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FACTORS AFFECTING THE EVOLUTION AND BEHAVIORAL ECOLOGY OF THE MODERN BEARS¹

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Abstract: The present distribution and abundance of the ursids is but an ephemeral reflection of an evolutionary path that began with the first identifiable bear, the dawn bear (*Ursavus elmensis*), 20 million years ago in the early Miocene epoch. Although the dawn bear was only the size of a fox terrier, by the Pleistocene its descendants had evolved into some of the largest terrestrial carnivores the world has known. Most bear species evolved in the northern hemisphere although some dispersed and reached South America, Africa and Southeast Asia.

Each species had to cope with ecological changes that affected interspecific competition or the availability of food. Apparently the black bear was sufficiently adapted to have survived largely unchanged from what it was like a million years ago. Numerous species went extinct, leaving only the 8 still present today. Some understanding of the evolutionary pressures that the modern bears have evolved through may help us to understand their behavioral ecology.

During the Pleistocene, bears at higher latitudes grew large and ecologically plastic while those closer to the equator remained small and became ecological specialists, as predicted by Geist's (1987) dispersal theory. Adaptations of the teeth of ancestral bear species allowed them to be both herbivores and carnivores. This allowed them to develop large size and broad ecological plasticity. Large body size enabled bears to conserve heat, capture large prey, defend carrion, travel great distances, and, as vegetation increased in the diet, to survive on qualitatively poorer food. Quantity and quality of available food and the degree of sexual dimorphism influenced the size of the home range and the evolution of social behavior in each species.

Bears show a great deal of individual variation in behavior and may exploit different subniches as a result of learned behavior. Slight differences in phenotype may also influence exploitation of subniches. Recent literature indicates that some terrestrial bear species are more active predators than previously thought and some evidence suggests a degree of scaling between the size of bears and the size of their prey. Social signalling appears to have been influenced by life in forest habitats but is not well understood. We give a preliminary interpretation of the social organization of the present day bears through the interactive framework of proximate ecological pressures, phylogenetic history, and learning.

There are likely few populations of bears anywhere in the world whose behavior has not been significantly influenced by man. This may confound our understanding of their behavior and ecology. Remaining populations of bears may not be able to adapt successfully to the combined effects of human predation, disappearing habitat, and climatic change.

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The bears are a fascinating group to analyze in an evolutionary context because of the remarkable variation in their adaptations. The largest species are about 10 times heavier than the smallest. The degree of sexual dimorphism ranges from species with none to those in which males are twice the size of females. Bears have evolved specialized niches as carnivores, herbivores, and myrmecophages, while retaining the functional ability to be omnivores. Pandas, which normally eat only 2 species of bamboo will still eat meat, while polar bears, which specialize in hunting seals, also eat berries. The home ranges of different species can range from less than 10 km² to over 100,000 km².

The present day distribution and abundance of the ursids is but an ephemeral reflection of an evolutionary path that began with the appearance of the first identifiable bear, the dawn bear, 20 million years ago in the early Miocene epoch (Kurtén 1976). Consequently, a brief examination of the evolutionary history of modern bears may help in interpreting the available information on their present day behavioral ecology. The dawn bear was only about the size of a fox terrier, but even after 10 million years, its descendent *Protursus*, from the mid-Miocene of Europe, was only modestly larger.

About 5 million years ago in the mid-Pliocene the world climate became drier (Kurtén 1976, Guthrie 1984)

and, in the northern hemisphere, the biomass and diversity of plants suitable for ungulates reached its zenith (Guthrie 1984). Savannas and steppes became widespread. At higher latitudes and altitudes the climate ameliorated and vegetation became abundant during interglacial periods. Mammal groups such as ungulates dispersed, speciated, and became larger (Geist 1978, 1987). During this period, the first identifiable bear species of the genus *Ursus*, *U. minimus*, appeared in the late Pliocene deposits of Europe. It probably gave rise to the present day members of the genus as well as several extinct species.

Coincident with this large increase in the biomass and diversity of prey species, there was an explosion in the diversity of predators. From the late Pliocene through the Pleistocene, the bears speciated and evolved into some of the largest terrestrial carnivores known (Kurtén 1968, Kurtén and Anderson 1980). During this period, several species of bears evolved, dispersed, and disappeared. An important point is that many more species once existed than do today. For example, several species of the genus *Tremarctos* lived in southeastern North America (e.g., the Florida cave bear, *T. floridanus*) and South America. Today only the spectacled bear (*T. ornatus*) survives in the northern Andes. Similarly, the large short-faced bears (*Arctodus* spp.) of North America, the cave bears of Eurasia (e.g., *Ursus spelaeus* in Europe), various popula-

¹ Invited paper

tions of brown bears (*U. arctos*) in Europe, Asia, and North Africa, and the Langebaanweg bear (*Agriotherium africanum*) of South Africa (Kurtén 1966, 1967, 1968; Hendey 1977) all thrived and subsequently went extinct. In general though, the bears were most successful where they originated, in north temperate areas.

Each species had to cope with a series of climatic changes that in turn affected interspecific competition or altered food availability. A few, such as the American black bear (*U. americanus*), were sufficiently adapted to survive changing ecological conditions and exist today, largely unmodified from what they were like a million years ago. The brown bears and polar bears (*U. maritimus*) of today are morphologically similar to, though smaller in size, than their Pleistocene ancestors (Kurtén 1976).

An important consideration when analyzing the behavioral ecology of the present day bears is the possible effect of man. Because of incessant hunting and habitat change, it is likely that few remaining populations of bears behave quite as their ancestors did. For example, large numbers of brown bears were once a common sight in continental North America (Storer and Tevis 1955). Can we assume that the habitat preferences and behavioral ecology of remnant populations in places like Yellowstone or southeastern British Columbia are unchanged from those of their predecessors? Probably not, but it may not be possible to evaluate the changes that have taken place. Similarly, the habitat occupied by remnant populations of other species may be significantly different from that in which they originally evolved. Obviously, we can only work with the information at hand but we need to remain conscious of possible biases.

In this paper, we have followed the taxonomy outlined by Nowak and Paradiso (1983) in which the giant panda (*Ailuropoda melanoleuca*) is considered an ursid. We refer to all races and populations of *U. arctos* as brown bears and group other bears, except for the spectacled bear, into the genus *Ursus*.

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THE SIZE OF BEARS

The modern bears are all medium- to large-sized mammals, ranging from 27 kg for the female Malayan sun bear (*U. malayanus*) (Nowak and Paradiso 1983) to over 800 kg for an exceptionally large male polar bear in prime condition (DeMaster and Stirling 1981). The latter represents a remarkable increase in body size, relative to their small Miocene ancestor, the dawn bear, 20 million years ago. About 15 million years later, when *Ursus minimus* first appeared, it weighed approximately 50 kg, similar to the maximum weight of the male Malayan sun bear, the smallest of the present day ursids. Kurtén (1976) noted that its canines were thin and sharp but the molars had already become enlarged and better adapted for feeding on vegetation, adaptations that together may have made it possible for the bears to evolve a large body.

Even when the smaller species of bears are included, the ursids are significantly heavier than all other families of carnivores (Gittleman 1985). Clutton-Brock and Harvey (1983) summarized 4 major advantages of large body size: the ability to produce large neonates or litters, reduction of relative heat loss, the ability to catch and handle larger prey or travel greater distances in search of food, and the ability to survive on qualitatively poorer food. Except for the production of altricial offspring in small litters, an anomaly imposed by physiological constraints (Ramsay and Dunbrach 1986), all these advantages were probably important to bears in the evolution of large body size.

Reduction of the ratio of surface area to volume with increased body size would have aided thermoregulation in an increasingly seasonal climate at higher latitudes. In this respect, the increased body size of bears was consistent with trends in other Ice Age mammals. In an analysis of the evolution of Ice Age mammals, Geist (1987) noted that speciation of cervids and caprids followed predictions made by his dispersal theory. In particular species that colonized higher latitudes with increasingly seasonal climates where productivity pulses became larger, became more ecologically plastic, and developed more ornate social organs (e.g., horns and antlers). In contrast, dispersal into lower latitude environments with less seasonal variability led to paedomorphism (i.e., the retention of primitiveness) and ecological specialization. As was the case for the ungulate genera studied by Geist (1987), the biggest bears were also north temperate species of the late Pleistocene, such as the cave bear of Europe and the short-faced bears of North America (Kurtén 1976). The largest modern ursids are also north temperate species. In comparison, the bears in sub-tropical climates (sun bear, sloth bear [*U. ursinus*], and spectacled bear), and the giant

panda of southeastern China, were removed from seasonal pulses in productivity. All are smaller than their northern relatives, less sexually dimorphic and most have become ecologically specialized (Laurie and Seidensticker 1977, Schaller et al. 1985, Lekagul and McNeely 1977).

It may be that bears were capable of broad ecological plasticity because the morphological adaptations of their teeth allowed them to evolve into a niche combining herbivory and predation (Kurtén 1976). Their grinding post-canine teeth enabled them to process large amounts of vegetation in the seasonal pulses of high productivity. However, the digestive tract of extant ursids is not highly modified from that of other carnivorous mammals (Bunnell and Hamilton 1983), which may have influenced body size. In a study of digestibility of different diets by 2 captive brown bears, Bunnell and Hamilton (1983) demonstrated that digestive efficiency declined as the proportion of vegetation increased. In particular, they noted that cellulose was poorly digested, especially in comparison to meat. Similarly, Schaller et al. (1985) found that dry matter digestibility of bamboo leaves by pandas varied seasonally between only 12 and 23%. Pandas are able to obtain carbohydrates by digesting hemicellulose from the cell wall of the plants but, as in all bears, they cannot digest cellulose. In comparison, Sinclair (1975) found that ungulates living on green grass assimilate about 80% of their diet, including 40-60% of the cellulose and hemicellulose (Van Soest 1982). Guthrie (1984) noted that non-ruminants cannot usually extract all the necessary amino acids, fatty acids, vitamins, and other vital dietary constituents from 1 or 2 species of plants. Consequently, he speculated that as non-ruminants moved toward increasing proportions of vegetation in the diet, they probably had to move over larger areas to find a variety of plant species to provide all the requirements. The same would apply if there was only a small number of digestible species but they were widely distributed at low density, in discontinuous patches, or both. Although Guthrie (1984) was speculating about the evolution of ground sloths, the same could have applied to the ancestral ursids. As the non-ruminant bears evolved into a progressively more herbivorous niche, they would likely have needed larger home ranges to ensure an adequate vegetative food base and allow for seasonal and annual variation in its distribution and productivity.

A vegetative diet alone is not a sufficient stimulus to produce large size, as is illustrated by several successful taxa of small mammals. Small animals are more vulnerable to predation than are large ones so they need to remain adjacent to escape habitat such as holes in the

ground, trees, or thick vegetation. To survive in open habitat, a mammal must be able to defend itself from predators or be fast enough to escape them. Consequently, as the body size of some bear species increased, they probably occupied more open habitat for longer periods, and were able to increase the proportion of vegetation in the diet. Their larger size also made them better able to defend themselves from predators. As the diet became progressively more vegetative, there would have been continuing pressure for body size to increase so enough vegetation could be ingested and processed to substitute for a high quality diet of animal material. Larger body size also made it possible to travel more in search of patchy food resources and to store and carry more fat with which to survive during periods of seasonal or unpredictable food shortage. With increased body size and well-developed canines, some bears were able to kill ungulates and other mammals, defend carrion from competitors, and protect themselves from other predators. Through this unique combination of being able to be predators, scavengers, and herbivores, they were able to exploit several food bases.

Small predators are restricted to small prey, so that one benefit of being large is that an animal can kill both small and large prey (Gittleman 1985). For example, brown bears are capable of taking advantage of relatively small animals such as ground squirrels and salmon in circumstances where their abundance makes such behavior energetically or nutritionally worthwhile (e.g., Stonorov and Stokes 1972, Murie 1981). Even so, the ratio between the size of the bear and its prey may be misleading since the predator's large size may be necessary to move heavy stones or earth to catch ground squirrels or to stay warm while standing in cold water for protracted periods while fishing for salmon. In the case of the more carnivorous bear species, their maximum size may have been influenced by the maximum size of generally available prey, as will be discussed below.

SEXUAL DIMORPHISM

Sexual dimorphism is strongly associated with polygynous breeding and is classically thought to result from sexual selection. Trivers (1972) proposed that variation in the degree of parental investment was the principal factor that determined if an animal bred monogamously or polygynously. However, in a subsequent review, Ralls (1977) noted that much of the theory about the evolution of sexual dimorphism was based on avian models and was not as applicable to mammals. In particular, she found that although a high degree of investment in the

offspring by both parents was a good predictor of monogamy, the converse was less reliable. In addition, the degree of parental investment does not explain why sexual dimorphism has evolved more frequently in large mammals than in small ones.

Sexual dimorphism in body size is present in all the modern ursids except possibly the sloth bear, for which there are too few data available to be certain (Table 1). As far as we have been able to determine, sexual dimorphism characterized most of the extinct Pleistocene bears as well.

In general, sexual dimorphism increases as species become larger (Clutton-Brock et al. 1977). Although quantitative weight data are not available for most bears, sexual dimorphism tends to increase with size in the 3 species of North American bears (Fig. 1). However, in the 3 North America species, the development of sexual dimorphism is only significantly different between black and polar bears (Tukey's test $P < 0.05$). It is also particularly interesting to note that a similar pattern of increasing sexual dimorphism in relation to increasing body size is present in North American brown bear populations (Fig. 1).

The bears did not develop anything resembling the antlers of the Ice Age ungulates (Geist 1987). However, we suggest the significant development of sexual dimor-

Table 1. Weights and approximate degree of sexual dimorphism in bears.^a

Species	Mean weight (kg)		Ratio (male:female)
	Males	Females	
Sloth bear	55-145		>1.0
Giant panda	97-107	86-89	1.1 to 1.2
Malayan sun bear	27-65		approximately 1.2
Giant short-face bear	350-375	250-270	approximately 1.4
Spectacled bear	140-175	110-120	approximately 1.4
American black bear	82-165	58-95	1.5 (range 1.1-1.7)
Brown bear	145-389	93-207	1.6 (range 1.2-2.2)
Asiatic black bear	110-150	65-90	1.7
Polar bear	271-322	147-197	1.8 (range 1.6-2.0)
European cave bear	410-440	205-220	approximately 2.0
Florida cave bear	230-250	115-125	approximately 2.0

^a Data for American black bear from Bunnell and Tait (1981); polar bear weights based on a random sample of 100 adult males and 100 adult females from Svalbard and 4 different populations in the Canadian Arctic (Lønø 1970; Canadian Wildlife Service, unpublished data); brown bears from Interagency Grizzly Bear Committee (1987); spectacled bear from M. Rosenthal and D. Weinhart (unpublished data) and Nowak and Paradiso (1983); other extant species from Nowak and Paradiso (1983); and, for extinct species from Kurtén (1967) and Kurtén (1976), based on estimates of body size.

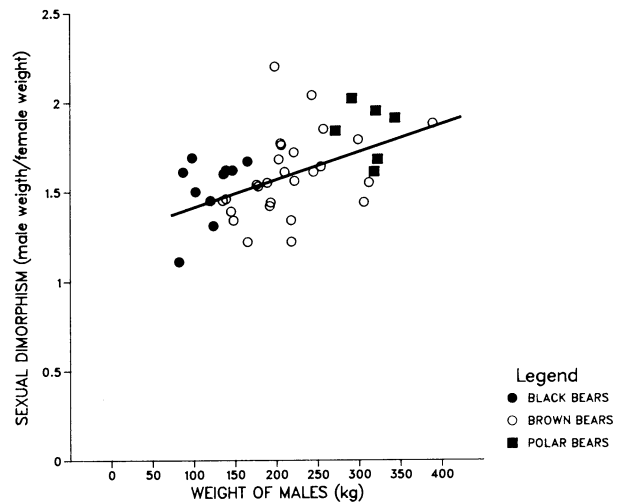


Fig. 1. Sexual dimorphism of black, brown, and polar bears as a function of body size. Black bear weights from Bunnell and Tait (1981); brown bear weights from Interagency Grizzly Bear Committee (1987); polar bears weights from Lønø (1970) and Canadian Wildlife Service unpublished data. Line indicates regression line for North American brown bear populations (slope of regression is significantly greater than 1 ($P < 0.05$)).

phism in the size of the body and the canine teeth of males, especially in the north temperate fossil and extant species, function for display, threat, and fighting. Kadosaki et al. (1986, 1989) compared the skull morphology of brown bears and Asiatic black bears (*U. thibetanus*) in Japan. They found that, although sexual dimorphism was detectable in all measured parts, the difference was significant only in the canine teeth. In both species, they found the degree of sexual dimorphism went from greatest to least in the following characters: canines, teeth except canines, length of tooth rows, and skull size. Since the diet of males and females of each species is similar, the significant enlargement of the canine teeth in males, beyond that which would be expected because of their larger size, probably function for intrasexual threat display and weapons. For example, in male polar bears, the canine teeth are important in intraspecific agonistic behavior. The canines of males are often badly broken in intraspecific fighting; a feature that is absent in females (Ramsay and Stirling 1986). Similar, though more exaggerated, development of canine teeth characterized other Pleistocene predators, such as the saber-toothed cats (*Smilodon* spp.) (Kurtén and Anderson 1980), and likely also functioned partly for social display.

Intense intraspecific conflicts between adult males of several species of bears have been reported (e.g., sun bears, Laurie and Seidensticker 1977; polar bears, Ramsay and Stirling 1986) and, although conclusive evidence relative to mating success is absent, it seems likely that

large body size confers reproductive advantage when competing with conspecifics. Bunnell and Tait (1981) also suggested that the larger size of male ursids, relative to females, may have evolved in part to favor the establishment of larger home ranges and a subsequent increase in potential mates (see Table 2). Ramsay and Stirling (1986) speculated that intense intrasexual competition between male polar bears for females, caused by the somewhat unpredictable distribution of females on the moving sea ice and the consequent inability of males to defend areas that would reliably include oestrus females, resulted in greater intrasexual competition for females than is found in terrestrial bears. Further, they suggested that the marked sexual dimorphism in polar bears is a consequence of the intense intrasexual competition between males for breeding opportunities with females. However, their hypothesis does not explain the apparently similar degree of sexual dimorphism exhibited by some populations of brown bears (Fig. 1), or the extinct terrestrial European and Florida cave bears (Kurtén 1966, 1967). An alternate hypothesis is that the large terrestrial Pleistocene bears, the large-bodied populations of brown bears, and the polar bear simply reflect the trend toward greater dimorphism with increased body size (Clutton-Brock et al. 1977).

One other ecological factor may have had a significant influence on the development of sexual dimorphism in the bears. Clutton-Brock and Harvey (1978) reported that within the primates, sexual dimorphism is greater in terrestrial than in arboreal species. They suggest this is because increased weight does not influence intersexual competition for food in ground dwelling species. In contrast, if males of arboreal species were larger than

females it might put them at a competitive disadvantage when feeding on thin stems or the ends of branches. This may also be a factor influencing sexual dimorphism in bears. Even though there are few reliable data on weights of adult male and female sun bears, sexual dimorphism is reduced and both are apparently quite arboreal (Laurie and Seidensticker 1977). Male and female sloth bears and giant pandas are of similar size and both are capable climbers, though they mainly feed on the ground. Finally, the least sexually dimorphic of the 3 North American ursids (Fig. 1, Table 1), the black bear, also makes the greatest use of trees. The spectacled bear and Asiatic black bear exhibit a similar degree of sexual dimorphism to the American black bear (Table 1), feed arboreally in some areas, make nests in trees to aid feeding, and sometimes rest in the nests as well (Schaller 1968, Peyton 1980). The spectacled bear is much less sexually dimorphic than was its extinct nearest relative (Table 1), which may have been influenced by feeding arboreally.

BEARS AS PREDATORS

The degree of active predation by the 3 bear species found in North America varies from the carnivorous polar bear to the less predatory brown and black bears. Because of their extensive use of vegetation, brown and black bears have not generally been thought to be significant predators. However, several more recent and quantitative studies have forced this premise to be revised (e.g., Cole 1972, Franzmann et al. 1980, Stewart et al. 1985, Reynolds and Garner 1987, Boertje et al. 1988, and other papers in this volume).

Throughout the carnivores, there is a strong correlation between the size of a predator and the size of its prey (Rosenzweig 1966, Gittleman 1985, Vezina 1985, Earle 1987) that, at first glance, might not appear to apply to the bears. For example, the polar bear seems 'oversized' when compared to its major prey, the ringed seal (*Phoca hispida*) (Fig. 2). Similarly, brown bears in several areas make extensive use of small prey. However, when the weight of each species of bear is plotted in relation to the weight of the largest prey it is now known to take regularly, the relationship for solitary carnivores derived by Earle (1987) fits fairly well (Fig. 2). The largest regular, though less frequently captured, prey species of the polar bear is the bearded seal (*Erignathus barbatus*) (Stirling and Archibald 1977, Smith 1980), which weighs up to about 360 kg (Kelly 1988). In addition, they occasionally kill white whales (*Delphinapterus leucas*) weighing up to about 600 kg (Lowry et al. 1987, Smith and Sjara 1990), and walrus (*Odobenus rosmarus*) up to about 500 kg (Kiliaan and Stirling 1978).

Table 2. Home range sizes of adult bears.

Species	Mean home range (km ²)(S.D.)	
	Males	Females
Giant panda ^a	8.5 (0.9)	4.6 (0.6)
Asiatic black bear ^b	12.6 (9.1)	
American black bear ^c	81 (55)	27 (20)
Brown bear ^d	631 (442)	242 (186)
Polar bear ^e	-	96,924 (78,453)

^a Schaller et al. (1985); Johnson et al. (1988)

^b Hazumi and Maruyama (1986)

^c Alt et al. (1980), Amstrup and Beecham (1976), Garshelis and Pelton (1981), Hellgren and Vaughan (1987), LeCount (1980), Lindzey and Meslow (1977), Manville (1983), Pelchat and Ruff (1986), Reynolds and Beecham (1980), Rogers (1987a)

^d Interagency Grizzly Bear Committee (1987)

^e Amstrup 1986

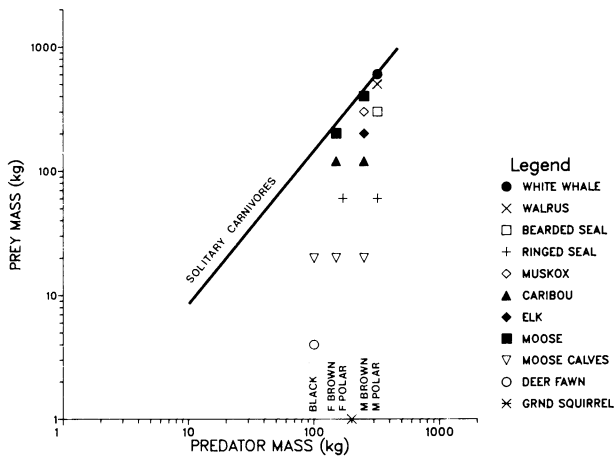


Fig. 2. Size of known prey of black, brown, and polar bears plotted in relation to the regression line of body weight of solitary carnivores (Earle 1987) and the weight of their largest regular prey. References by prey species as follows: white whale, Smith (1980), Lowry et al. (1987), Smith and Sjare (1990); walrus, Kiliaan and Stirling (1978); bearded seal, Stirling and Archibald (1977), Smith (1980), Kelly (1988); ringed seal, Stirling and Archibald (1977); muskox (D. Ruben, pers. commun.); caribou, Reynolds and Garner (1987), Boertje et al. (1988); elk, Cole (1972); moose, Mysterud (1973), Franzmann et al. (1980), Stewart et al. (1985), Boertje et al. (1988); deer fawn, Ozaga and Verme (1982), Mathews and Porter (1988); ground squirrel, Murie (1981).

Boertje et al. (1988) reported that adult male brown bears killed an average of 3.3 to 3.9 adult moose (*Alces alces*) (400-500 kg) per year whereas lone adult females killed significantly fewer (0.6-0.8 moose/year). Female brown bears with cubs killed no adult moose. All classes of bears killed moose calves but females without cubs killed at a higher rate than did the other 2 groups. In the area studied, brown bears were primary predators of moose and killed 4 times more animal biomass than they scavenged. Mysterud (1973) also reported 2 adult moose killed by brown bears in Norway but the sex of the bears was not known.

Lone adult female brown bears killed an average of 0.9 to 1.0 caribou (*Rangifer tarandus*) per year in east central Alaska (Boertje et al. 1988). Reynolds and Garner (1987) also documented killing of caribou by brown bears on the Alaskan North Slope. Most of the animals killed were calves but some adults were taken as well. Adult females were involved in 64.7% of the chases but were only observed feeding on 37.3% of the carcasses, compared to 58.5% for males. However, it is likely that several of the carcasses that adult males were observed feeding on were killed by other smaller bears (Reynolds and Garner 1987). D. Ruben (pers. commun.) of Paulatuk, Northwest Territories, also observed an adult male brown bear kill an adult female muskox (*Ovibos moschatus*) (approximately 250 kg) near Fallaise Lake, Northwest Territories, in 1984.

On the basis of circumstantial evidence and an observed attack by 2 subadult brown bears that drew blood from a lone adult bison (*Bison bison*), brown bears are suspected to occasionally kill young bison, although none has been confirmed (M. Meagher 1973 and pers. commun.). Observations have also been made of individual brown bears testing lone bison by approaching them and then leaving when the bison ignored them, refused to run, and kept on feeding (M. Meagher pers. commun.). Healthy adult male bison may be too large and well armed for a bear to attack without risk of serious injury to itself. Testing likely helps a bear to identify a sick or weak animal. Bison also have a clumped distribution, especially during critical periods such as calving (Calef and Van Camp 1987), which may also make predation by bears difficult. In a review of historical material, Roe (1970) found evidence of brown bears scavenging on dead bison but it appears that predation was uncommon.

Black bears also demonstrate predatory behavior and have been found to be significant predators of moose calves (Franzmann et al. 1980). The smaller body size of black bears probably precludes them from being a significant predator on adult moose. Recently, it has also become apparent that black bears can be important predators of neonate white-tailed deer (*Odocoileus virginianus*) (Ozaga and Verme 1982, Mathews and Porter 1988). The maximum size of prey taken regularly by black bears is not known but, from Figure 2, it should be about 151 kg for a 100 kg bear. The vulnerability of prey of different sizes to predation by black and brown bears probably influences niche separation between them.

Peyton (1980) reported seeing the hide of a woolly tapir (*Tapirus pinchaque*) with blunt scars from being attacked by a spectacled bear. Villagers had found and killed the wounded animal. Although Tschudi (1844, cited in Peyton 1980) reported that spectacled bears preyed on deer, guanaco (*Lama guanicoe*), and vicuña (*Vicugna vicugna*), there are no supporting quantitative data.

Recent studies of the energetics of polar bears also suggest that body size may have a significant influence on how bears hunt. Hurst et al. (1982) found that the energy required for the plantigrade polar bear to move is about double that for most other mammals. To move at the modest speed of 7 km/hr, uses 13 times more energy than lying. This probably explains the polar bear's preference for lying and still-hunting for seals (Stirling 1974, Stirling and Latour 1978). Lunn and Stirling (1985) calculated that unless a 320 kg adult polar bear captured a flightless snow goose in late summer in 12 seconds or less, it would cost the animal more energy that it would gain if it was successful. The lower ratio of surface area

to volume, and heavier deposits of fat on adult bears (particularly males and pregnant females) mean they can run much shorter distances than subadults because they overheat more quickly and are unable to dissipate heat quickly enough to be able to continue high levels of exertion. Although there are no data available at present to compare the cost of locomotion of brown and black bears, we suggest that it would also be easier for smaller and leaner subadults to run longer distances than adults. If so, this would probably mean that larger animals would make most of their kills after a short burst of running from ambush, similar to the lion (*Panthera leo*). Coincidentally, the lion is the only other mammal known in which the metabolic cost of movement is about double that of most other mammals (Chassin et al. 1976). Not surprisingly, Schaller (1972) found that female lions caught medium-sized prey twice as often as males. He suggested that the females were more successful on the faster medium-sized prey because they were faster than the more cumbersome males.

The relationships between brown and black bears and their prey may not be as simple as the regression in Earle (1987) or Figure 2. We suggest that body size and energetics are significant factors in determining how bears of different body sizes hunt ungulates. Learning is probably also important. We predict that most kills made by adult males will be after a short rush from ambush or after stalking to close range and that most kills that require a longer chase will be made by adult females with cubs and by subadults. There is some support for this hypothesis. Cole (1972) noted that subadult or subordinate young bears appeared to be the most effective predators on elk (*Cervus canadensis*). He also reported separate incidents of elk being killed by 2 subadult bears hunting together in chases that lasted 15 and 20 minutes each. On the Alaskan North Slope, only 1 of 17 brown bears of known age and sex observed chasing caribou was an adult male (Reynolds and Garner 1987). The remaining 16 chases were made by adult females and subadults.

For the omnivorous bears, sexual dimorphism does not appear to confer benefits in the area of resource segregation (Bunnell and Tait 1981). However, in the North American bears, sexual dimorphism appears to become more pronounced with increasing predatory behavior (Fig. 1). Ralls (1976) suggested that sexual dimorphism could be related to niche exploitation as well as to a polygynous breeding social system. Sexual dimorphism in birds of prey is thought to function partially to separate niches and reduce intersexual competition (Selander 1972). We suggest partial niche separation of males and females could be important in the predatory bears and

may also have influenced the development of sexual dimorphism. As already noted above, adult male brown bears kill far more adult moose than do lone females, whereas the reverse is true for the killing of moose calves. In the case of the sexually dimorphic and polygynous polar bear (Ramsay and Stirling 1986), the adult males appear to prey most frequently on bearded seals and occasionally kill white whales. From data collected throughout the Canadian Arctic, 93% (14/15) of the bearded seal kills that were found while still in the possession of a polar bear were being consumed by adult males. Females predominantly kill the smaller (60 kg) ringed seal. There is some segregation of different age and sex classes of polar bears by habitat type (Ramsay and Stirling 1986). Much of this appears to result from females with cubs minimizing the risk of infanticide by avoiding adult males. Considering the large degree of sexual dimorphism in polar bears, segregation might also be influenced by differences in the vulnerability of different sized species of prey.

Surplus killing has been documented in wolves (*Canis lupus*) (Miller et al. 1985) and other carnivores (Kruuk 1972). Similarly, surplus killing of domestic sheep by brown bears has been reported in Norway (Mysterud 1975) and of harp seal pups (*Phoca groenlandicus*) off the coast of Newfoundland by polar bears (T. Øritsland, pers. commun.). Lowry et al. (1987) reported polar bears killing several white whales at 1 location and leaving some uneaten. In the Canadian Arctic, we once observed a polar bear kill a ringed seal, feed extensively on it and then kill 2 more within the next hour but leave them uneaten. It is not clear why animals do this. Although the benefit to other bears, particularly subadults, of scavenging on the remains is probably considerable, this seems an unlikely explanation.

Another difference between bear species relates to the length of time spent processing a kill. Polar bears usually feed once on a seal kill and then abandon the remains, which sometimes are substantial (Stirling 1974, Stirling and Archibald 1977). The only exceptions to this pattern of carcass use are a few adult males that we have seen kill an adult bearded seal and apparently remain with it, possibly for several days. In contrast, brown bears are well known for remaining for several days with an animal they have killed, or 1 they are scavenging (e.g., Boertje et al. 1988). This difference in how long polar and brown bears remain with their kills may also relate to the rate at which prey can be captured in each ecosystem, prey size, and gross energy value in relation to alternate food sources, and the number of potential inter- and intraspecific scavengers that might attempt to contest ownership.

INTER- AND INTRASPECIFIC COMPETITION

Interspecific and intraspecific competition between bears, including predation (e.g., Miller 1985, Ross et al. 1988), has been significant in their evolution. Cubs of all the predatory species of bears are sometimes killed by adult male conspecifics (e.g., Jonkel and Cowan 1971, Taylor et al. 1985, Dean et al. 1986, LeCount 1987) as well as by other mammalian predators (e.g., Rogers and Mech 1981, Ramsay and Stirling 1985, Paquet and Carbyn 1986). Intraspecific predation has not been reported for any of the subtropical species of bears, although it may occur.

In a comparison of black and brown bears in different biogeoclimatic zones in North America, Herrero (1978) found that brown bears are consistently 1.5 to 2.0 times the size of black bears. He further concluded that black bears had retained the forest dwelling niche of their ancestors while the brown bear moved to exploit more open habitat types as well as forests. When faced with a serious threat, the strategy of a female black bear is to send her cubs up a tree safe from danger, flee, and return for her cubs when the threat has passed. In contrast to black bears, the larger brown bears protect their cubs by standing their ground or attacking the perceived threat directly (Herrero 1978). Although the cubs are capable of climbing trees, they apparently do so much less frequently in response to danger than do black bears. Female polar bears, which live in open habitat, also defend their cubs by direct attack, even if threatened by an adult male twice her size or a helicopter hovering over her head. Along the southwestern coast of Hudson Bay, where polar bear family groups spend significant amounts of time on land during the late summer and fall, we have never seen cubs attempt to climb trees, even though large trees are present in some areas. In lieu of trees as escape habitat in the High Arctic, female polar bears with cubs, and lone subadults often climb 100 m or more up a hillside above the sea ice and dig a pit to lie in where they can see around them before sleeping. This precaution appears to be in response to the threat of intraspecific predation.

A plausible hypothesis to explain why the black bear did not move out of the forest may be that it was not large enough to protect its young, or possibly itself, on the ground from larger carnivores (Herrero 1978). During the Pleistocene, there was an abundance of large terrestrial predators in the open country, including the cursorial giant short-faced bear (*Arctodus simus*), one of the most powerful terrestrial mammalian predators to evolve anywhere (Kurtén 1967, Kurtén and Anderson 1980). With the passing of the giant short-faced bear during the Pleistocene extinctions, its open country habitat was

occupied by the brown bear. Brown bears crossed the Bering land bridge in the late Pleistocene and invaded western North America via Alaska, and presumably continued to exclude the black bear from the plains.

No brown bears occurred in eastern North America during the Pleistocene. In this situation, the now extinct black bear (*Ursus americanus amplidans*) often became as large as brown bears and their remains are still occasionally mis-identified as such (Kurtén and Anderson 1980). Present day black bears in eastern North America are still larger than their western counterparts that share habitat with brown bears. Kurtén (1963) has speculated that the extinction of the Florida cave bear and the eastern short-faced bear (*A. pristinus*) may have been brought about by competition from the large eastern race of black bears and invading brown bears from the north. In this context, although black and brown bears first appeared together in the fossil record in Europe about the late Miocene or early Pliocene, only the brown bear exists there today, possibly because it displaced its smaller competitor (Kurtén 1976).

Another open country habitat occupied by brown bears in North America is the tundra, north of the tree line. In parts of northern Canada, Harington et al. (1962) suggested that brown bear populations have diminished as a result of overhunting. Coincidentally, Jonkel and Miller (1970) noted a possible increase in the numbers of black bears recorded in various tundra areas and suggested this might be because of reduced competition or threat from brown bears.

The other forest dwelling bears are able to climb trees although the extent to which they do so varies. Spectacled bears and sun bears are excellent climbers and feed arboreally. Sun bears lack hair on the soles of their feet, which has been suggested to be an adaptation to aid climbing (Bunnell 1987). Although pandas feed predominantly on the ground, unattended young are still vulnerable to predation (Schaller et al. 1985). They use trees for escape habitat under some circumstances, including when harassed by courting males, but the presence of leopards (*Panthera pardus*), which are known to kill pandas occasionally, may reduce the overall value of that escape strategy.

The subtropical sloth bear is also an expert climber but the cubs remain on the ground when the female is in a tree. If threatened, the female leaves the tree immediately and flees on the ground, her cubs sometimes departing ahead of her (Laurie and Seidensticker 1977). They attribute this behavior to the presence of the leopard, a significant arboreal predator, which sometimes kills sloth bears (Kurt and Jayasuriya 1968). Consequently, climbing a

tree is ineffective for escape and might make the bear more vulnerable to predation. They also note that large ungulates are more likely to stand and fight predators, or attack them, than run away. They suggest the presence of elephants (*Elaphus maximus*) and rhinoceros (*Rhinoceros unicornis*), which are capable of pulling down or pushing over even medium-sized trees, further reduce their value as escape habitat for sloth bears. Despite its small size, the sloth bear is known to attack humans if surprised and is regarded as dangerous by local people (Laurie and Seidensticker 1977). Like the much larger brown bears, aggressive behavior may be a consequence of not being able to rely on trees for escape.

Interspecific competition from mammals other than bears may have played a significant role in preventing bears from invading some areas. Alternatively, an absence of competitors for a particular niche may have facilitated evolution and dispersal. For example, the sloth bear apparently was able to enter the myrmecophagic niche in southern Asia because areas of suitable habitat were unoccupied by the 3 other allopatric mammalian myrmecophages present (Laurie and Seidensticker 1977). In South America, there are 5 sympatric species of myrmecophages, which appear to occupy all available habitat, and there are no bears that eat ants or termites (Laurie and Seidensticker 1977). However, in temperate North America and northern Asia, where there are no mammalian myrmecophages, ants may form a significant part of the diet of black and brown bears (e.g., Hatler 1972, Vereschagin 1976).

Pruitt and Burghardt (1977) note that the mountain gorilla (*Gorilla gorilla beringei*) appears to occupy a similar niche in central Africa to that occupied by the black bear in North America. Similarly, there are numerous species of primates in northern South America and other tropical regions. What role, if any, primates may have had on distribution patterns of the modern bears is unknown.

Although there are no bears in southern Africa today, bears of the genus *Agriotherium* have been found in Pliocene deposits dating back between 4 and 5 million years (Hendey 1977). The Langebaanweg bear is the largest terrestrial predator recorded from southern Africa and, from its large jaws and the degree of development of its incisors and canines, appears to have evolved into a largely carnivorous niche. Its muzzle was short and broad and the palate was even shorter than that of the short-faced bears of North America. The sagittal crest was high and the zygomatic arch was wide, which are also indicative of strong musculature indicative of a carnivore. Apparently *Agriotherium* was a short-lived, but wide-

spread, genus that first evolved in Europe during the Miocene but during the Pliocene spread to North America, Asia, and Africa (Hendey 1977). They were apparently extinct by the end of the Pliocene. It is possible, though unknown, that in the northern hemisphere they were out competed by other species of bears. However, the present day lack of ursid successors in central or southern Africa is puzzling, considering the large and variable food base, unless the rapid evolution of other carnivores and primates (including humans) into available niches excluded them after the passing of the Langebaanweg bear.

It is likely that interspecific, and possibly intraspecific, predation influenced the behavior of temperate bears during winter denning. Bears differ from other hibernating mammals in that their body temperature drops only a few degrees and they are capable of rapid arousal (Folk et al. 1972). This may be necessary because females give birth to altricial young and probably have to give them continuous attention to ensure their survival. However, from the number of reports in the literature on the killing of bears in their dens by other predators, including ursids (e.g., Paquet and Carbyn 1986, Ross et al. 1988), it is clear that bears in dens must also be able to arouse themselves quickly, if necessary, to protect themselves and their cubs from being killed.

INDIVIDUAL VARIATION

In general, biologists who have worked with bears have been impressed with how variable the behavior of individuals appears to be. Similarly, most of us have the distinct, if unquantified impression that bears remember a great deal about particular areas and how to do things. The success that circuses have had with training bears also suggests they are good at learning new tasks. Yet, with the exception of a very few quantitative studies such as Bacon and Burghardt (1976a, b), there is little more than an anecdotal appreciation in the literature of their ability to learn or remember things. As long-lived mammals that spend most of their lives within a home range and show strong seasonal fidelity to particular locations, bears probably learn much about the area, including where and how to find food or other necessities under a variety of circumstances. The variability in the ways bears from the same population behave within a particular area may be influenced by both genetic factors and learning. If there is a lot of variability within the habitat (e.g., in food types and availability, cover, and topography), over time there will be differences in some of the experiences individual bears have while feeding.

Thus, through learning, some bears may develop individual differences in food preferences, vary in the degree to which they prey on live animals, or respond to disturbances. Individuals will develop behavioral patterns that are molded by their own experiences. Similarly, some behaviors will be learned by cubs while accompanying their mothers during the long period before weaning. However, there has been no attempt in the literature to review or quantify the aspects of learning noted above.

An unexplored but possibly fertile area for investigation is that of individual variation in niche exploitation by different individuals within a population as a result of variations in their morphology. In a recent review, Lomnicki (1988) argued for the adaptive significance of individual variation within populations. Similarly, Wallace (1982) suggested that the higher degree of phenotypic variation that sometimes occurs among the offspring from the same parents, compared to those of unrelated animals, could be adaptive because, in the case of a shortage of resources, the survival of at least some of the progeny may be possible. Kurtén and Anderson (1980) noted that Erdbrink (1953) listed 232 recent and 39 fossil species and subspecies of brown bears in what they describe as "... a waste of taxonomic effort which ... is unparalleled". Ignoring the unrealistic amount of taxonomic splitting that was done, the fact remains that there is substantial morphological variation in the skulls of these mammals. This was brought home to us recently when we examined a small sample of skulls from male brown bears collected from the southern Caucasus Mountains in the U.S.S.R. In broad terms, the shapes varied from what we think of as normal for a brown bear to one with a shortened face and high forehead reminiscent of a panda to another that was elongated rather like a wolf skull. A similar amount of variation was reported and illustrated for brown bears in Hokkaido by Kadosaki et al. (1989:27, Fig. 2). The consequences of such variation in phenotypic expression on the development of different feeding strategies by individual bears is unknown. Possibly the variability in skull morphology is greater in a species like the brown bear because its habitat and the food resources are highly variable. Does this allow different individuals within a population to specialize in particular subniches? The retention of such variability in skull morphology in brown bears from fossil through recent species (Erdbrink 1953) suggests there may be some benefit we do not understand. In comparison, based upon a superficial comparison of polar bear skulls, the same amount of obvious variability was not present either within populations or between them. The diet and habitat of polar bears are probably less variable

than those of brown bears but we do not know if that accounts for a lack of comparable variability in the skulls.

SOCIAL ORGANIZATION

In general, the present day bears tend to live most of their lives as solitary individuals, with social groups being limited to females with cubs and male-female pairs during the breeding season. There is no indication from the fossil record that the ancestors of the modern bears were any more gregarious (Kurtén 1976). As with other species, their social organization appears to have been influenced by the risk of predation, intraspecific competition, and the distribution of resources (Wrangham and Rubenstein 1986).

It is possible that some of the ancestral ursids might have been vulnerable to significant predation because of their small size. However, it appears that as body size, teeth, and claws increased in size through the Pliocene and Pleistocene epochs, bears were probably not as vulnerable to predation from non-ursids. As a result, there was probably little significant pressure to aggregate for the purpose of group defence or vigilance. We suspect that, similar to the modern bears, the threat of predation by other species of bears, or males of their own species, might have had a significant influence on their behavior and ecology. The smaller bears might have used trees as escape habitat while larger species could stand and fight if necessary.

Intraspecific competition, including predation by large males, has been suggested to be important in population regulation of North American black and brown bears (e.g., Kemp 1972, Stringham 1983). The importance of this factor to other species is unknown. Intraspecific predation also occurs in polar bears (Taylor et al. 1985) but in the open habitat of the arctic sea ice it may be less important than in the forest (Ramsay and Stirling 1986). Cubs develop rapidly and are able to outrun adult males by the time they are 6 months old. Nevertheless, 1 consequence of intraspecific competition, including the threat of predation, is differential distribution of bears by age and sex class. For example, adult female polar bears with cubs on the sea ice during the breeding season, and on land in Hudson Bay during the non-breeding season, tend to segregate themselves from habitats where adult males are most abundant (Stirling et al. 1977, Ramsay and Stirling 1986, Derocher and Stirling 1990a).

Home ranges of bears, for which data are available, are extremely variable (Table 2) and have a high degree of overlap with conspecifics. In most cases, this probably indicates that resources are widely distributed and not

defendable. Group defence of a home range would probably not be any more energetically beneficial since it is unlikely the defendable area would increase enough to support a group of bears.

Intraspecific competition for patchy and ephemeral resources, and the evolution of a largely vegetarian diet, which necessitates a large food intake because of a non-ruminant digestive tract, likely acted against the formation of large social groups of bears. Groups of bears would be likely to exhaust food patches more quickly than individuals so they would have to move more frequently in search of new feeding areas. The effect of additional travel could be negative because the large size and massive build of bears appears to reduce their energetic efficiency of movement (Hurst et al. 1982). If there is a similar trend in other species of bears, it is likely that intraspecific competition would negate feeding in groups except in exceptional circumstances where there is a high density of high quality food, such as at a salmon stream or a garbage dump.

In considering why bears are not found in sleuths, it is insightful to compare their social organization to that of lions. Bears and lions both give birth to altricial offspring so that substantial postpartum care is required. In lions, the mother-offspring bond is the basis of group formation (Packer 1986). Also like bears, the ancestors of lions were solitary carnivores, as most other felids still are today (Packer 1986). Most studies attribute group living in lions to the benefits associated with the advantages of killing large prey, but Packer (1986) argued that group living in lions appears to have evolved despite possible disadvantages of group hunting. The kin-based structure of female prides results from natal area philopatry (Packer 1986) and may represent the rudimentary mechanism from which higher levels of sociality develop. A major advantage of group living in lions may be protection of the cubs from infanticidal males, resulting in increased reproductive success that negates possible disadvantages of group hunting (Packer 1986, Packer et al. 1988).

Both infanticide and natal area philopatry are closely paralleled in ursid ecology, yet all ursids remain solitary. However, there are 2 important differences. Female lions can come into oestrus at any time of year compared to bears, which are seasonal breeders. Thus, a male lion may be able to mate with a lioness if he kills her cubs, regardless of the season, something unlikely with bears. Consequently, infanticide is a less important stimulus for group living in bears than in lions. We suggest food size and density may constitute the critical difference. By hunting together, lions are able to obtain large enough units of high quality food, often enough, that all the

members of the group can be fed within their territory. Except for brief periods in special circumstances, such as at salmon streams, bears cannot do this because the prey available to them are distributed at densities lower than those in lion habitat. For brown bears, killing an ungulate is a rare enough event that it may be advantageous not to share it. Additionally, in temperate regions, the cooler climate may act to preserve a carcass, making it more beneficial for an animal to guard it for continued use. The warmer climate in lion habitat, plus the abundance of scavengers, may make it advantageous to share a kill and ensure consumption by kin. Although brown bears, especially subadults, are occasionally cursorial hunters of mammals as large as elk or caribou (Cole 1972, Reynolds and Garner 1987), and may hunt in pairs (Cole 1972, M. Meagher pers. commun.), the rate at which they are able to kill does not approach that of lions. If bears hunted in sleuths, they would have to travel extensively between kills, as do packs of wolves, because of the low density of prey species. Each bear would receive a reduced caloric return from each kill because of the need to share. However, compared to wolves, long distance travel by bears is slow and likely much more costly in the energetic sense, so that solitary hunting is the best overall strategy.

While feeding on a vegetarian or omnivorous diet, individual bears are capable of sustaining and protecting both themselves and their cubs in most circumstances without the assistance of conspecifics. Consequently, there is little apparent nutritional benefit in becoming more socially developed. Even in the completely carnivorous polar bears, the small size of their major prey item, ringed seals, probably negates any potential advantage from hunting as a group or sharing a kill with any conspecific except offspring. Like brown bears hunting ungulates, the rate at which polar bears are able to kill large prey such as bearded seals or odontocete whales does not appear to be frequent enough to stimulate the development of group hunting. Nevertheless, large numbers of polar bears will scavenge together at whale carcasses or dumps, as do brown or black bears, though in those circumstances each animal still behaves independently.

Lastly, in contrast to lions, many past and present ursid species hibernate and this may restrict the development of sociality. By way of analogy, there is a fairly wide range in the development of sociality in ground squirrels. Apparently what characterizes the most social species is a prolonged association between adults and subadults that can only occur with short, or absent, periods of hibernation (Armitage 1981). Even though some pres-

ent-day bears may not hibernate in warmer regions, their herbivorous diet in a forest environment does not lend itself to the development of sociality as discussed above.

In contrast to the varied diet of omnivores such as black bears, more than 99% of the diet of the giant panda consists of stems, branches, and leaves of only 2 bamboo species (Schaller et al. 1985). There is seasonal variation in the use of each species and the parts of the plants that are eaten but, since bamboo grows year-round at high density, pandas can normally obtain all their metabolic requirements within much smaller areas than other species of bears (Table 2). This is probably strongly influenced by the additional fact that there is no seasonal variation in bamboo quality (Schaller et al. 1985). Thus, there is no need for the panda to either change diet or hibernate. Even so, they show little social organization.

Probably because of their solitary existence, female bears appear to be induced ovulators (Bunnell and Tait 1981). There is little advantage to ovulating spontaneously if the chance is good there would not be a male nearby at the time. From observations in zoos and in the field (Meyer-Holtzapfel 1957, Hornocker 1962, Sparrowe 1968, Herrero and Hamer 1977), it appears that male and female pairs may remain together for up to 2 weeks. Males may try to sequester females to isolated areas where they are less likely to encounter competing males (Herrero and Hamer 1977, Ramsay and Stirling 1986) and copulation usually occurs many times. Intrasexual competition between males for mating privileges can be intense and some females may mate with more than 1 male (Sparrowe 1968). Since female bears may have multiple ovulations (Ramsay and Stirling 1986), it is possible for members of the same litter to have different fathers (Bunnell and Tait 1981). For example, Hornocker (1962) observed a female brown bear that mated 10 times with 4 males in 2 hours. How frequent polyandrous mating is, and what effect it may have had on the evolution of the social organization of bears is unknown.

Nevertheless, some sociality does exist although its function may not necessarily be fully understood. For example, during the ice-free period in western Hudson Bay, 2 to 14 or more adult males may aggregate closely and show extreme tolerance of conspecifics (Kolenosky 1987, Derocher and Stirling 1990b). In this circumstance, considerable ritualized fighting may also take place in which combatants are not injured (Latour 1981). Two adult female polar bears, each with cubs, were observed interacting non-aggressively, and even attending each other's cubs on occasion, over a period of 6 weeks while feeding together at a garbage dump (Lunn 1986).

It is also possible that the apparently solitary forest-dwelling bears are more social than previously thought. Reassociation of family groups after breakup has been reported (Reynolds and Beecham 1980, Garshelis and Pelton 1981). In black bears, female offspring tend to settle in or adjacent to the home ranges of their mothers (Rogers 1987a) while male cubs disperse. Rogers (1987b) also suggested that female black bears can recognize independent offspring and behave in a beneficial manner dictated by genetic relatedness.

COMMUNICATION

Because bears are solitary animals and are usually difficult to observe, their methods of communication are not well understood. The degree to which bears vocalize varies between species. Herrero (1978) suggested that black bears are more vocal than brown bears because they are more of a forest animal and have restricted visibility. Other forest species such as spectacled bears, sloth bears, and sun bears also seem to be quite vocal (Laurie and Seidensticker 1977, Peyton 1980, Bunnell 1987). Pandas in zoos vocalize during oestrus (Kleiman et al. 1979) while those in the wild have a repertoire of approximately 11 identifiable sounds (Schaller et al. 1985). In contrast, in our experience, polar bears vocalize little. Females and cubs may call to each other if they become separated, or if the female is leaving a site and wants the cub to follow. Males snort and chuff (Wemmer et al. 1976) during intrasexual agonistic behavior but otherwise they lack the distinctive calls that characterize other carnivores.

Several species of bears mark trees. The function of this behavior has not been confirmed experimentally but the information conveyed likely includes territorial marking and possibly the status of the individuals.

The use of scents, including pheromones, have not been documented in bears though they are likely present. For example, we have tracked individual adult males on the sea ice during the breeding season in the spring, when their paths may cross the tracks of dozens of other bears. There is no discernible response until a male crosses the path of a lone adult female. Recognition is instant and he then follows the track until he catches up to her or is distracted by another female. We do not know how a male polar bear recognizes the track of a lone, and presumably oestrus, adult female but it is clear that he can. It seems likely a chemical stimulus is involved.

In general, the presence of color patterns in bears is fairly conservative, especially when compared to some other carnivores (Nowak and Paradiso 1983). However, contrasting color patterns on the body may help commu-

nicate an animal's presence, especially in a forest habitat. The existence of color patterns and contrast is greatest in lower latitude species such as the spectacled bears and pandas in particular, but also to a lesser degree in the sloth bear. Sun bears, Asiatic black bears, spectacled bears, and usually American black bears, have a patch of white on the chest. The muzzle of these smaller forest bears, and even part of the face of the sun bear, are much lighter in color than the rest of the head or upper body (see Nowak and Paradiso 1983, Bunnell 1987). By comparison, there is less contrast in the body color patterns of brown bears. In the polar bear, which lives in the most open habitat of any species of bear, there is no contrast in body color at all, with the exception of the black nose and eyes. Schaller et al. (1985) suggested the complex body markings of the panda sent important signals to conspecifics and Ewer (1973) thought that the chest markings in bears possibly served to accentuate a threat posture when an animal stood on its hind legs. Bears in general tend to approach conspecifics in a head-on manner so that concentration of the marking patterns in the chest and facial areas would enhance identification and communication. Head and neck orientation, ear position, and the orientation of the mouth and teeth are probably all important though they have been little studied.

Tails in the ursids are conspicuous by their small size. In many carnivore species, tails serve an important function in communication and in many instances are highly patterned (Ewer 1973). Even in other species with short tails such as the lynx (*Lynx canadensis*), the tail is held upright and is used in maintaining social contact and communication (Ewer 1973). The absence of a functional tail may have been influenced by the relatively non-social nature of the bears and the fact that the most important displays seem to involve frontal and bipedal display.

MANAGEMENT IMPLICATIONS

It is not possible to predict the direction in which bears may evolve but it is obvious from the generation time involved that change will be slow. Large species evolve more slowly because of low rates of reproduction and high rates of extinction (Stanley 1979). This may not bode well in a world which appears to be changing ever more quickly, especially when, as Peters (1983:196) has noted, "Evolution has favored smaller species, and large size tends to be an evolutionary dead end".

All extant populations of bears have been hunted, displaced from habitat, or impacted in some other way by the presence of man. It is difficult to assess the effect this

may have had on the evolution of the modern bears but it has probably influenced aspects of their learned behavior such as movement patterns and diet preferences. As the habitat available for bears continues to decrease, we reduce the genetic variability that remains available to the species. This may alter the pattern of natural selection because genetic drift increases in smaller populations (Allendorf 1983).

Large carnivores are sensitive indicators of ecosystem health and could be used to define the minimum area necessary to preserve intact ecosystems (Eisenberg 1980). However, it is estimated that areas in excess of 10^6 km² are required for mammals 50 kg and larger to persist through evolutionary time (i.e., 10^5 to 10^6 years) (Belovsky 1987). This estimate assumes a scenario of no major climatic change. It is clear that bears will never regain the vast expanses in which they evolved, so it is vital for us to ensure that the remaining populations have large enough areas of appropriate habitat. Yet, it is also apparent from the size of the home ranges of most species of bears (Table 2) and the minimum population sizes required to maintain an adequate genetic pool that large geographic areas will be required if bears are to survive. Solution of this dilemma will require creative thinking. Somehow, we will need to delineate and manage large areas of the most optimal remaining wild and semi-wild habitat for a variety of equally important priorities, one of which is the conservation of large carnivores, including bears.

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