should have been near his maximum weight. His weight was less than half that of similar-size males at that time. He seemed to be fit and his teeth were in excellent shape. On examination, however, we discovered that his maxilla was broken through (Fig. 27.10), and there was a pronounced gap in his palate. The front portion of his upper jaw was attached only by the skin and musculature of his lips. His ability to bite and hold large prey was seriously compromised. How this injury was sustained is not clear. He has not been recaptured, and given the bear's lean state just before the harshest season of the year, I suspect he did not survive the winter.

In addition to trauma of various kinds, an array of maladies occurs at low frequencies in polar bears just as they do with other wild and domestic mammals including humans. For example, a very large male in the Beaufort Sea died of gastric dilatation and volvulus (Amstrup and Nielsen 1989). This is a condition in which the alimentary organs, including the stomach and much of the intestine, rotate around the mesenteries that support those structures in the abdominal cavity. Blood



FIG. 27.10. Broken upper jaw of a large male polar bear captured in the Beaufort Sea in autumn 1999. Because they rely on strong jaws to catch and hold large prey animals, such injuries are probably fatal to polar bears. Photo by Steven C. Amstrup.

Reported diseases and parasites of polar bears are few. In 21 years of research in Alaska, I have not seen any evidence of ectoparasites. In an extensive review of ursid parasites, Rogers and Rogers (1976) found that seven endoparasites had been reported in polar bears. Only *Trichinella* spp., however, had been observed in wild animals. The three species of nematode and three species of cestodes that had been reported in captive polar bears had not occurred in the wild. *Trichinella* can be quite common in polar bears and has been observed throughout their range. Concentrations of this parasite in some tissues can be high, but infections are not normally fatal (Rausch 1970; Dick and Belosevic 1978; Larsen and Kjos-Hanssen 1983; Taylor et al. 1985). Arctic foxes (*Alopex lagopus*) are common carriers of rabies and they routinely interact with polar bears. However, only one instance of rabies has been confirmed in a polar bear (Taylor et al. 1991). Although polar bears are not immune to diseases and parasites, they seem to be plagued by fewer of these problems than most terrestrial mammals.

Male polar bears, like males of other ursids, will kill and eat dependent cubs (Hansson and Thomassen 1983; Larsen 1985; Taylor et al. 1985; Derocher and Wiig 1999). Although this activity does not account for a large percentage of the mortality, it is a curious cause of death in young bears. A male bear that kills cubs fathered by another probably confers some survival advantage to cubs he fathered by eliminating possible competitors for resources. Also, female bears undergo a lactational anestrus. By killing her cubs, a male interrupts that anestrus, and theoretically could breed with the female, inducing her to have his

that occur between breeding and emergence of cubs onto the sea-ice in spring, there is no selective advantage to a male if he kills cubs he fathered a year before. For the benefits of infanticide to be maximized, the male also must have some reasonable assurance of being around when the female comes back into estrus. In terrestrial bears with limited home range sizes and the ability to defend definable territories, it may be reasonable for a male bear to keep track of a female during the several days between loss of her cubs and onset of estrus. For polar bears, with no territories or other restrictions on movements, the likelihood of a male remaining with a female for that period seems small. In two cases of infanticide I observed in the Beaufort Sea, the male and female involved were already separated by dozens of kilometers the day after the cubs were killed, and they were going in opposite directions. In one case, the male and female were >200 km apart 2 weeks after the male killed her cubs. At least in that case of infanticide, it seems very unlikely that breeding was the goal of the male.

Polar bears will eat the flesh of their own kind, and often a bear that kills another will eat it. The killing of young cubs is probably not motivated by predatory instincts. Small cubs provide a very limited amount of energy, especially considering the risk of injury to a predatory male imposed by the defending female. Males that kill cubs may not even consume them (Derocher and Wiig 1999; S.C. Amstrup, unpublished data), perhaps due to their limited energy value. In terrestrial bears, harassment, or infanticide by large males may be a mechanism of density-dependent population regulation (McCullough 1981; Young and Ruff 1982; Stringham 1983). Derocher and Wiig (1999) also speculated that infanticide may be a density-dependent phenomenon, increasing in frequency with population size. Harassment of subadults by adult males at scavenging sites (Smith 1980) also may be an important regulating factor among polar bears. Infanticide has been detected more often in the Svalbard area than in other parts of the polar bear range where relative densities may be lower (Taylor et al. 1985). In all areas, however, frequencies of infanticide and cannibalism appear to be low enough that understanding their significance to population regulation is difficult. Infanticide in polar bears may be nothing more than an atavistic trait carried over from their terrestrial ancestors, and quantitative effects male polar bears have on their population are unknown.

AGE ESTIMATION

Polar bears can be assigned to age classes based on examination of the skull and dentition. As with other mammals, progressive closure of skull sutures is adequate to separate young and adult polar bears (Manning 1964). Hensel and Sorenson (1980) assigned living polar bears to approximate age classes based on reproductive status, physical measurements, and tooth replacement and wear. Ages of cub-of-the-year and yearling polar bears can be assigned without error by observation of dental eruption despite huge variation in size and weight in these age classes. In the autumn and early winter of their first year, permanent canines of young polar bears appear as small cones barely longer than the incisors. Early in the second year of life, canines have grown, but still appear conical in overall cross section. By autumn and early winter, as the second birthday approaches, canines have taken on the shape of mature teeth with a distinctive base and crown. More precise assignment of polar bear ages can be made, as in other ursids, by counting cementum annuli in microscopic cross sections of tooth roots (Stoneberg and Jonkel 1966; Hensel and Sorenson 1980; Calvert and Ramsay 1998).

MANAGEMENT AND CONSERVATION

Hunting. Early Eurasian explorers viewed polar bears as fearless marauders (Larsen 1978). They killed polar bears in self-defense, before they could become a threat, or just because they could. For centuries,

the Beaufort Sea and other parts of the polar basin, many of these individuals spent the summer on land instead of remaining with the sea-ice as it retreated to the north. Commercial hunters eliminated polar bears from St. Matthew Island by the early 1900s (Hanna 1920). Likewise, overwintering commercial whalers, along with local residents, may have nearly eliminated the bears that once dened along the north coast of Alaska (Leffingwell 1919).

Although the wanton destruction of polar bears by Arctic explorers decreased during the 1900s, polar bears continued to be harvested in large numbers through the middle of the century. In recognition of the polar bear's increasing vulnerability to human activities, the five nations (the Soviet Union, Canada, Denmark, Norway, and the United States) with jurisdiction over polar bear habitats negotiated the International Agreement on Conservation of Polar Bears (Treaty). The Treaty, negotiated in 1973 and ratified in 1976, prohibited the taking of polar bears from aircraft or large motor vessels or in areas where they were not taken by traditional means in the past (Prestrud and Stirling 1994). This prohibition created a de facto sanctuary in the central polar basin. A resolution appended to the Treaty requested governments to prohibit the taking of cubs or females with cubs, and hunting in denning areas during periods when pregnant females are moving into them or are denning. Another resolution requested governments to establish an international system to identify and control the trafficking of hides (Lentfer 1974; Stirling 1986; Prestrud and Stirling 1994). Finally, the Treaty required each signatory nation to conduct research and cooperate in management and research of populations that overlap jurisdictional boundaries.

Subsequent to the Treaty, most polar bear populations continue to be hunted. Hunting is not allowed in Svalbard, although a limited number of polar bears there are killed each year in defense of life and property. Hunting in the other jurisdictions, with two exceptions (see below), is limited to Native people continuing a centuries-long tradition. Modern Native hunters, in most areas, use snow-mobiles and high-powered rifles and can be more effective in harvesting polar bears than ever before. Shooting by local hunters accounted for 85% of the deaths of adult female polar bears documented in the Beaufort Sea during the 1980s and early 1990s (Amstrup and Durner 1995). Despite the effects of technology on abilities of hunters to kill polar bears, a combination of government regulations and user's agreements has kept hunting by Native people in balance with the allowable yields of most populations.

In Canada, where the largest numbers of polar bears are harvested, the take is regulated by a quota system and, with specific exceptions, is limited to Native people (Prestrud and Stirling 1994). Quotas are developed through the best available scientific information and enforced through a system of harvest tags distributed by the local hunters and trappers organizations. Representatives of the hunters groups work with scientists to help set quotas throughout Canada, and are fundamental participants in all management processes. In some parts of Canada, Native hunters use a fraction of their allotted quota tags to guide sport hunters, who may be non-Native (Prestrud and Stirling 1994). Such hunts generate significant financial returns for small northern communities. Sport hunts also have resulted in smaller harvests and a higher proportion of males in the harvests. Sport hunters are not as efficient as local people in catching polar bears, and they strive for larger bears, which are most commonly males. Both the shifted composition of the harvest and the smaller total take resulting from the use of quota tags for sport hunts benefit the hunted populations. The Canadian quota system, whether tags are used for sport hunts or not, has resulted in strict controls on the size of the harvest and exceptionally high quality reporting of harvest composition. Although the Canadian polar bear harvest is larger than that in any other nation, that harvest also is the most scientifically controlled and the best managed. Vigorous efforts are being made to improve harvest monitoring where it is weak, and to implement quotas in the provinces of Quebec and Ontario, where they

Hunting in Greenland is limited to “professional” hunters who derive all of their income and sustenance from hunting and fishing. Theoretically, non-Native people could become professional hunters if they established long-term residence in remote areas and gave up all other income sources. In practice, however, this requirement has limited polar bear hunting to Native Greenlanders. The size of the harvest in Greenland is limited only by availability (which is controlled by weather and ice conditions) and the requirement that polar bear hunters use dog teams rather than snow-mobiles to pursue polar bears. In 2000 and 2001, the Greenland Home Rule Government began intensive work with hunters to improve harvest monitoring and work toward harvest limits and a quota system (Amalie Jessen, Vice Director, Greenland Home Rule, Department of Industry, pers. commun. June 2001).

In northern Alaska, the harvest is regulated by agreements among the local users and international agreements between Inupiat hunters in Alaska and Inuvialuit hunters in Canada (Treseder and Carpenter 1989). Current population estimates (Amstrup et al. 1986, 2001) suggest the harvest in northern Alaska is under the maximum sustainable yield. There currently are no restrictions on the harvest by Native Alaskans in western portions of the state, and harvests there largely have been regulated by availability of bears to hunters. A new agreement between Russia and Alaska, however, will soon bring more control and better monitoring to this region (see below).

The biggest threat from hunting may be in Russia. That conclusion is ironic because under Soviet management, hunting was banned in 1956. After the fall of the Soviet regime, however, management of hunting and other uses of renewable resources has suffered from lack of funding and absence of enforcement. So, although shooting polar bears is still illegal, there is nothing to stop such activity when it occurs. This is cause for concern because the economic gains from organized hunting are potentially great and other opportunities to generate income in northern Russia are extremely limited. Also, Russia controls nearly half of the Arctic and much of the world’s polar bear habitat. A potentially uncontrolled harvest over such a broad area could be a problem with far-reaching implications.

Risks of excessive take in Russia have been partially addressed by the Agreement between the Government of the United States of America and the Government of the Russian Federation on the Conservation and Management of the Alaska–Chukotka Polar Bear Population. This agreement, signed on 16 October 2000, followed more than 8 years of discussions and negotiations between the local Native people and government representatives of both countries. Although still awaiting congressional ratification, this agreement recognizes the needs of Native people to harvest polar bears for subsistence purposes and includes provisions for developing binding harvest limits, allocation of the harvest between jurisdictions, compliance, and enforcement. Each jurisdiction is entitled to up to one half of the harvest limit. The agreement reiterates requirements of the 1973 multilateral Treaty and includes restrictions on harvesting denning bears, females with cubs, or cubs <1 year old, and prohibitions on the use of aircraft, large motorized vessels, and snares or poison for hunting polar bears. The agreement does not allow hunting for commercial purposes or commercial use of polar bears or their parts. It also commits the parties to the conservation of ecosystems and important habitats, with a focus on conserving polar bear habitats such as feeding, congregating, and denning areas. As with the agreement between the Inuvialuit of northwest Canada and the Inupiat of Alaska (Treseder and Carpenter 1989), the commitment of the users seems likely to assure that in western Alaska and in the eastern Russian Arctic, harvests will be kept within sustainable limits. The remainder of the Russian Arctic is still of concern.

In sum, although hunting can still pose a threat to the welfare of polar bears, it is maintained at sustainable levels in most jurisdictions by a combination of regulations and user’s agreements. In the jurisdictions where formal agreements or rules are lacking, the need for limits on

movement, feeding, and breeding patterns and could result in exposure to contaminants (Amstrup et al. 1989; Amstrup 1995). In the Beaufort Sea of Alaska, polar bears have been exposed to activities related to hydrocarbon exploration and development for >30 years. Throughout those same 30 years, the population appears to have grown (Amstrup et al. 2001). The population growth during industrialization of the Beaufort Sea coast suggests that management of potential negative interactions between polar bears and humans has been successful. Proposed activities indicate increased vigilance may be necessary to continue those management successes. Oil development activities currently span >160 km of the Beaufort Sea coastal area, but proposed developments would more than double that. The potential for direct and indirect interactions between polar bears and humans only can increase with greater numbers of people and more activities, and more area under development.

If management is to respond properly to the added perturbations that could result from more expansive developments, the processes bringing about natural changes in polar bear populations must be understood. For example, responses to perturbations vary with population size if density plays an important role in population regulation. This means that when numbers are near carrying capacity, populations regulated largely by density-dependent factors may compensate for increased levels of mortality by increasing recruitment (McCullough 1979; Clutton-Brock et al. 1982). Such compensation would result in greater resilience of the population to perturbations than could be predicted from recruitment and survival rates measured prior to the perturbation. Accurate prediction of effects of human activities could only be made, therefore, if population-regulating factors and mechanisms are understood.

The potential for disturbances of denning polar bears may be especially great because undeveloped young must remain in a maternal den that protects them from the rigors of the arctic winter until they are approximately 3 months old (Lentfer and Hensel 1980; Stirling 1990; Stirling and Andriashek 1992; Amstrup 1993; Amstrup and Gardner 1994). Although polar bears may be less sensitive to activities near their dens than previously assumed (Amstrup 1993), the potential for disruptions can only increase as human activities in the Arctic escalate. The general distribution of dens is now known worldwide, but it is still largely unexplained. Except for some critical habitat requirements that can be defined, why bears chose to den at particular sites is unknown. The influences of slope, aspect, and elevation are beginning to be understood (Durner et al. 2001, 2003), although we do know that some bears make mistakes in their choices (Clarkson and Irish 1991). We have made much progress in describing the kinds of habitats polar bears prefer for denning. If we are to adequately manage human activities that could interfere with denning, however, we must either know how to predict which specific sites polar bears will use or learn how to detect newly established dens under the snow.

Global Warming. With reasonable management flexibility, the future of the polar bear as it relates to interactions with humans appears bright. Even in areas of intense industrial activity, such as the Alaskan Beaufort Sea, polar bear populations have flourished. Given adequate vigilance, humans and polar bears should be able to continue to coexist for the foreseeable future.

Significant larger concerns loom on the horizon, however. Evidence that the average temperatures of the globe are increasing continues to mount (Stirling and Derocher 1993). Along with increasing temperatures, the extent of the sea-ice in the Northern Hemisphere has declined from about 12.5 to 11.5 million km² during the past 25 years (Gloersen and Campbell 1991; Vinnikov et al. 1999). Reductions in the amount of time polar bears of southern regions can spend hunting on the sea-ice already may have resulted in significant declines in productivity. Body weights of female polar bears and numbers of independent

of warmer temperatures and earlier ice melt are likely to be felt there sooner than in more northerly parts of the polar bear range. In fact, in areas where the heavy sea-ice limits access to food (Messier et al. 1992; Ferguson et al. 2000b) and where productivity traditionally has been lower than Hudson Bay (Amstrup et al. 1986, 2000), a milder climate may actually benefit polar bears in the short run. Thinner ice cover and shorter ice seasons of time could enhance primary productivity in northerly areas and such increases could be passed through the food chain. Ultimately, however, if sea-ice cover continues to decline, polar bears worldwide will suffer. Polar bears are so closely tied to the presence of the sea-ice platform from which to hunt, mate, and carry on other life functions that continuing extensive declines in ice coverage will restrict their productivity and could ultimately threaten their survival.

Contaminants. Throughout the 1900s, numerous organic compounds were released into the global environment. Organochlorine pesticides like chlordane, dichlorodiphenyltrichloroethane (DDT), hexachlorocyclohexanes (HCHs), and hexachlorobenzene (HCB) have been used in agricultural areas worldwide and in many undeveloped areas to control mosquitoes and other insects that pose a threat to human health. Many of these compounds are resistant to physical as well as biological degradation and persist in the environment for extended periods. Their persistence allows these compounds to be spread by atmospheric and oceanic circulation, and many have concentrated in the Arctic.

The position of polar bears at the top of the Arctic food chain means they are likely to build up high body burdens of these compounds. Recent studies have verified that likelihood (Norstrom et al. 1998) and raised concerns for health effects of such contamination. The highest concentrations of many chlorinated hydrocarbon compounds have occurred in polar bears of western Russia, Svalbard, and portions of the Canadian High Arctic (Bernhoft et al. 1997; Norstrom et al. 1998). Wiig et al. (1998) hypothesized that environmental contaminants could have caused pseudohermaphroditism by disrupting normal endocrine function of Svalbard polar bears. Although linking contaminants to pseudohermaphroditism remains hypothetical, more recent studies have explicitly linked contaminants to polar bear health. Bernhoft et al. (2000) found significant negative correlations between immunoglobulin (IgG) levels and polychlorinated biphenyl (PCB) and HCB levels in the plasma of Svalbard Polar bears. PCBs and HCB also were negatively correlated with plasma levels of retinal and thyroid hormones in Svalbard polar bears (Skaare et al. 2001). Although specific maladies were not identified, IgG and thyroid hormone levels are associated with a broad variety of health-related systems. Their depression by external contaminants must be of concern. A study nearing completion in summer 2001 provided the strongest evidence yet that pollutants can reduce biological function in polar bears. Wild free-ranging polar bears in Canada, where contamination levels are relatively low, and in Svalbard were captured and vaccinated with harmless viruses. Blood samples collected 5 weeks after vaccination revealed reduced immune system response in the heavily polluted Svalbard polar bears (Skaare et al. 2002).

Although population-level effects of reduced ability to build immunity to disease have yet to be observed, it is clear that organochlorine contamination places polar bears at greater risk to a variety of possible environmental challenges. Use of some of these compounds has been dramatically reduced in recent years, and those reductions may already be reflected in polar bear tissues (Norstrom et al. 1998). Many other chemicals have been introduced in recent years, however, and risks they may cause will continue to create polar bear management uncertainties for decades to come.

RESEARCH NEEDS

Understanding Movement Patterns. With modern radiotelemetry

life cycle (Garner et al. 1990, 1994; Gloersen et al. 1992; Messier et al. 1992; Amstrup et al. 2000; Ferguson et al. 2001). Just as clearly, distribution and availability of prey are important in movement patterns of polar bears (Stirling and Øritsland 1995). The links between sea-ice, prey, and polar bears, however, are still poorly understood. If we are to explain the movements and activities of polar bears, we need to understand the ecological and energetic components of the predator-prey interactions (Lunn et al. 1997). Also, we need to understand explicitly how that interaction is mediated by the volatile sea-ice platform on which seals and bears depend. At present, descriptions of sea-ice patterns in the Beaufort Sea are too general to provide needed explanations (Stirling et al. 1981; Gloersen et al. 1992). Many logistical obstacles will make understanding seals, sea-ice, and the activities of polar bears a formidable task. Given that polar bears may be important indicators of the health of the arctic marine ecosystem (Stirling and Derocher 1993), overcoming such obstacles is necessary.

Recent measurements, derived from many observations of numerous individuals, are unequivocal and indicate polar bears are among the most mobile of all quadrupeds (Amstrup et al. 2000). However, physiological evaluations suggest that walking polar bears are energetically inefficient (Best 1982; Hurst et al. 1982a, 1982b). The physiology of locomotion in polar bears clearly needs to be reevaluated in light of their known extensive travel. Furthermore, the cues polar bears use to navigate during long movements need to be understood. No other animal is transported as far "in the blind" as are female polar bears that den on drifting pack ice. Going to sleep in one location and waking up, months later, 1000 km from that location must challenge abilities to return, but somehow polar bears are able to do so.

An obvious shortcoming of the data on movements of polar bears is that they were collected with satellite telemetry. Building platform satellite radiotransmitters (platform transmitter terminals or PTTs) into neck collars and attaching them to polar bears has provided previously unobtainable insights into polar bear movements and behaviors (Amstrup et al. 1986, 2000; Messier et al. 1992; Amstrup and Gardner 1994; Bethke et al. 1996). However, the necks of male polar bears are larger than their heads, and radio-collaring does not work for them. Neck collar radios also cannot be fitted to subadults, for fear of injury that could result as they grow and the collar does not. Hence, inferences regarding the movements of all members of the population must be extrapolated from the movements of females only. Males and subadults constitute a large portion of the population, and are often the most likely to be harvested or otherwise interact with humans. Failing to understand what they do is a significant limitation. Males are not only necessary to maintain the population, they also may play a role in limiting population size (McCullough 1981; Young and Ruff 1982; Stringham 1983). Polar bear populations can sustain higher harvests of males than of females (Taylor et al. 1987), but males also appear to be more vulnerable to human hunters. If male polar bears move in patterns that are significantly different than those of females, adjustments to management plans that are currently based on telemetry results from females (Treseder and Carpenter 1989; Nageak et al. 1991) might be required.

There is no satisfactory method of long-term attachment of transmitters to males, and information on movements or activities of male bears is minimal. A limited number of satellite radiotelemetry observations from seven male polar bears suggested that movement rates, distances moved, and areas occupied do not differ greatly between males and females (Amstrup et al. 2001). Those observations corroborated the tag and recovery findings of Lentfer (1983), Schweinsburg et al. (1981) and Stirling et al. (1980, 1984) as well as the correlations between genetic and telemetric population groupings (Paetkau et al. 1999). Clearly, as management needs intensify, better knowledge of the movements of all components of the population will be necessary. Nonetheless, an understanding of the movements of males comparable to that now available for females remains a challenge.

for a period of time. We often lack, however, an understanding of why animals select particular locales or habitats. Visits to land in the Beaufort Sea region, for example, appear to be increasing. Time on land and near shore exposes bears to anthropogenic risk factors and increases the probability of humans being injured by bears. Direct interactions between people and bears have increased markedly in recent years, and that trend can be expected to continue. If those interactions are to be handled properly, managers must know why bears are in areas frequented by people, which bears they are, and how to minimize prospects of bears and people ending up at the same places at the same time.

Research also is needed to understand how to predict probabilities of polar bear occurrence at various locations. When trying to understand the potential of a harvest or other human perturbation on highly mobile species that occur in overlapping management units, we need a way to convert retrospective telemetry data into predictions of the probability of occurrence at locales of interest. As the need for intensive management grows with increasing human presence in the Arctic, predicting where bears will be at particular times and understanding why they are there will be essential.

Maternal Denning. Worldwide, most available denning information has been derived from visual surveys. Except in Alaska and Canada, few animals have been followed to dens by radiotelemetry. Outside Alaska, most radio-collared polar bears have not been resighted on emergence to confirm denning outcome. Still fewer have been monitored long enough to assess patterns of fidelity to den sites or habitat types. Hence, data that might provide an understanding of the significant differences in denning patterns worldwide are not available. Why polar bears in different regions choose to den where they do is largely unknown.

The absence of comparative data among different geographic regions minimizes our understanding of the influence of different sea-ice, climate, and biotic conditions on the chronology and geographic distribution of denning. Polar bears in dens are more vulnerable to anthropogenic as well as natural disturbances than at other times in their life cycle. Therefore, denning data that are comparable over broad geographic regions are essential to interpretation of proposed increases in human uses of the Arctic.

Estimating Numbers. Worldwide, 20 populations of polar bears currently are recognized (see Fig. 27.8). The total combined number of bears in those populations is thought to be between 21,500 and 25,000 (Lunn et al. 2002, Table 1). Population estimates vary in quality from educated guesses in some of the populations to rigorous values complete with confidence intervals in others. Because most of the populations are hunted and many are subject to other potential human perturbations, better estimates of abundance are needed. Optimistic population estimates in the 1950s and 1960s resulted in excessive harvest and declines in Beaufort Sea polar bear numbers (Amstrup et al. 1986). Other populations also were suffering from overharvest at that time (Prestrud and Stirling 1994). Managers need reliable estimates of population size and trend to prevent overharvests from recurring. Despite over 30 years of polar bear capture, however, estimates of population size and trend have been elusive. Failures of past capture-recapture efforts to provide reliable estimates apparently resulted from biases caused by heterogeneity in capture or survival probabilities (Seber 1982; Hwang and Chao 1995). Amstrup et al. (2001) and McDonald and Amstrup (2001) improved estimates of numbers of polar bears by modeling heterogeneity in capture probability with covariates. Their analyses also pointed out many shortcomings of past efforts as well as weaknesses in available data. Estimates of population size based on mark and recapture data are dependent on the number of animals marked and the number of occasions during which marking occurs. Larger numbers of marked animals increase probabilities of capture and reduce the variance of the estimated population size. Increased numbers of occasions

Understanding Reproduction. Delayed implantation is known mainly from animals that are tractable in the laboratory. How it works in ursids and how they use it to their advantage in highly variable environments is poorly understood. The timing of implantation, and hence that of birth, appears to vary geographically and also among individual females. It is likely dependent on body condition of the female, which in turn depends on a variety of environmental factors. The interaction between environmental and physiological factors that controls timing of birth and onset of lactation is simply not understood. Further research is necessary to understand how global warming and other broad-scale changes in Arctic conditions may affect reproductive processes.

Estimating Survival. Because polar bears are harvested in most areas and also increasingly exposed to other human perturbations, understanding the processes of reproduction and survival is essential. Estimating the numbers of cubs produced in polar bear populations can be logistically difficult, but is technically straightforward. Estimating survival, on the other hand, is both logistically and technically challenging. Making reasonable estimates of survival continues to provide a stumbling block for researchers and managers alike. Although estimates of survival derived from radiotelemetry studies are consistent with ecological theory (Amstrup and Durner 1995; Eberhardt 1985), the lack of concordance among estimates derived by different methods is troubling. The best estimates derived without the aid of telemetry (Derocher and Stirling 1995a; Lunn et al. 1997) are not in the range thought to be necessary to sustain populations (Eberhardt 1985). Also, telemetry estimates can be derived only for females because male polar bears will not retain radio-collars. As management needs intensify, precise estimates of survival of independent juvenile polar bears as well as adult males will need to be developed while survival patterns of females and dependent young are reevaluated.

Jurisdictional Inequalities. Most current information about polar bears has been derived from studies in Alaska, Canada, and Svalbard. Large portions of the Arctic either have not been studied or have been the site of less consistent efforts. These inequalities create difficulties when we attempt to manage shared populations or wish to draw conclusions applicable over large regions of the Arctic. The greatest information gap is in the Russian Arctic. Russia controls nearly half of the world's Arctic habitat and undoubtedly many of the world's polar bears. However, few detailed studies have occurred or are planned. Lack of funding has environmental research over most of Russia at a standstill. Limited availability of logistics support, concerns over personal safety, and political restrictions on activities in many geographic regions further inhibit studies that might be accomplished in Russia by researchers from other countries.

The inability to study polar bears in Russia and limitations in information from previous work are significant. As indicated under Management and Conservation Issues, the future of polar bears in Russia may be less secure than in any other jurisdiction. Contamination of bears in portions of the Russian Arctic is high. Poaching is thought to be on the increase, and dramatic increases in harvest could result from the current economic unrest and absence of regulatory capacity. Some of the highest density maternal denning areas in the world are within Russian boundaries. The earliest work on maternal denning of polar bears was done by Soviet scientists. All of that work preceded the development of modern telemetry and other new technologies. Hence, those findings are dated and not directly comparable with current studies in other jurisdictions. The limited telemetry data from Russia has precluded discovery of new denning areas there. Large concentration areas on a few offshore islands in Russia have been known by conventional observations for decades. Much of the Russian Arctic, however, has a long linear coastline similar to that of Alaska. Scattered denning undoubtedly occurs there. Also, the long linear coast, as in Alaska, may encourage denning in the heavy offshore pack ice. No denning studies

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