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26

Grizzly Bear

Ursus arctos

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NOMENCLATURE

COMMON NAMES. Brown bear, grizzly bear, Kodiak bear
SCIENTIFIC NAME. *Ursus arctos* Linnaeus

The grizzly bear inspires fear, awe, and respect in humans to a degree unmatched by any other North American wild mammal. Like other bear species, it can inflict serious injury and death on humans and sometimes does. Unlike the polar bear (*Ursus maritimus*) of the sparsely inhabited northern arctic, however, grizzly bears still live in areas visited by crowds of people, where presence of the grizzly remains physically real and emotionally dominant. A hike in the wilderness that includes grizzly bears is different from a stroll in a forest from which grizzly bears have been purged; nighttime conversations around the campfire and dreams in the tent reflect the presence of the great bear. Contributing to the aura of the grizzly bear is the mixture of myth and reality about its ferocity, unpredictable disposition, large size, strength, huge canines, long claws, keen senses, swiftness, and playfulness. They share characteristics with humans such as generalist life history strategies, extended periods of maternal care, and omnivorous diets. These factors capture the human imagination in ways distinct from other North American mammals. Precontact Native American legends reflected the same fascination with the grizzly bear as modern stories and legends (Rockwell 1991).

Dominance of the grizzly in human imagination has played a significant role in the demise of the species. Conquest of the western wilderness seemed synonymous with destruction of the great bear. The challenge of the twenty-first century is to avoid repeating and attempt to correct the errors of the nineteenth and twentieth centuries.

Ursus arctos is widely distributed throughout the Palearctic (Europe and Asia) and Nearctic (North America) faunal regions. In the Palearctic, *U. arctos* is commonly referred to as the brown bear, whereas in North America it is called the grizzly bear in the lower 48 states and most of Alaska. Typically only the coastal populations of Alaska or those in Canada are referred to as brown bears. Here, we use the terms interchangeably recognizing that there is only one species with different common names. The grizzly bear is one of eight species of bears distributed worldwide, and one of six members of the genus *Ursus*. The brown/grizzly bear occupies a diverse array of habitats, from arctic tundra, to boreal and coastal forests, to the mountain forest/grassland ecotone. Classified as an omnivorous carnivore, its diet varies widely over its North American range. To a large degree, abundance of high-quality foods dictates body size, reproductive rates, and population density. Human influences on the landscape continue to alter once pristine habitats to the detriment of grizzly bears. Habitat degradation and losses coupled with human-caused mortality are the major conservation issues the species has faced historically and continues to face today.

Subspecies. By necessity, early classification relied heavily on paleontological and morphological data, but such classifications of ursids were inconclusive at best (Kurtén 1968; Kitchener 1994; Waits et al. 1999). Merriam (1918) proposed over 90 subspecies that described the geographic variants of *U. arctos*, but this classification is considered obsolete (Waits et al. 1998a). As summarized by Craighead and Mitchell (1982) and Waits et al. (1998a), Rausch (1963) identified two extant subspecies of brown bears in North America primarily from skull measurements. He classified bears from the mainland as *U. arctos horribilis* Ord and those from the Kodiak Island archipelago as *U. a. middendorffi* Merriam. Rausch (1963) reconsidered his earlier classification (Rausch 1953) of the bears from the Alaska Peninsula as being a distinct subspecies (*U. a. gyas* Merriam). Kurtén (1973) used skull measurements from Rausch (1963) to propose three North American subspecies, *U. a. middendorffi* from Kodiak Island archipelago, *U. a. dalli* Merriam of southern coastal regions of the Alaska panhandle, including the islands of Admiralty, Baranof, and Chichagof (ABC), and *U. a. horribilis* for all other brown bears. Finally, Hall (1984) used cranial and dentition dimensions to propose seven North American subspecies. Five were restricted to Alaska: (1) *U. a. middendorffi* (Kodiak islands), (2) *U. a. gyas* (Kenai Peninsula), (3) *U. a. dalli* (northwest panhandle), (4) *U. a. sitkensis* Merriam (southeast Alaska including ABC islands), and (5) *U. a. alascensis* Merriam (the remaining mainland). The subspecies *U. a. stikeenensis* Merriam was restricted to coastal British Columbia, Washington, and Oregon, and *U. a. horribilis* included all inland brown bear populations in Canada and the lower 48 states. The generally accepted current classification is that proposed by Rausch (1963), but this is likely to change based on DNA analysis.

With the advent of DNA analysis and the technological advancements in this field, we now know considerably more about evolution of ursids and subspecific classification within species (Waits et al. 1999). Using mitochondrial DNA (mtDNA) of brown bears across their geographic range, several researchers have defined five mtDNA lineage groups defined as clades (Cronin et al. 1991; Taberlet and Bouvet 1994; Kohn et al. 1995; Randi et al. 1995; Taberlet et al. 1995; Talbot and Shields 1996; Waits et al. 1998a). Clade I brown bears are from southern Scandinavia and southern Europe; Clade II are from the ABC islands; Clade III are from eastern Europe, Asia, and western Alaska; Clade IV are from southern Canada and the lower 48 states; and Clade V are from eastern Alaska and northern Canada (Fig. 26.1).

The mtDNA phylogeny does not support any of the historic taxonomic classifications (Waits et al. 1998a). There is no support for *U. a. middendorffi*, *U. a. horribilis*, or *U. a. gyas*. The classification by Kurtén (1968) and Hall (1984) of bears from the ABC islands and adjacent mainland probably is incorrect. Brown bears from the ABC islands constitute the oldest and most genetically unique mtDNA clade in the New World and are a sister taxa to the polar bear (Talbot and Shields 1996; Shields et al. 2000). However, as stated by Waits et al. (1998a:415), "a revision of the taxonomy of North American brown bears in accordance with the phylogenetic species concept (Cracraft 1983) would result in drastic changes in the current classification. The most frequently recognized subspecies, *U. a. middendorffi*, would be abolished, and 4 new subspecific distributions would be added. But it seems unreasonable to dramatically alter the current taxonomy based on the results from a single mtDNA region." Additional research using

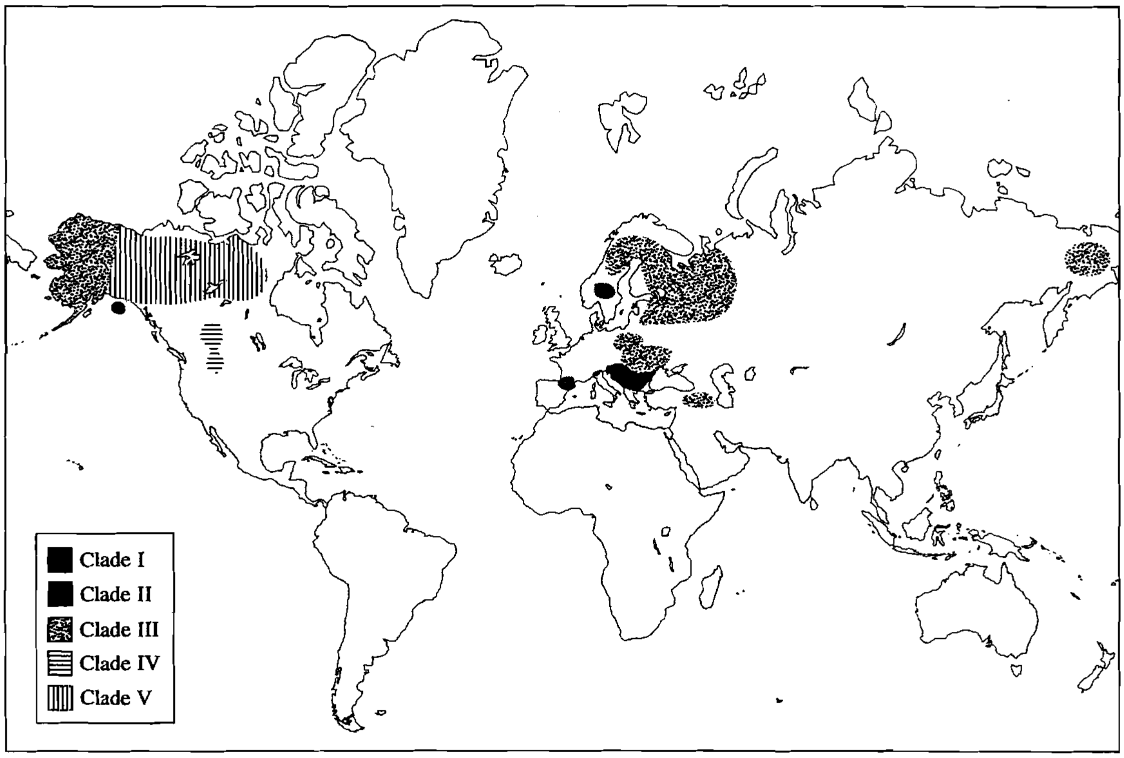

FIGURE 26.1. Worldwide geographic distribution of the five mitochondrial phylogenetic clades in the brown/grizzly bear. SOURCE: After Waits et al. (1999).

additional genes, particularly from the Y chromosome, is needed for taxonomic clarification (Waits et al. 1998a).

Evolution. Thenius (1959) and Kurtén (1968) provided much of the original paleontological work on the Ursinae. Herrero (1972), Martinka (1974), and Craighead and Mitchell (1982) provided excellent summaries, which we paraphrase here. All living and fossil bears of the genus *Ursus* descended from *U. minimus*, a small, forest-dwelling bear of the Pliocene. The grizzly bear differentiated from the Etruscan bear (*Ursus etruscus*) in Asia during the middle Pleistocene (2–3 million years ago). The earliest records of *U. arctos* are from about 500,000 years ago from Choukoutien, China. The species entered Europe some 250,000 years ago during formation of glacial land bridges (Pasitschniak-Arts 1993). Speciation occurred during a period of extensive glaciation in northern continental areas. Forests were replaced with tundra, and adaptation to these open habitats was a key element associated with genetic separation of the grizzly from its forest-dwelling ancestors (Herrero 1972). Steppe and tundra forms dominated late dispersal, and it appears that the grizzly did not successfully colonize Alaska until the Wisconsin glacial period (Herrero 1972). Recession of the continental ice sheets allowed expansion into most of North America by the early Holocene (Martinka 1974).

DISTRIBUTION

Historical Range. Following recession of the ice sheets, *Ursus arctos* was widely distributed across North America (Fig. 26.2). Distribution expanded eastward to Ontario (Peterson 1965) and Ohio and Kentucky (Guilday 1968), and southward to Mexico (Storer and Tevis 1955). The range possibly extended northeast as far as Labrador (Speiss 1976; Speiss and Cox 1977). Distribution apparently receded following this eastward expansion in response to unfavorable environmental conditions (Guilday 1968).

Before European settlement of the North American continent, the brown bear had a wide distribution (Roosevelt 1907; Wright 1909; Dobie 1950; Storer and Tevis 1955; Herrero 1972; Stebler 1972;

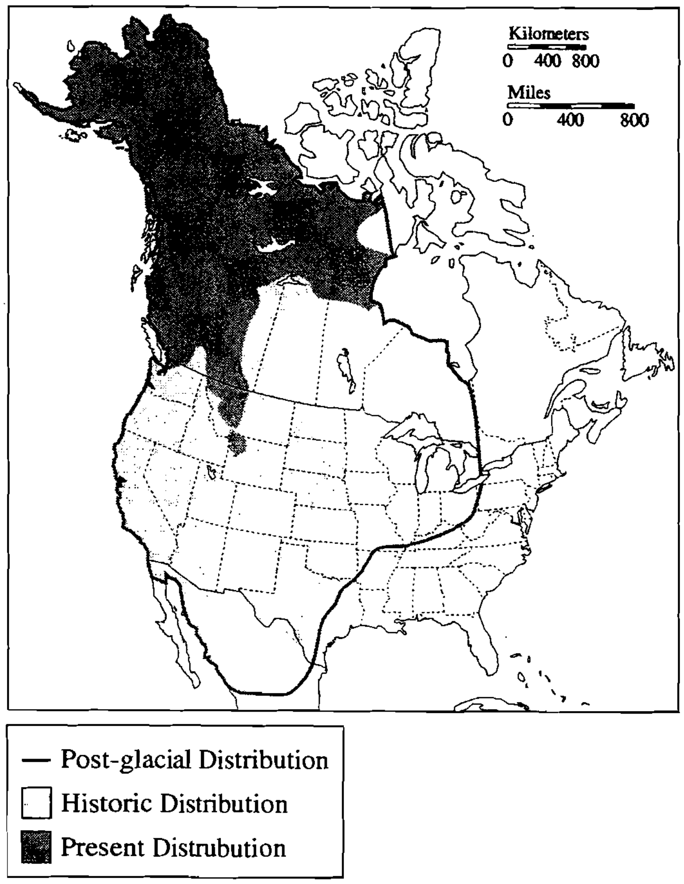

FIGURE 26.2. Postglacial, historical, and current distribution of the brown/grizzly bear. SOURCE: Data from Rausch (1963), Martinka (1976), Servheen et al. (1999).

TABLE 26.1 Estimated characteristics of grizzly bear populations in North America, with sample sizes in parentheses

Study Area	Density (Bears/100 km^2)	Litter Size	Reproductive Interval[a]	Age at First Litter (years)	Weight (kg) Adult Male	Weight (kg) Adult Female	Cub Mortality Rate	Percent Adult Male[a]	Hunted?
Interior population									
East Front Montana	0.7	2.2 (41)	2.6 (11)	6.0 (4)	—	125	—	54	Yes
Flathead	8.0	2.2 (26)	3.1 (17)	6.1 (7)	176 (22)	114 (16)	0.18	37	Yes
Eastern Brooks	0.4	1.8 (13)	—	—	179 (26)	108 (31)	—	49	Yes
Alaska Range	1.5[b]	2.2 (36)	4.2[c] (38)	7.6[c] (8)	224[d] (24)	135[d] (32)	0.29	33	Yes
Nelchina	1.0	2.1 (64)	3.8[c] (44)	5.6[c] (24)	269[d] (12)	144[d] (21)	0.30	27[e]	Yes
Tuktoyaktuk	0.4	2.3 (18)	3.3[c] (8)	6.4[c] (10)	195 (16)	124 (36)	—	33	Yes
MacKenzie Mountains	1.2	1.8 (6)	3.8 (5)	—	148 (20)	110 (28)	—	—	Yes
Glacier National Park	4.7	1.7 (35)	—	—	—	—	—	—	No
Yellowstone 1959–1970	—	2.2 (173)	3.2 (68)	5.7 (16)	245 (33)	152 (72)	0.26	46	No
Yellowstone 1975–1989	—	1.9 (232)	2.6 (20)	5.7 (23)	193 (65)	134 (63)	0.15	55	No
Western Brooks	2.4	2.0 (6)	4.1[c] (16)	7.9[c] (14)	182 (26)	117 (35)	0.44	42	No
Kluane Park	3.7	1.7 (11)	—	7.7 (7)	145 (26)	98 (16)	—	—	No
Northern Yukon	2.8	2.0 (6)	4.0[c] (4)	7.0[c] (3)	173 (59)	116 (35)	—	51	No
Coastal population									
Kodiak Island	28.0	2.5 (29)	4.6[c] (41)	6.7[c] (12)	312 (10)	202 (16)	0.37	38	Yes
Alaska Peninsula	18.4	2.3 (200)	3.0 (81)	4.4 (9)	357 (21)	226 (63)	0.40	28	Yes
Admiralty Island	40.0	1.8 (32)	3.9 (7)	8.1 (7)	260 (10)	169 (18)	0.20	—	Yes
McNeil Sanctuary	—	2.2 (137)	3.8 (37)	6.5 (11)	257	160	0.31	55	No

SOURCE: Adapted from McLellan (1994).

NOTE: Cautious interpretation is necessary because variables have been collected in different ways among studies.

[a] Due to a variety of methods used in their derivation, comparisons must be done cautiously.

[b] The original estimate was for bears > 1 year old. This value was adjusted to all bears by multiplying by 1.3 (Miller 1988).

[c] Includes incomplete intervals and births.

[d] Spring-only weights and adjusted by 1.28 for females and 1.24 for males.

[e] Adult sex ratio changed from 53% to 27% male during the study period due to intensive harvests.

these bears lost about 32% (±10%) of their body weight. These results are comparable to those in a study of captive nonlactating (335 g/day) and lactating (490 g/day) brown bears of similar mass (Farley and Robbins 1995). Weight loss during winter was highly variable for grizzly bears in a northern Northwest Territories study (Nagy et al. 1983b). Total weight loss during the denning period averaged 190 g/day during a 256-day period for two adult males (24% of body mass), but only 20 g/day for the same time period for a subadult male (5% of body mass). Five adult females lost on average 180 g/day over a 249-day period (30% of body mass) and subadult females lost 100 g/day (34% of body mass). Pearson (1975) documented an average of 200 g/day loss over a 220-day period in four grizzly bears in the southern Yukon. These animals lost 28–43% of their fall mass during the denning period.

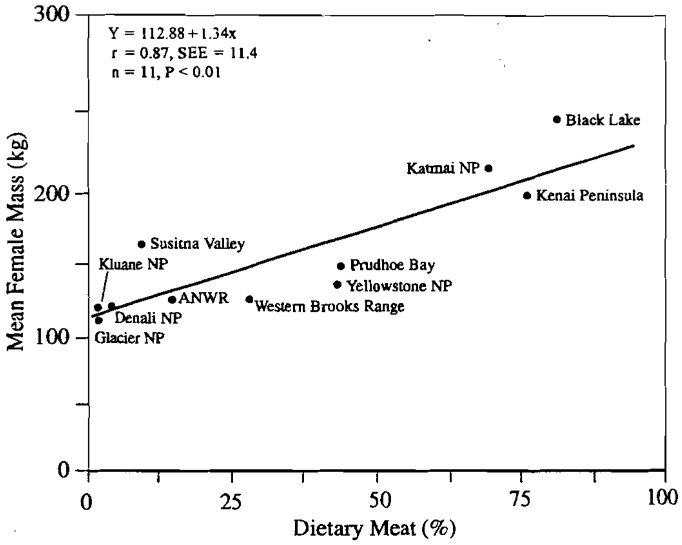

FIGURE 26.3. Body mass of adult female brown bears and the amount of meat in the diet. SOURCE: Data from Hilderbrand et al. (1999a).

Depending on availability and quality of spring forage, bears can continue to lose body mass until resources improve (Troyer and Hensel 1969; Craighead and Mitchell 1982; Blanchard 1987). Weight increases rapidly in the fall. Pearson (1975) measured a 410 g/day gain for a 126-day period for an adult male and a 640 g/day gain over 16 days for a subadult female in August.

Bears continue to grow throughout their life, but the sexes grow differently. Kingsley et al. (1983) fitted growth curves to age-specific data from spring and fall captures from northern Canada (Fig. 26.4). Although the curves are specific to that area, they illustrate general patterns in grizzly bear growth, seasonal weight dynamics, and the magnitude and allocation of weight gain through life. In that area, males took nearly 14 years to reach 95% of their maximum weight, whereas females required 9 years. The maximum rate of increase in basal weight was similar for the two sexes. When females divert resources into reproduction, they stop growing. Fall weight of males is related to spring weight, but increases approximately 28%; winter maintenance is remarkably constant at 22% (Fig. 26.5). Weight gain more than triples during the first summer, and declines continuously thereafter. Mature females cycle more weight than males, both relatively (Fig. 26.5) and absolutely (Fig. 26.6). Gain and loss in females continues to increase through maturity, until the oldest females cycle 70% of their spring weight. The relative gain and loss of weight in females exceeds that for males from the age of first reproduction onward. Females have greater weight fluctuations than males because females must expend energy in gestation and lactation (Kingsley et al. 1983). Several researchers (Troyer and Hensel 1969; Glenn 1980; Nagy et al. 1984; Blanchard 1987; Kingsley et al. 1988) established similar relationships of various body measurements with age and weight.

Pelage. Throughout their range, brown bears vary from light blond to black (LeFranc et al. 1987). Many specimens have silver or cream tipping on the guard hairs, creating a grizzled appearance; hence the origin of the name grizzly bear. Cubs in their first year are typically with blond to white guard hairs on the head, shoulders, and back; legs are darker. Russell et al. (1978) considered about half the grizzlies in Jasper National Park as brown, with some yellowish tinge on the sides and back. The rest have prominent blond, yellow, or silver-tipped guard hairs on the sides, back, and neck. Heads are brown to yellow, the hump is darker than the head, and the legs are darker yet. In the Yukon, Pearson (1975) classed about 75% of the brown bears as brown, mostly chocolate, with grizzled silver or yellow guard hairs. The rest are blond to yellow, usually with a dorsal stripe along the back, and darker legs.

Knight et al. (1981) reported five major color patterns in pelt characteristics of Yellowstone grizzlies. The most prevalent have medium to dark brown underfur; brown legs, hump, and underparts; light to medium grizzling on the head and part of the back; and a light-colored girth band or patch behind the forelegs. Other patterns include (1) an overall gold or silver appearance and brown underparts, with an occasional dark back stripe; (2) no distinct silver tipping, giving a general black or brown appearance; and (3) medium to dark brown underfur, rump, legs, and hump, with medium to heavily grizzled forequarters and face. Subadults often appear multicolored with various shadings of red, blond, brown and great variation in silver tipping. Light-colored "yolks" on the chest and dark stripes on the back are common. These patterns fade as the bear matures into one of the four patterns described in adults.

Molt. Latitude, sex, and age influence molting of hair in the brown bear. Brown bears replace their hair annually. In general, adult males begin to molt first, followed by young males and other lone individuals; females with dependent young molt last (Pearson 1965, 1975; Quimby and Snarski 1974; Nagy et al. 1983a). Molt is generally complete by late July or August. Color, color pattern, and general appearance change markedly over time (Pearson 1965, 1975; Quimby and Snarski 1974; Nagy et al. 1983a). Quimby and Snarski (1974) found that dark-colored bears predominated in spring and fall, whereas lighter colors predominate during summer. They attributed these trends to differences in timing of emergence, sex-specific differences in color, bleaching, and observability. Rausch (1953) and Troyer and Hensel (1969) examined spring hides with rub marks, suggesting that molting may begin at emergence from dens; they noted substantially less rubbing in the fall.

Skull and Dentition. The skull of the brown/grizzly bear is highly variable across the North American range. It is stout and heavy (Fig. 26.7) and sexually dimorphic (Merriam 1918; Rausch 1953, 1963; Kurtén 1973; Craighead and Mitchell 1982; Pasitschniak-Arts 1993). Records of skull measurements from dead bears (Byers and Bettas 1999) provide potential maxima for the species. The largest skull length and width recorded for the Alaskan brown bear are 45.56 and 32.54 cm, respectively.

The skull grows and changes in dimension throughout life. Cubs have an oval-shaped skull, which lengthens during the active growth phase and reaches standard configuration at sexual maturity (Zavatsky 1976). Condylobasal length and zygomatic width are frequently measured skull characteristics, with the later continuing to increase after length is attained (Rausch 1963). Rausch (1963) presented the most comprehensive study comparing skull morphology throughout North America. Variation in mean condylobasal length is clinal with an increasing gradient along the coastal zone from British Columbia to the end of the Alaska Peninsula. A similar gradient was evident along the Arctic Coast. Bears from the interior are smaller.

The dental formula is I 3/3, C 1/1, P 4/4, M 2/3 (LeFranc et al. 1987; Pasitschniak-Arts 1993), however, some premolars can be missing (Glass 1974). Craighead and Mitchell (1982) incorrectly reported the dental formula for molars as 3/2. The skull of *U. arctos* can be distinguished from that of *U. americanus* based on molar measurements. The most accurate method (Gordon 1977) separates brown bears from black bears based on the first mandibular molar (M_1). A crown length greater than 20.4 mm or width greater than 10.5 mm indicates *U. arctos;* smaller measurements indicate *U. americanus*. This method showed no overlap for the two species in a sample of 128 skulls of all ages and both sexes. Grinnell et al. (1937) and Storer and Tevis (1955) separated the species based on the greatest crown length of maxillary molar 2 (M_2); it is seldom <38 mm in *U. arctos*, and seldom >31 mm in *U. americanus*.

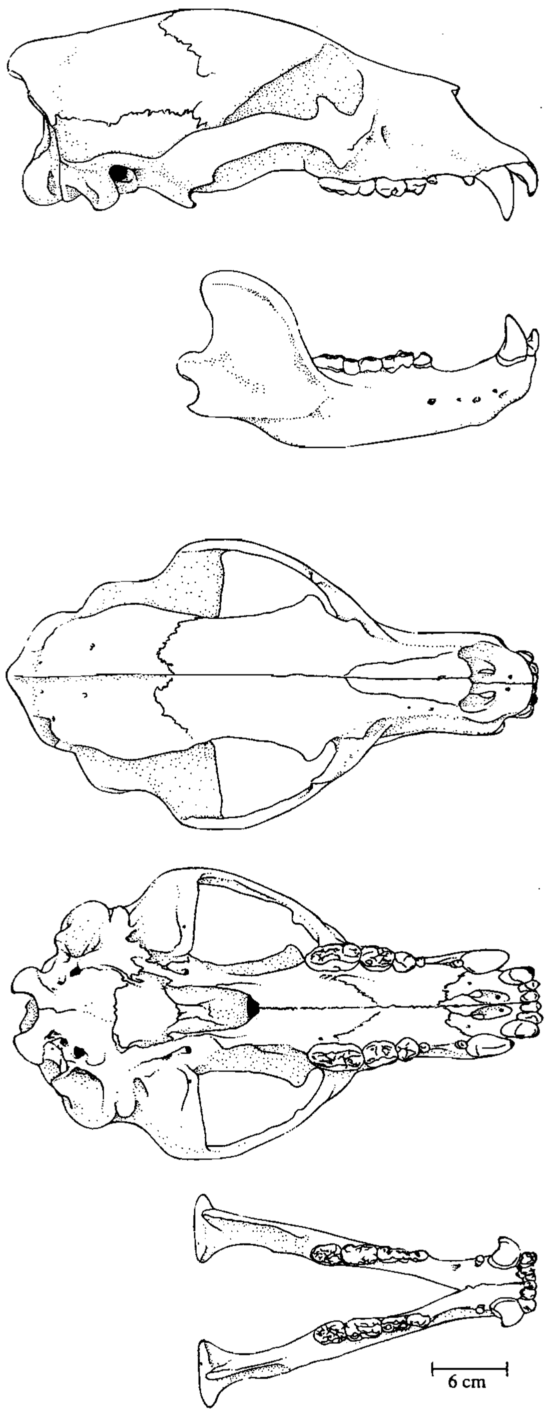

FIGURE 26.7. Skull of the brown/grizzly bear (*Ursus arctos*). From top to bottom: lateral view of cranium, lateral view of mandible, dorsal view of cranium, ventral view of cranium, dorsal view of mandible.

GENETICS

The six ursine bears (sun bear, *Helarctos malayanus;* American black bear; Asiatic black bear, *Ursus thibetanus;* brown bear; polar bear; and sloth bear, *Melursus ursinus*) have a nearly identical karyotype with populations. These factors are linked to body size, which depends on nutrition (Stringham 1990; Hilderbrand et al. 1999a). The brown bear has a low reproductive rate relative to other mammals, a trait that critically affects survival in the presence of humans (Pasitschniak-Arts 1993; J. J. Craighead et al. 1995).

Early research into the reproductive biology of the species was based on field observation and examination of reproductive tracts from dead specimens (Craighead and Mitchell 1982). With the advent of radiotelemetry, biologists have been able to follow individual females through several breeding cycles. Such studies have provided more accurate insight into reproduction of the species and inherent variation among populations. Estimates of male reproductive success are possible with the development of DNA fingerprinting techniques (F. L. Craighead et al. 1995).

Breeding Season. The breeding season is narrowly defined as that period when copulation occurs, or more inclusively the period of male–female consorting, plus pre- and postcopulatory behavior (LeFranc et al. 1987). Variations among populations in breeding season chronologies are influenced by definition, length of study, numbers of observations, habitats, and biological differences among areas. However, it is nearly impossible to determine the exact date of conception under natural conditions, so no studies provide such detailed information. Data compiled from 20 different study sites across North America suggest that, on average, the breeding season (broadly defined) begins around mid-May and ends in early-July (Fig. 26.8).

J. J. Craighead et al. (1995) provided detailed breeding data from Yellowstone National Park during an 8-year period. Earliest date of observed copulation was 18 May and latest was 11 July, a period of 55 days. The period of observed copulation in any given year averaged 29 days with a range of 17–45 days. They predicted a mating season of approximately 63 days. Dittrich and Kronberger (1963) reported a mating season of approximately 72 days from captive brown bears. The earliest recorded date from the 20 North American studies (Fig. 26.8) was 21 April (courtship association), whereas the latest recorded was early August (breeding pairs). Average time between recorded start and end dates for the 20 reported studies was 49 days, with a minimum and maximum time for any one study of 25 and 92 days, respectively.

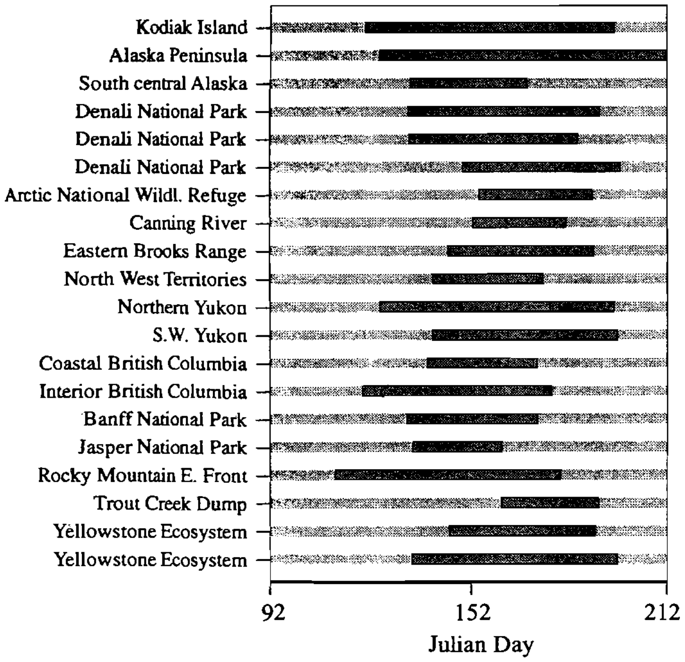

FIGURE 26.8. The period of male–female association, breeding plus postcopulatory association, for grizzly bear populations. Julian days 92 and 213 are the first day of April and last day of July, respectively. SOURCE: Data from LeFranc et al. (1987), Table 7.

Copulation. Copulation by grizzly bears is vigorous and prolonged (Craighead and Mitchell 1982). Vigor of the male, receptivity of the female, and privacy of the event (J. J. Craighead et al. 1995) influence duration. Probably the best data set available on observed copulation comes from Yellowstone National Park during the mid-1960s, when the open-pit garbage dumps were still operating (J. J. Craighead et al. 1969, 1995). The mean duration of 64 successful copulations (≥ 10 min) was 24.3 min, with more than half being <24 min; the longest observed was 60 min.

Brown bears are promiscuous. Females mate with multiple males and may have a litter with offspring sired by different males; males can sire litters with multiple females in a breeding season (F. L. Craighead et al. 1995, 1998). Dominant males attempt to sequester a receptive female during her estrous period (Hornocker 1962; Herrero and Hamer 1977; Hamer and Herrero 1990; Brady and Hamer 1992). Plasticity is associated with this reproductive behavior. Mating can occur at concentrated food sources (Glenn et al. 1974; J. J. Craighead et al. 1995) or in poor-quality foraging sites (Herrero and Hamer 1977; Hamer and Herrero 1990; Brady and Hamer 1992). Pair bonds can last several weeks (Murie 1944; Herrero and Hamer 1977; Hamer and Herrero 1990) or may last only a few hours (Craighead et al. 1969). Females may enter estrus (defined here as the period of sexual receptivity) more than once (Dittrich and Kronberger 1963; Reynolds and Hechtel 1984; Reynolds 1989, 1992; J. J. Craighead et al. 1995). Not all breeding results in cub production the following spring, particularly in subadult females (Craighead and Mitchell 1982; J. J. Craighead et al. 1995).

Age at Puberty. Age of first litter production in brown bears varies widely geographically (LeFranc et al. 1987; Blanchard 1987; Stringham 1990; McLellan 1994), and is related to age at maturation and body size (Blanchard 1987; Stringham 1990), which is positively related to diet quality (Hilderbrand et al. 1999a) (Table 26.1). Nagy and Haroldson (1990), however, cautioned against interpreting body size–habitat relationships in the absence of information on population density. Age at first conception is estimated in brown bears by following subadult females through their first litter production. Age is generally determined from tooth sectioning, but in some cases can include known-age animals. However, the conventional method for calculating age of first conception, using only bears whose first litters are observed, gives a low-biased estimate (Garshelis et al. 1998). Cub production can be detected by actual observation of offspring or indirectly by examination of condition of mammae or ovarian structures (Stringham 1990).

Female brown bears do not reach sexual maturity until 3.5 years old (Hensel et al. 1969; Ballard et al. 1982; Craighead and Mitchell 1982; Aune et al. 1994), with some females producing first litters at age 4. In Yellowstone National Park, for example, from a sample of 15 females observed long enough to produce their first litters, 7, 5, 2, 0, and 1 produced first litters at age 5, 6, 7, 8, and 9 years of age, respectively. Mean age of first litter production from this sample was 5.9 years (J. J. Craighead et al. 1995). Mean age at first litter production varies from as low as 4.4 years for a growing population on the Alaska Peninsula (Miller and Sellers 1992) to as high as 8.1 years on Admiralty Island (Schoen and Beier 1990) (Table 26.1).

Litter Size. The number of cubs varies among individuals and populations but is typically one to three/litter. Litters of four are rare (Onoyama and Haga 1982; Bunnell and Tait 1985; Wilk et al. 1988; Sellers and Aumiller 1994; Case and Buckland 1998), but litters as large as six (Wilk et al. 1988) have been documented. However, adoption and/or exchange of cubs among different maternal females has been observed (Erickson and Miller 1963; Glenn et al. 1974; Barnes and Smith 1993), making empirical documentation based on field observations difficult. Mean litter size has been correlated with adult female body mass; intake of dietary meat, primarily salmon and ungulates (Bunnell and Tait 1981; Stringham 1990; McLellan 1994; Hilderbrand et al. 1999a); and garbage (Stringham 1986). Litter size also has been related to latitude (Bunnell and Tait 1981; Stringham 1984), climate, and a climate-carrion index (Picton 1978; Picton and Knight 1986); there are exceptions (Wielgus and Bunnell 2000). Litter size also is age related, with needs for the next denning cycle, they tend to concentrate their activity seasonally in the most productive habitats available.

On the north slope of Alaska and the barren grounds of northern Canada, brown bears occupy a treeless landscape. In the central arctic, esker complexes and riparian tall shrub habitats were preferred by bears throughout the year (McLoughlin 2000). Bears in these regions rely extensively on herbaceous plants, roots, and berries when seasonally available (Gebhard 1982; Hechtel 1985; Phillips 1987). Meat from scavenging or predation on caribou (*Rangifer tarandus*), ground squirrels, and microtines also is seasonally important (Nagy et al. 1983b; Hechtel 1985; Phillips 1987; Gau 1998).

In Alaska and British Columbia, bears use a variety of habitats including old-growth forests, coastal sedge meadows, and south-facing avalanche slopes. During early summer, most bears use alpine and subalpine meadows. From midsummer through early fall, they move to coastal habitats and concentrate along streams to feed on spawning salmon (LeFranc et al. 1987; Schoen et al. 1994). Not all bears follow this typical pattern of habitat use; some do not visit salmon streams (Schoen et al. 1986), but remain in high-elevation habitats throughout the year. Mace and Waller (1997) observed that habitat selection often varies among individuals, even in an environment that appears consistently similar to humans. During late fall, bears alternately fish or use berry-producing habitats (LeFranc et al. 1987; Schoen et al. 1994).

Grizzly bears in the northern Rocky Mountains rely on a fairly predictable sequence of habitats that provide seasonally available forage. Seasonal habitats are often separated into (1) a spring/early-summer preberry period, when bears forage on a variety of locally available graminoids, forbs, and roots; and (2) a summer/early-fall berry-producing period when bears fatten on locally available berry corps (LeFranc et al. 1987; Mace and Waller 1997; Herrero et al. 2000). During spring, bears are generally in lower elevation habitats eating emergent vegetation and winter-killed ungulates. During late spring, they move to higher elevations following the phenological advance of vegetal foods. During summer, bears move to lower sites to exploit habitats with early-ripening berry crops. They repeat their altitudinal movements, following the ripening fruits to higher elevations during early fall (Darling 1987; Hamer and Herrero 1987; Mace and Waller 1997).

In the Greater Yellowstone Ecosystem (GYE), the pattern of seasonal elevation use is similar to that found for other populations occupying interior western mountains (Mealey 1980). During the spring, grizzly bear use of ungulates, both scavenged and as neonate prey, is extensive (French and French 1990; Gunther and Renkin 1990; Green 1994). The annual percentage of energy obtained from ungulate meat is considerably higher in the GYE than for other interior populations (Hilderbrand et al. 1999a). Use of ungulates abates during summer as bears use habitats that supply a variety of graminoids, forbs, and root crops (Mattson et al. 1991a). Yellowstone lacks significant berry-producing habitats. Consequently, bears use high-elevation sites to feed on whitebark pine (*Pinus albicaulis*) nuts (Blanchard and Knight 1991; Mattson et al. 1991a) and army cutworm moths (*Euxoa auxiliaris*) at insect aggregation sites (Mattson et al. 1991b; French et al. 1994).

In much of Alaska and northern Canada, habitats occupied by the grizzly bear are not significantly altered by humans. However, in the contiguous 48 states and some portions of southern Canada, most of the productive lands are dominated by humans. As a result, grizzly bear populations are relegated to "what's left," which usually constitutes the most remote and rugged mountainous areas; these may not represent what historically were "the best" habitats (Craighead and Mitchell 1982; Gibeau 1998). For bear populations in these areas, human settlement and alteration of the landscape limits habitat choices.

Home Range and Movements. Since 1970, movements and patterns of landscape use by brown bears have been investigated throughout North America (LeFranc et al. 1987). Movement patterns can be extremely variable within and among populations of brown bears. Movements are influenced by many factors, including key food items, breeding, reproductive and individual status (i.e., dominance), security, and human disturbance. Such factors dictate the pattern and extent of the landscape used throughout a season, a year, and the life of an individual, and define its home range (Burt 1943). It is generally believed that animals establish home ranges because it is more efficient to exploit familiar rather than unfamiliar areas (McLellan 1985).

Boulanger and White (1990) observed that use of different home range estimators could produce confusion in interpretation due to differences among the estimators themselves and not the behavior of the animal being studied. For brown bears, differences may also be influenced by sample size, which is typically small for wide-ranging bears (Nagy and Haroldson 1990). Most authors reporting brown bear home ranges used Mohr's (1947) minimum convex polygon method (Table 26.2); some lack sufficient locations to accurately estimate true home range size because the polygon method is sensitive to sample size (Gustafson and Fox 1983; Bekoff and Mech 1984).

More recently, kernel estimators (Worton 1989) have been employed to estimate home range extent for grizzly bears, with more attention paid to the adequacy of sample sizes (Blanchard and Knight 1991; Holms 1998; McLoughlin 2000). With the application of global positioning system technology, future knowledge of movements and range extent for brown bears will improve (Arthur and Schwartz 1999; Schwartz and Arthur 1999).

Though direct comparisons of home range statistics are difficult, several consistent patterns of grizzly bear home range size are evident. Craighead and Mitchell (1982) suggested that movements and range use by brown bears could be separated into two distinct patterns based on whether or not the population had access to high-quality food resources that concentrated individuals. Where brown bear populations have access to dependable, high-quality food resources, traditional patterns of movement to exploit them are well established. Average seasonal, annual, and life ranges for bears in these populations are typically smaller than those reported for populations that do not rely on dependable concentrated foods. For example, brown bear populations with access to rich salmon fisheries on the coast of Alaska have some of the smallest annual ranges observed in North America (Table 26.2). In contrast, annual ranges for brown bear populations in interior Alaska that do not use salmon were much larger. In the GYE, range sizes reported during years when bears were feeding extensively in open garbage dumps (Craighead 1976) were significantly smaller than those reported after dumps were closed (Blanchard and Knight 1991).

Differences in annual range size observed among study areas have generally been attributed to differences in habitat quality and distribution (Blanchard and Knight 1991). In support of this, McLoughlin et al. (1999) found a significant negative correlation between an index of primary productivity and grizzly bear home range size. However, Nagy and Haroldson (1990) speculated that social factors such as kinship, density, and population structure, all of which are influenced by turnover rates (human-caused or natural), may also affect range size observed in different regions.

Another consistent finding is that adult male bears typically have annual ranges that are several times larger than those observed for adult females (Table 26.2). This pattern usually is attributed to breeding activity of males (Blanchard and Knight 1991) or increased energy demand due to larger body size (Harested and Bunnell 1979; McLoughlin et al. 1999). Ranges of adult males overlap those of several females. During the 13-year study conducted by Blanchard and Knight (1991), multiannual or life ranges for most adult male bears did not plateau over time, but increased annually with additional radiotracking. Multiannual ranges of females were more likely to plateau at some maximum size (Blanchard and Knight 1991).

Seasonal ranges for specific sex and age classes of bears can be very restricted. Spring and early-summer ranges of females with cubs are often the smallest (Pearson 1975; Russell et al. 1979; Aune and Kasworm 1989; Blanchard and Knight 1991). This is attributed to the lack of mobility of young cubs and/or the need for security of cubs to reduce intraspecific predation. Sizes of late-summer and fall ranges, which coincide with the hyperphagic period of intense foraging (Nelson et al. 1983b), are usually more variable where key fall foraging opportunities are temporally and spatially unpredictable.

TABLE 26.3. Chronology of denning for brown bears in North America

Location	Latitude (°N)	Who Dens?	Denning Period[a]									
			Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June
NW Alaska	68	All		ooo•	oooo	++++	++++	++++	++++	++oo	o•o	
Central Alaska	62	All	o	o•oo	o+++	++++	++++	++++	++++	+ooo	•ooo	o
SE Alaska	57	All		oo•	oooo	oo++	++++	++++	+++o	oooo	•ooo	
NE Kodiak Island	57	Not all adult males		oo	•ooo	oooo	++++	++++	++oo	oooo	•ooo	oooo
SW Kodiak Island	57	All		oo	ooo•	oooo	++++	++++	oooo	oooo	•ooo	oooo
Banff NP, Alberta	52	—			oo++	++++	++++	++++	+++o	oo		
NW Montana	48	All			o•o	++++	++++	++++	+++o	o•o		
NW Montana	48	All		ooo	•ooo	o+++	++++	++++	+ooo	•ooo	oo	
Yellowstone NP	44	All		o	o•++	++++	++++	++++	++++	oo		
Yellowstone NP	44	All	o	oooo	o•oo	ooo+	++++	++oo	ooo•	oo		

SOURCE: Adapted from Linnell et al. (2000).

[a] Each month is divided into four quarters. Shown are (•) the quarters containing the average entrance and emergence dates, (o) the range of quarters in which bears began to den or emerge, and (+) the quarters during which all bears were denned.

and presumably conserving energy by entering a constructed or natural cavity, and hibernation as physiological adaptations that allow bears to survive for several months without food or water. This same distinction can logically apply to brown bears. Thus, as a necessary prerequisite to the behavioral aspects of denning, brown bears must first attain a hibernating physiology.

Physiologically, North American black, grizzly, and polar bears are true hibernators (Folk et al. 1976; Hellgren 1998). This condition allows bears to go up to 7 months without eating, drinking, defecating, or urinating (Folk et al. 1976; Nelson 1980). Yet female bears can support fetal development and lactation, as young are born in midwinter during the denning period (Nelson 1973). Unlike other true hibernators such as ground squirrels, bears can be aroused almost instantly for defense (Nelson 1973). Nelson et al. (1983a) reported that the physiological condition is not readily and/or intermittently attained in response to fluctuating weather and suggested that a neurocircumannual cycle is involved. Bears are generally thought to be in a physiological state of hibernation well before they enter dens in the fall. This is indicated by the predenning lethargy described by Craighead and Craighead (1972) and for the period (stage II, walking hibernation) after emerging from dens in the spring (Nelson et al. 1983b). Hellgren (1998) provided a good review of literature pertaining to the physiology of hibernation in black, brown, and polar bears.

A comprehensive summary (Table 26.3) of denning chronology for brown bear populations worldwide was compiled by Linnell et al. (2000). They reported that almost all brown bear populations studied in North America exhibit denning behavior. An exception occurs on a portion of Kodiak Island, Alaska, where >25% of radiocollared male bears remained active through at least one winter of a 6-year study (Van Daele et al. 1990). These males reportedly spent much of their time bedded, intermittently traveling short distances, and appeared to be in a state of "walking hibernation" (Nelson et al. 1983b).

Food availability and weather conditions are proximal factors that influence timing of den entry among most brown bears (Craighead and Craighead 1972; Van Daele et al. 1990). Den entry and duration also are somewhat correlated with latitude; brown bears in northern latitudes enter dens earlier and remain longer than bears at more southerly latitudes (Fig. 26.9). Pregnant females generally enter dens earlier and emerge later than other sex and age classes. Males are typically the last class of brown bear to enter dens in the fall and the first to emerge in the late winter or early spring (Linnell et al. 2000). Duration of denning may be as short as several weeks for adult males or as long as 7 months for females that emerge from dens with cubs. Females that emerge from dens with cubs may loiter near the den for several weeks (Craighead and Craighead 1972; Vroom et al. 1977).

Linnell et al. (2000) also summarized den and den site characteristics for brown bear populations worldwide (Table 26.4). The typical den documented for North America brown bears is excavated (Linnell et al. 2000), often under trees where root systems provide stability for the roof. Use of natural cavities or caves as dens has been observed less frequently, but is typical in study areas where natural structures are available, such as southeastern Alaska (Schoen et al. 1987). Van Daele et al. (1990:265) stated that "suitable den sites were those that remained dry throughout the denning period, and provided adequate soil depth and stability for excavation of a den or a suitable natural cavity." Thus, suitable den sites are probably not limiting in most populations of brown bears in North America; however, local exceptions may occur. Linnell et al. (2000) concluded that natural cavities were reused more often than excavated dens. Reynolds et al. (1977) and Miller (1990a) found that excavated dens in Alaska did not persist long enough for reuse to occur.

Specific sites and habitats chosen for dens are highly variable both within and among study areas, and show the considerable behavioral plasticity with regard to environmental condition exhibited by bears. Van Daele et al. (1990) concluded that brown bears likely used the most suitable denning habitat within their home range and local tradition plays a role in selection and construction. Habitats used for denning vary from open tundra to forested sites, depending on availability to local populations (Harding 1976; Vroom et al. 1977; Judd et al. 1986; Schoen et al. 1987; Van Daele et al. 1990). Selection of den sites with a

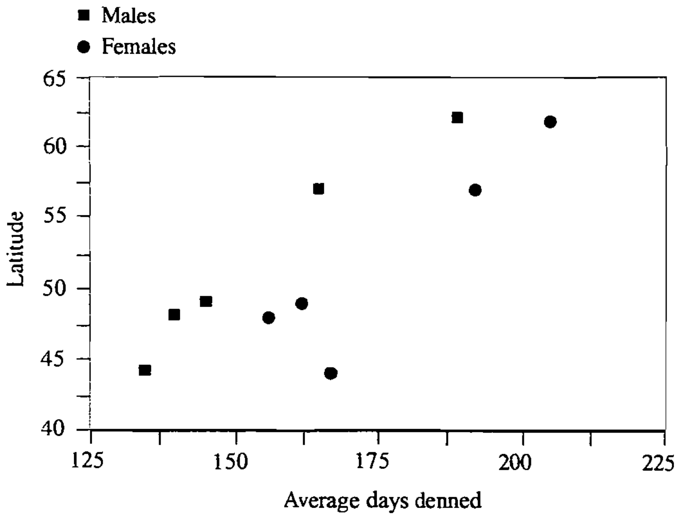

FIGURE 26.9. Average days denned relative to latitude for five interior brown bear study areas. SOURCE: Data from Aune et al. (1986), Judd et al. (1986), Schoen et al. (1987), Miller (1990a), Mace and Waller (1997).

diets because of the combination of their absolute energy requirements and relatively small mouth. In the wild, male bears are more carnivorous than females (Jacoby et al. 1999). Meat eating by adult males provides the necessary calories to maintain a large body size, which leads to sexual dimorphism (Hilderbrand et al. 1999a).

Due to high digestibility and energy content, animal matter is arguably a highly valuable bear food (Welch et al. 1997; Hilderbrand et al. 1999a). However, a bear's ability to acquire these foods may be compromised by its size, its status in the social order, or the needs of its dependent offspring. Bears are most successful when feeding on animals that are abundant and vulnerable to their predatory skills. Bears inhabiting the coastal regions of Alaska and British Columbia commonly feed on spawning salmon, often centering their activities at falls, where upstream movement of fish is impeded. Under these circumstances, bears can be quite efficient predators. Many bears have access to this high-quality food for nearly the entire active season because of extended availability afforded by sequential runs of several salmon species. At Karluk Lake, Alaska, brown bears killed up to 79% of salmon migrating upstream (Gard 1971). In other coastal areas, bears may feed on postspawning salmon with little impact on the salmon run (Clark 1957). For some interior bear populations, trout provide a high-quality seasonal food. In the GYE, an estimated 30–50 grizzly bears forage annually on spawning cutthroat trout (*Oncorhynchus clarki*) in tributary streams of Yellowstone Lake (Reinhart and Mattson 1990).

In contrast to coastal environments with anadromous fish, meat is much less available and more difficult to obtain for interior brown bear populations. Use of ungulates as prey and carrion is common and seasonally important. Following spring emergence, brown bears feed on winter-starved ungulates including caribou, moose (*Alces alces*), elk (*Cervus elaphus*), and bison (*Bison bison*). Bears can also be effective predators. In early summer, neonates are actively hunted. Moose, caribou, and elk calves are seasonally important foods (Ballard et al. 1981; Larsen et al. 1989; Gunther and Renkin 1990; Hamer and Herrero 1991; Green et al. 1997; Mattson 1997; Gau 1998). Marine mammals, rodents, and ground-nesting birds and their eggs are eaten when available (Nagy et al. 1983b; LeFranc et al. 1987).

In the southern Rocky Mountains, army cutworm moths and ladybird beetles are valuable seasonal foods (Klaver et al. 1986; Mattson et al. 1991b; White 1996). Bears forage on moths in the talus where they are vulnerable to predation. Studies from Glacier National Park (White et al. 1999) indicate that a foraging bear can consume as many as 40,000 moths/day, ingesting approximately 20,000 kcal. These insects are high in lipid content (Kevan and Kendall 1997) and represent one of the most calorie-rich foods consumed by bears (White et al. 1999). Cutworm moth aggregation sites can attract large numbers of bears (French et al. 1994), but are geographically limited in North America.

Fruits of blueberries, huckleberries, buffaloberry, devil's club, bearberry, and other species are seasonally important foods for bears throughout much of their range in North America. High carbohydrate content makes berries important summer and fall foods. When available, bears spend up to 50% of the day foraging on berries; foraging efficiency is related to fruit abundance, size, and distribution (Welch et al. 1997).

Roots, corms, and bulbs are commonly used by bears in the Rocky Mountains and interior Alaska. Roots of hedysarum (*Hedysarum* spp.) are dug in all mountainous and arctic habits of Canada and Alaska, but are not a major diet item south of Canada (LeFranc et al. 1987). Here, biscuitroot, glacier lily, and yampa are seasonally important. These foods are typically higher in starch and digestible energy than herbaceous foods. They can serve as alternate fall foods during years when berry crops fail.

Whitebark pine nuts are an important fall food wherever the species is abundant in the contiguous United States (Mattson et al. 1991a; Mattson and Reinhart 1997). Almost all seeds consumed by bears are excavated from the middens of red squirrels (Mattson and Reinhart 1997). Pine nuts are high in fat and one of the most energy-rich foods consumed by bears. When abundant, they use pine nuts to the exclusion of most other foods. Unfortunately, whitebark pine has been eliminated or significantly reduced over much of its former range by an exotic fungus, white pine blister rust (*Cronartium ribicola*) (Kendall and Arno 1990). Most stands persist in the GYE where the climate is dryer. However, even there, rust is present and spreading (Smith and Hoffman 1998).

Geophagy, the purposeful consumption of soils, has been documented in the GYE (Mattson et al. 1999a). Soils consumed were high in potassium, magnesium, and sulfur. This behavior peaked primarily during March–May and secondarily during August–October and occurred during peak consumption of ungulate meat and mushrooms. Mattson et al. (1999a) speculated that bears were consuming soils to remedy potassium deficiencies incurred during hibernation, stimulate motility, and reduce parasites and harmful bacteria in the intestines.

Anthropogenic foods (i.e., garbage, livestock feed, pet food, bird seed, human foods, garden crops, honey) are used by brown bears wherever humans and bears coexist (Herrero 1985). Open garbage dumps can be a source of highly nutritious foods when available. Use of dumps can lead to food conditioning, habituation, and increases in property damage and human-caused bear mortality. In the GYE, considerable effort has gone into eliminating availability of anthropogenic foods (Meagher and Phillips 1983). These efforts have been largely successful in reducing incidents of bear–human conflicts. Here and in other regions where bears and people live in close proximity to one another, most conflicts occur during years when important natural foods fail (Blanchard 1990; Riley et al. 1994; Blanchard and Knight 1995).

DEMOGRAPHICS

Sex and Age Composition. Constructing the sex and age composition of a grizzly bear population is difficult. Sample method, sample size, number of years of study, sightability, natural variation during the study period, human harvest, age of adults, and other factors all influence estimates. Capture records and visual observations are biased by differential capture and sighting probabilities. Harvest records can be biased by selective harvest regulations (protection of females with offspring) and differential vulnerability of different gender and age classes to harvest. With ground-based trapping operations and helicopter capture, potential biases exist due to heterogeneity of capture for certain age–gender classes of bears (Miller et al. 1997). For example, adult females with cubs tend to be underrepresented in samples because of their secretive nature (Miller et al. 1987, 1997). Aerial observations can be subject to error and misclassification, with certain groups of bears underrepresented and others overrepresented (Erickson and Siniff 1963; Dean 1987; O'Brien and Lindzey 1998). At best, reconstruction of sex and age composition for grizzly bear populations based on field observations and capture records is an approximation. LeFranc et al. (1987) provides a summary of gender and age composition from several populations in North America. Many studies are constrained by small sample sizes. Miller (1997) provided a "weighted snapshot" estimate of population composition designed to reduce bias associated with different rates of movements between males and females.

A sample of multiple-year studies and relatively large sample sizes suggests ratios among adults, subadults, yearlings, and cubs vary widely (Table 26.5). The proportion of cubs in any population is a reflection of reproductive performance and early mortality, and should in general be higher for more fecund populations. Cub production varies yearly (Craighead et al. 1974), so as multiple-year sampling increases, a more accurate picture of age structure emerges. As expected, yearlings usually make up a smaller proportion of the population than cubs due to mortality during the first year of life. The proportion of adults, particularly adult males from populations that are harvested, tends to be lower than from unharvested populations (Miller 1990b). Ages of males and females in harvested populations are younger and older, respectively, with intensive harvest (Miller 1990b), although not in all cases (Miller 1997).

The sex ratio in bear populations tends to be skewed toward females, particularly in harvested populations (Table 26.5). Although sex ratio at birth can favor males (see Reproductive Rates), in general,

TABLE 26.7. Cause-specific mortality (%) from a sample of grizzly bear studies in North America

Number of Deaths	Natural	Hunter Harvest[a]	Citizen Killing[b]	Management Control[c]	Accident[d]	Unknown	Location	Reference
22	4.8	81.0	—	—	14.2	—	Noatak, AK	Ballard et al. 1991
14	28.6	64.3	7.1	—	—	—	Northwest Territories	Clarkson and Liepins 1994
10	—	60.0	30.0	—	10.0	—	Kananaskis Country, AB	Carr 1989
83	16.9	19.3	36.2	12.0	2.4	13.2	Interior mountains of Canada and United States	McLellan et al. 1999
38	15.8	50.0	26.3	2.6	5.3	—	Flathead River, BC	McLellan 1989b
35	28.5	2.8	34.3	17.1	2.8	14.3	Swan Mountains, MT	Mace and Waller 1998
43	11.6	25.6	27.9	32.5	2.3	—	Rocky Mountain front, MT	Aune and Kasworm 1989:213
365	1.6	29.3[e]	19.7	39.2	3.0	7.1	Yellowstone Ecosystem (1959–1972)	Craighead et al. 1988
145	13.8	8.3[f]	42.8	24.8	6.9	3.4	Yellowstone Ecosystem (1973–1985)	Knight et al. 1988

NOTE: Data include known and probable deaths, except in the Greater Yellowstone Ecosystem, which includes possible deaths.

[a] Hunter harvest includes only bears harvested legally during a sport-hunting season.

[b] Citizen killing includes defense-of-life or property killing, poaching, mistaken identification, and malicious killing. In some cases, killing of bear for defense of life or property is legal.

[c] Management control represents removal of problem bears by agency staff.

[d] Accident includes train and automobile kills, electrocution, and research deaths.

[e] Legal hunting ended in Montana and Wyoming in 1973 and 1974, respectively. Management control includes humane removals and trap casualty.

[f] Data span 1973–1985. Legal hunting occurred in 1973 only.

83%; survival for nontransported bears was 89%. Survival was largely affected by whether the bear returned to the capture site; return rates were most affected by distance transported and age and gender of the bear. Return rates decreased at distances of ≥75 km, and subadult females returned the least. Because of low survival and high return rates, transporting grizzly bears should be considered a final action to eliminate a conflict situation. However, transporting females must be considered a viable technique because some translocated females have contributed to the population through successful reproduction.

Causes of Mortality. Bears die for a number of reasons, primarily human related (Table 26.7). Natural mortality can result from old age, intra- and interspecific killing, starvation, rock or snow avalanche, den collapse, or unknown reasons. Natural mortality constitutes a greater proportion of total mortality for dependent young (Nagy et al. 1983b). Cubs and yearlings are killed by conspecifics, although the cause of mortality in dependent young is often unknown because few are radiocollared; loss of dependent young from marked mothers is generally considered mortality. McLellan et al. (1999) found different mortality rates due to natural causes among gender–age classes, with adult females having a higher rate than adult or subadult males. Work by Mace and Waller (1998) supports this.

Hunting, management removal, and defense of life and property by citizens can constitute as much as 90% of all recorded mortalities for adult bears (Table 26.7). Even in areas with no hunting, human-caused mortality dominates. Deer and elk hunters killing grizzly bears in self-defense, hunters mistaking a grizzly bear for a black bear, and malicious killing are major causes of bear deaths in Montana (Craighead et al. 1988; McLellan et al. 1999). Agency removal of problem bears either by euthanasia or relocating to zoos and shooting by citizens protecting livestock, homes, and campsites constitute a major mortality factor in many areas (Table 26.7).

Most bears die during the nondenning season. Although an occasional mortality is documented during winter (McLellan et al. 1999), most deaths occur when bears are active. Aune and Kasworm (1989) and Mace and Waller (1998) found that most grizzly bears in Montana died during autumn. Natural mortality was prominent during spring and summer, whereas management removal was the primary cause of loss during autumn. Mortality due to mistaken identification by black bear hunters was the leading cause of subadult female mortality. Adult males were most likely to die during ungulate hunting season in defense-of-life killings by hunters. Subadult males were equally susceptible to malicious killing and mistaken identification (Mace and Waller 1998).

Because most bears are killed by humans, proximity of kills to human facilities and access routes (roads, trails, back country sites) are common. Aune and Kasworm (1989) found that of 43 grizzly bear mortalities on the Rocky Mountain front, 63% occurred within 1 km of the nearest road. Knight et al. (1988) found that the majority of grizzly bear deaths in the GYE were clustered near foci within and on the periphery of Yellowstone National Park. Major population sinks included communities such as West Yellowstone, Cooke City, and Gardiner, Montana; recreational developments, sheep grazing allotments, and various other human concentration areas. Also, diverse attractants such as apple orchards, outfitter camps, and locations where people have persistently fed individual bears or unlawfully disposed of garbage enticed bears into conflict situations, especially during periods of natural food shortage. Hunter harvest also tends to be greater in areas with enhanced human access (Miller 1990b). On Chichagof Island in southeastern Alaska, increased cumulative miles of road construction was strongly correlated with fall brown bear harvests from 1978 to 1989 (Titus and Schoen 1992). This happened even after closure of hunting seasons, because of defense-of-life and property kills and illegal kills (Titus and Beier 1991; Schoen et al. 1994).

Grizzly bears, like most other animals, are afflicted with an array of parasites and diseases (LeFranc et al. 1987). Occasionally a bear succumbs to such ailments, but documenting cause of death is difficult, particularly under natural conditions. Animals carrying a heavy load of parasites can die from starvation, malnutrition, or in a conflict situation. The parasite may ultimately be the cause of their demise, but the proximal cause may differ. We are unaware of a documented major die-off in a grizzly bear population linked either to parasites or diseases.

Intraspecific Killing. On occasion, grizzly bears kill one another. Adult males have been implicated as the killers in nearly 78% of the 27 documented cases where the age and gender of the killer is known (McLellan 1994). Of 57 cases of intraspecific killing, cubs of the year are the greatest victims (44%, $n = 25$), but adult females are also killed (18%, $n = 10$). Some adult female victims are protecting their cubs. Victims are of all age and sex classes, indicating that intraspecific killing is not limited to infanticide (McLellan 1994). Adult females have also been implicated in killing cubs (Hessing and Aumiller 1994). In 10 cases where age and gender of the killer were known, adult females were implicated in 5 (McLellan 1994).

There are two competing theories on the impacts of intraspecific killing in bear populations (Miller 1990c, 1990d). One suggests that greater mortality of adult bears will result in increased survival of young bears, particularly cubs. Although some studies have demonstrated a negative relationship between recruitment of subadults and number of adult male bears (McCullough 1981, 1986; Stringham 1983), Stringham (1983) and others (Miller 1990c; Garshelis 1994; McLellan of data indicating it would be beneficial in other areas where intensive bear management was adopted.

Hunting affects population composition in different ways, and regulations can affect the composition of harvests (Miller 1990e; Van Daele et al. 1990). Because bears are promiscuous, regulations that direct harvests toward males and away from adult females permit higher hunter quotas (Taylor et al. 1987). In early spring, hunters kill primarily males because they are the first to emerge from dens. Females accompanied by newborn cubs are the last to emerge from dens. Similarly, males are the last to enter dens in the fall, so late fall seasons have higher proportions of males. In central Alaska, females constituted 18% of the spring season hunter kill before 1 May, but >40% of the harvest after the third week in May (Miller 1990a). In the fall, females represented 53% of the kill during the first week of September, but <43% of the kill during October (Miller 1990a). Bears enter dens later on northern Kodiak Island and are more vulnerable to hunters during fall seasons than on southwestern Kodiak Island (Van Daele et al. 1990). In Alaska and Canada, regulations prohibit shooting females accompanied by cub-of-year or yearling offspring, which contributes to a male bias in hunter harvests. In the Yukon, a point system is used that provides incentives for outfitters to avoid harvesting females (Yukon Renewable Resources 1997). It is difficult for hunters to distinguish between males and female bears unless the female is accompanied by offspring or the male is exceptionally large. Regardless of regulations, male bears are more vulnerable to hunters than female bears because they range more widely and are more likely to encounter areas frequented by hunters (Bunnell and Tait 1980). Correspondingly, across North America, males constitute between 64% (Yukon) and 85% (northern Canada) of hunter harvests (Table 26.8).

Hunting regulations can influence the composition of hunted populations of bears (Reynolds 1993; Miller 1997). In an extremely heavily hunted population in south-central Alaska that included spring and early-fall seasons, population composition (bears ≥ 2 years) shifted from 70 males/100 females to 21 males/100 females over a 10-year period. For bears >5 years old, sex ratio shifted from 53 males/100 females to 26 males/100 females. In this area, 58% of the bears harvested during this period were males (Miller 1997). Percentage males in the harvest is a potentially misleading statistic to use in evaluating harvest level because as the proportion of males in the population declines, the proportion of females in the harvest will increase (Frasier et al. 1982). Populations in which hunter effort is not uniformly distributed will also frequently show a prevalence of males in hunter harvest greater than in the population because males have larger home ranges and a correspondingly higher chance of encountering hunters (Bunnell and Tait 1980). In a heavily hunted area of Alaska, there was no significant change in the age of males or females in the population, although there was a tendency for both sexes to be older following the period of heavy hunter kills (Miller 1997). In spite of these changes in population composition in this area, grizzly bear density was not significantly changed (Miller 1995a). In another portion of Alaska, heavy hunting pressure caused a decline in grizzly bear density (Reynolds 1990).

Reporting Rate. Not all bear deaths are detected and recorded. Miller (1990b) indicated that unreported sport or nuisance kills and wounding losses could represent significant sources of mortality that managers should consider. Studies by McLellan et al. (1999), for example, show that without the aid of radiotelemetry, management agencies would have been aware of only 46–51% of grizzly bear deaths and 54–66% of human-caused deaths. Large portions of radio-collared grizzly bear deaths in British Columbia are legal, reported sport kills. However, even in British Columbia, the management agency would have only recorded 53–59% of the mortalities and 67–83% of the human-caused deaths. In rural northwestern Alaska, less than half the grizzly bear sport and subsistence harvest is reported (Miller 1990b). In Montana, where hunting is illegal, agencies would have recorded only 38–41% of deaths and 44–55% of human-caused deaths (McLellan et al. 1999). In the GYE, Knight et al. (1988) suggested that the overall fraction of recorded deaths of grizzly bears ranges from 40% to 60%. They concluded that most deaths due to legal hunting, removal by management agencies, and road kills were confirmed, whereas 32 of 73 (44%) of deaths associated with illegal activities were not confirmed. In a subsequent analysis of the Yellowstone data, Mattson (1998) concluded that there was a high prevalence (60–76%) of radio-marked bears among recorded deaths, and different causes of mortality were not reported equally. He cautioned against use of a simple correction for unknown, unreported mortality.

Density. For brown/grizzly bears, like most species, density (number/unit area) is a key population parameter. High-density bear populations can exist in areas with abundant and uniformly distributed food resources. Low-density bear populations exist in areas where food resources are sparse and/or patchy with long distances between patches (or where there has been excessive human killing of bears). The highest documented grizzly bear density in North America is about 140 times greater than in low-density areas (Table 26.9).

The greatest brown bear densities in North America occur in coastal areas of Alaska, where bears thrive on summer and fall runs of salmon. Coastal maritime climate leads to longer growing seasons, which also benefit bears. Documented densities in these areas are 175–550 bears (all ages)/1000 km^2 (Miller et al. 1997) (Table 26.9). Salmon import energy from rich marine systems into frequently nutrient-impoverished terrestrial systems. Because of this importation of energy, bears living in salmon-rich areas not only have more dense populations, but they are 1.5–3 times larger in body mass (Glenn 1980; Hilderbrand et al. 1999a). Populations with the lowest densities occur in the extreme northern part of North America, between the Alaska Range and the Beaufort Sea in Alaska, and in northern Yukon and Northwest Territories in Canada (Kingsley et al. 1988). Densities in these areas are typically <10 bears/1000 km^2 (Table 26.9). Higher densities can be maintained even in these northern environments in areas where caribou are abundant (Reynolds and Garner 1987). Migratory caribou, like anadromous salmon, are net importers of energy into these energetically impoverished northern systems. Nutrients from salmon that are imported into forest ecosystems and distributed as bear feces may be important for forests growing as far inland as Idaho (Hilderbrand et al. 1999b).

Techniques for estimating bear density are not standardized; consequently, density estimates presented in Table 26.9 are not directly comparable. In Alaska, however, 19 brown bear density estimates were obtained using the same techniques in different habitats; all are directly comparable and have measures of precision (Miller 1995b; Miller et al. 1997; Testa et al. 1998). These techniques required the use of radiocollars, which largely eliminate the problem of geographic closure common to other density estimation techniques.

Radio-marking techniques are not broadly applied outside of Alaska because of expense, need to capture bears to apply radiocollars, and low sightability of bears in heavily forested habitats. Instead, many researchers in Canada and the United States have focused on the development of techniques to estimate number of bears and density employing hair-snaring methods. With this procedure, bears are attracted to sampling stations with a scent lure. At each sampling station, barbed wire is strung between trees, and when the bear passes under the wire, a small tuft of hair is snagged in the barb of the wire (Woods et al. 1996, 1999). The follicles from these hair samples contain DNA, which can be used to identify individual animals. This technique is conceptually similar to techniques developed to identify bears based on photos taken when bears trip cameras (Mace et al. 1994). Advantages of these DNA and camera techniques include reduced need to mark bears or see them from aircraft. However, these techniques are labor intensive and expensive, and typically have problems identifying the area inhabited by the estimated population. This closure problem creates difficulties in estimating density. So far, the DNA and camera techniques are not standardized for design or data analysis, hence results from different areas may not be comparable. In Glacier National Park, U.S. Geological Survey researcher Kate Kendall has conducted the most extensive effort to estimate grizzly bear abundance using hair-snaring and

British Columbia and Montana. The λ value for the GYE was 0.97–1.12 (Eberhardt 1995). Stable population growth was estimated for grizzlies in the Kananaskis area of southwestern Alberta (λ = 0.99–1.01; Wielgus and Bunnell 1994) and the Selkirk Mountains of British Columbia and Idaho (λ = 1.00; Wielgus et al. 1994). A declining population was estimated for the Swan Mountains of Montana (λ = 0.977, 95% confidence interval [CI] = 0.875–1.046; Mace and Waller 1998). Some of these rates are point estimates based on small sample sizes. For nearly all estimates, the 95% CI bounds 1.0, making it impossible to determine true population trajectory. For a slowly reproducing species like grizzly bears, in which even a maximum lambda will always be close to 1.0, it will seldom be possible to have a 95% CI that does not overlap 1.0. Uncertainty primarily associated with subadult and adult female survival explains most of the variance associated with these estimates (Eberhardt et al. 1994; Hovey and McLellan 1996; Mace and Waller 1998).

Shaffer (1978, 1983) was the first to use stochastic models to help guide grizzly bear management in Yellowstone National Park. This pioneering work was the first PVA for any species. His model estimated a minimum viable population, or the smallest population size necessary with a 95% chance of remaining extant after 100 years. Initial simulations indicated that a population of 35 grizzly bears might be expected to survive 100 years. Because of uncertainty associated with his original estimate, Shaffer (1983) later suggested that this value should be increased to 50–90 bears. Later Suchy et al. (1985) updated these estimates to 40–125 or 50–225 bears depending on a low versus high mortality schedule. To be conservative, Suchy et al. (1985) recommended a population >125 be maintained to ensure a high probability of persistence for at least 100 years. Soulé (1987) and Shaffer (1992) expressed concern that targeting a minimum population level is inadequate for sound conservation and that larger populations are necessary to ensure long-term persistence of the species. More recent reviews of PVA (Boyce 1992; Boyce et al. 2001) have pointed out that traditional PVA models are demographically based; they lack a link to habitat, particularly habitat changes. Most PVAs do not consider genetic effects, including inbreeding depression, loss of evolutionary potential, and accumulation of harmful mutations (Allendorf and Ryman 2002).

AGE ESTIMATION

Assessing growth annuli in teeth is the most accurate means of age determination for many mammalian species (Thomas 1977; Fancy 1980). The technique has been applied to the canine (Rausch 1969), the lower third molar (Mundy and Fuller 1964), and the first upper and lower premolars (Matson et al. 1993) of brown bears. Because of the ease in collection, its vestigial nature, and small root size, the premolar is the tooth most commonly extracted from live bears. Eruption of permanent premolars occurs before denning in grizzly bears at about 8 months of age (Pearson 1975). The first annulus is formed during the denning season around the time the bear has its first birthday. By spring, the premolar of a yearling brown bear has the light cementum of the previous summer/fall and a single annulus of the winter just past (Matson et al. 1993). Each denning season, a new annulus is formed. Accuracy of the technique is dependent on tooth quality, experience of the technician, and age of the bear. For older bears (>9 years), errors for exact age can be as high as 70%; errors decline to 40% if accuracy within 1 year is acceptable (Matson et al. 1993). A thin annual layer of light cementum has been correlated with successful cub rearing in some female black bears (Carrel 1992; Coy and Garshelis 1992), but has proven unreliable in brown bears.

MANAGEMENT AND CONSERVATION

Conservation. As noted, grizzly bears south of Canada have been dramatically reduced in abundance and distribution to perhaps as few as 1000 individuals in mountainous areas of the northern Rocky Mountains near Canada and in the Yellowstone Ecosystem (Servheen 1999). Additionally, there may be a small transitory population in the North Cascades near the border with British Columbia (Servheen 1998, 1999). Grizzlies occupy only 1–2% of their historical range south of Canada. In the United States, healthy populations of brown bears remain only in Alaska, where some 31,700 individuals are estimated to live (Miller 1993; Miller and Schoen 1999). Even in Alaska, however, there are areas such as the Kenai Peninsula where the same decimating factors of excessive mortality and habitat destruction that reduced the population south of Canada have placed the persistence of brown bears at risk.

Habitat loss and human-caused mortality operate in southern Canada. Brown bears have been exterminated from the open plains in the provinces of Manitoba, Saskatchewan, and western Alberta (McLellan and Banci 1999). An estimated 25,300 brown bears remain in Canada (Banci et al. 1994; McLellan and Banci 1999). The most secure of these populations are in the high-density zones along the Pacific coast, but even here they were listed as threatened or vulnerable by McLellan and Banci (1999). Banci et al. (1994:140) noted, "It can no longer be assumed that there will be some areas of [Canada] that will be left natural and untrammeled and that can serve as refugia for grizzly bears and other wildlife that require large areas of relative solitude." In the far north of Canada, populations exist at densities that are close to prehistoric conditions, but because densities are naturally very low in northern Canada (Nagy and Haroldson 1990), these populations are inherently vulnerable.

Six and one-half years following listing under the Endangered Species Act, a recovery plan for grizzly bears was published (U.S. Fish and Wildlife Service 1982). The plan was revised in 1993. This revised plan presents recovery targets for grizzly bears in the Northern Continental Divide Ecosystem (Glacier National Park and vicinity), the GYE including Yellowstone National Park, the Cabinet/Yaak Ecosystem, and the Selkirk Ecosystem. The recovery plan also identified an objective of reestablishing a grizzly bear population in the Bitterroot Ecosystem and mentioned the need to develop a plan for the North Cascades of Washington State. When the targets identified in the recovery plan are reached, the U.S. Fish and Wildlife Service will propose removing grizzly bears from protection under the Endangered Species Act and returning management authority to state agencies responsible for wildlife management.

In the Northern Continental Divide Ecosystem (NCDE) and GYE recovery targets are based on numerical, distributional, and mortality objectives. Because of the difficulty of accurately estimating abundance, numerical targets in the recovery plan are based on counts of unduplicated females with newborn cubs (Knight et al. 1995). This segment of the population is most recognizable. Females accompanied by newborn cubs observed by qualified personnel are tallied based on location, date, pelage color, size, and number of cubs. Because cub production varies yearly, trends are based on a 6-year running average count. The target running average is 15 females with newborn cubs in the GYE, 22 in the NCDE (10 within Glacier National Park and 12 outside the park), 6 in the Cabinet/Yaak Ecosystem, and 6 in the Selkirk Ecosystem. This numerical target is conservative because not all females with newborn cubs are observed and there is a conservative protocol for excluding possible duplicate counts.

Recovery cannot occur unless recruitment exceeds mortality. Under the Recovery Plan (U.S. Fish and Wildlife Service 1993) for all recovery areas, maximum mortality level is set at ≤4% of the population estimate/year during any two consecutive years. The population estimate derives from an extrapolation on the number of females with newborn cubs based on a conservative set of assumptions about the proportion of the population constituted by females with newborn cubs. In addition to this numerical mortality limit, the plan specifies that no more than 30% of the mortality can be females. The female quota recognizes that a population of bears can persist with higher rates of mortality to males than to females. Mortality quotas established in the recovery plan have proven more difficult to achieve than numerical goals.

The recovery plan also recognizes that bears must be well distributed in each ecosystem. Recovery zones have been subdivided into bear management units (BMUs). Recovery targets identify the

Road density was measured based on moving window analyses. This technique involves randomly moving a window of 1 mi^2 across a map and summing the lengths of segments of roads and trails within the window (EPPL7, Minnesota Land Management Information Center, 658 Cedar Street, St. Paul, MN 55155). This technique precludes direct conversion of the above standards to metric equivalents.

These guidelines acknowledge the importance of large core areas with no roads and only low road density in the remaining grizzly bear habitat. However, these guidelines have been difficult to implement because of opposition to the extensive road closures required to meet them. Biologists also recognized that there was a seasonal component to grizzly bear use of the habitats influenced by roads. Acceptable levels of habitat security for bears require seasonal closures of roads and trails during periods when they are most commonly in these areas. Consequently, the guidelines listed above are under review in an effort to close roads in areas that will result in maximum benefit to bear habitat security. Although there is clear evidence of the detrimental impact of roads in grizzly bear habitat, the threshold of road density may vary among areas. J. J. Craighead et al. (1995) suggested that road density >1 km/6.4 km (0.25 mi/mi^2) has detrimental impacts on bear use of landscapes.

In addition to habitat loss by disturbance displacement, roads facilitate killing of bears by humans via hunting and control actions. These are the greatest sources of mortality to adult bears in the GYE (Weaver et al. 1986; Mattson et al. 1987). Risk of mortality was estimated as five times higher near roads (Doak 1995). On Chichagof Island in southeastern Alaska, where brown bears are legally hunted, there was a direct positive correlation between bear kill by hunters and cumulative kilometers of constructed roads (Titus and Beier 1991).

Habitat evaluation for grizzly bears requires knowledge about the abundance and distribution of food and shelter patches as well as knowledge about human influences that may make bears avoid some areas or expose them to higher risk of mortality. Excellent early work on evaluation of bear habitat concentrated on vegetation analyses was presented by Craighead (1977) and Craighead et al. (1982). More recent efforts to evaluate habitat incorporate similar vegetative analyses with those of mortality risks to brown bears and likelihood of disturbance avoidance of preferred habitats. Risks to bears come from many sources, and managers use cumulative effects models (CEM) to assess habitat values (Weaver et al. 1986; Schoen et al. 1994; Suring et al. 1998; Mattson et al. 1999b). CEM models assign qualitative importance scores to different components of the habitat and then sum these scores for all factors to obtain a measure of habitat value and overall risk. The first CEM for grizzly bears included measures of human-induced risk of mortality, habitat alteration, and displacement from habitat (Weaver et al. 1986). Each of these parameters incorporated numerous coefficients (Mattson et al. 1999b). The value for mortality was derived from indices of habitat quality and type and intensity of human activities. The value for habitat displacement included components of distance to cover and nature and intensity of bear activity in that habitat (Weaver et al. 1986).

A more recent approach integrates empirical information from telemetry studies into models to derive resource selection functions (RSF) (Schoen et al. 1994; Mace et al. 1996, 1999; Boyce and McDonald 1999; Merrill et al. 1999; see Carroll et al. 1999 for a review). RSFs are proportional to the probability of an area being used by an animal. The key to this approach is to correctly identify the important parameters; some include satellite imagery (greenness), elevation, human activity points, roads, and trails (Mace et al. 1999) or human numbers, human distribution, and abundance and quality of bear foods (Merrill et al. 1999).

South of Canada, grizzly bears once occupied the landscape continuously from mountain tops to valley bottoms and plains. With ever-increasing human presence in the valley bottoms and plains, bears have become isolated in islands of remaining mountainous and forested habitat surrounded by a threatening sea of subdivisions, agricultural fields, and pastures. Bears that venture beyond the borders of these remaining islands venture into areas described as "mortality sinks," which can drain the island population and threaten its viability (Knight et al. 1988). Identification of zones of connectivity or linkages between the islands is an essential element of habitat analyses, and numerous approaches have been described. Linkage zone models predict relative probability of grizzly bear movements through an area as a function of factors such as visual cover, riparian corridors, and anthropogenic features (Gibeau 1993; Servheen et al. 2001; Gibeau et al. 1996; Apps 1997). A simulation model was used to predict dispersal routes for grizzly bears based on permeability of different habitat types (Boone and Hunter 1996). Based on a literature review, whitebark pine/lodgepole pine (*Pinus contorta*) habitats were assigned high permeability values, whereas clear-cut and early-seral stage forests had low permeability. Walker and Craighead (1997) combined the permeability data and dispersal mortality risk to map potential dispersal routes for grizzly bears in the northern Rocky Mountains. These models can be used to plot the "least-cost path" for bears moving between ecosystems. These approaches recognize that the correct paradigm for a linkage zone is not a corridor that bears use to move between ecosystems, but rather an area of habitat between ecosystems that bears can safely occupy at low densities with acceptable levels of mortality risk.

Bears are archetypal flagship species—species so charismatic that they symbolize an entire conservation program (Simberloff 1999). The grizzly bear and other large carnivores are a flagship for the Yellowstone-to-Yukon Biodiversity Strategy (Y2Y), a broad program to maintain and restore natural diversity and ecological health of the Rocky Mountains. The Y2Y mission is to establish an interconnected system of core protected areas and wildlife movement corridors that extend from the GYE to the Yukon's Mackenzie Mountains (Tabor 1996; Tabor and Soulé 1999). The concept is premised on protecting existing core areas within existing national parks and preserves, state and provincial parks, and wilderness areas. Core areas will be interconnected with corridors, allowing migration of wildlife among them. Conservation benefits of Y2Y encompass more than the grizzly bear in the United States, and include large carnivores and other wildlife species. Such broad thinking is heretofore unheard of in North America and generally beyond traditional agency thinking or mandates. The vision has inspired over 200 conservation groups to work together beyond international boundaries. The research, planning, and implementation that has gone into the Y2Y effort will benefit the management of grizzly bears and other wildlife in North America that require large interconnected landscapes to support healthy populations.

RESEARCH NEEDS

One of the earliest studies of grizzly bears in North America was in Denali National Park (formerly Mount McKinley National Park) by the great naturalist Adolph Murie (Murie 1944, 1981). Using observational techniques, Murie discovered much about grizzly bear ecology before the development of effective means of immobilizing bears and tracking them with radiotelemetry. However, through observation he was unable to quantify some important parameters such as population density, reproductive and mortality rates, distances moved by individual animals, and characteristics of denning locations. Information on these awaited the pioneering studies of grizzly bears in Yellowstone National Park by the Craighead brothers using radiotelemetry techniques they developed (Craighead et al. 1963). Later, they pioneered the use of satellite monitoring of bears (Craighead et al. 1971).

Although the importance of telemetry techniques is well recognized, Craighead and Mitchell (1982) expressed concern that some biologists are overusing telemetry. They note that capture and handling imposes unnecessary stress on the animals, particularly from populations inhabiting similar environments. We agree with this concern and suggest that radiotelemetry is only one tool available to biologists. Application of such a tool must be employed when the technique is applicable to address a specific objective and answer certain questions. Telemetry studies must be well designed, adequately reviewed, and competently conducted. Scientific ethics requires that agencies proposing to conduct telemetry studies on grizzly bears or other rare animals must

Aune, K., and W. Kasworm. 1989. Final report. East Front grizzly studies. Montana Department of Fish, Wildlife and Parks, Helena.

Aune, K., M. Madel, and C. Hunt. 1986. Rocky Mountain East Front grizzly bear monitoring and investigations. Unpublished data. Montana Department of Fish, Wildlife and Parks.

Aune, K. E., R. D. Mace, and D. W. Carney. 1994. The reproductive biology of female grizzly bears in the Northern Continental Divide Ecosystem with supplemental data from the Yellowstone Ecosystem. International Conference on Bear Research and Management 9(1):451–58.

Ballard, W. B., T. H. Spraker, and K. P. Taylor. 1981. Causes of neonatal moose calf mortality in south-central Alaska. Journal of Wildlife Management 45:335–42.

Ballard, W. B., S. D. Miller, and T. H. Spraker. 1982. Home range, daily movements, and reproductive biology of the brown bear in southcentral Alaska. Canadian Field-Naturalist 96:1–5.

Ballard, W. B., L. A. Ayres, K. E. Roney, D. J. Reed, and S. G. Fancy. 1991. Demography of Noatak grizzly bears in relation to human exploitation and mining development (Federal Aid in Wildlife Restoration Final Report W-22-5, W-22-6, W-23-1, W-23-2, and W23-3, Study 4.20), Alaska Department of Fish and Game, Juneau.

Banci, V. 1991. The status of the grizzly bear in Canada in 1990 (Status Report). Committee on the Status of Endangered Wildlife in Canada.

Banci, V., D. A. Demarchi, and W. R. Archibald. 1994. Evaluation of the population status of grizzly bears in Canada. International Conference on Bear Research and Management 9(1):129–42.

Barnes, V. G., Jr., and R. B. Smith. 1993. Cub adoption by brown bears, *Ursus arctos middendorffi*, on Kodiak Island, Alaska. Canadian Field, Naturalist 107:365–67.

Bath, A. J. 1998. The role of human dimensions in wildlife resource research in wildlife management. Ursus 10:343–48.

Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62:821–41.

Bekoff, M., and L. D. Mech. 1984. Simulation analyses of space use: Home range estimates, variability, and sample size. Behavioral, Research Methods, Instruction and Computation 16:32–37.

Bielanska-Osuchowska, Z., and S. Szankowska. 1970. Histological and histochemical studies on the alimentary tract in the brown bear. Acta Theriologica 15:303–42.

Blanchard, B. M. 1987. Size and growth patterns of the Yellowstone grizzly bear. International Conference on Bear Research and Management 7:99–107.

Blanchard, B. M. 1990. Relationship between whitebark pine cone production and fall grizzly bear movements. Pages 362–63 *in* W. C. Schmidt and K. J. McDonald, comps. Proceedings of symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource (U.S. Forest Service General Technical Report INT-270). U.S. Department of Agriculture, Forest Service, Ogden, UT.

Blanchard, B. M., and R. R. Knight. 1991. Movements of Yellowstone grizzly bears, 1975–87. Biological Conservation 58:41–67.

Blanchard, B. M., and R. R. Knight. 1995. Biological consequences of relocating grizzly bears in the Yellowstone Ecosystem. Journal of Wildlife Management 59:560–65.

Boertje, R. D., W. C. Gasaway, D. V. Grangaard, D. G. Kelleyhouse, and R. O. Stephenson. 1987. Factors limiting moose population growth in Subunit 20E (Federal Aid in Wildlife Restoration Progress Report Project W-22-5, Job 1.37R). Alaska Department of Fish and Game, Juneau.

Boone, R. B., and M. L. Hunter. 1996. Using diffusion models to simulate the effects of land use on grizzly bear dispersal in the Rocky Mountains. Landscape Ecology 11:51–64.

Boulanger, J. G., and B. McLellan. 2001. Estimating closure violation bias in DNA based mark–recapture censuses of grizzly bears. Canadian Journal of Zoology 79:642–651.

Boulanger, J. G., and G. C. White. 1990. A comparison of home-range estimators using Monte Carlo simulation. Journal of Wildlife Management 54:310–15.

Boyce, M. S. 1992. Population viability analysis. Annual Review of Ecology and Systematics 23:481–506.

Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14:268–72.

Boyce, M. S., A. R. E. Sinclair, and G. C. White. 1999. Seasonal compensation of predation and harvesting. Oikos 87:419–26.

Boyce, M. S., and J. Waller. 2000. The application of resource selection functions analysis to estimate the number of grizzly bears that could be supported by habitats in the Bitterroot Ecosystem. Appendix 21B. Pages 231–46 *in* Grizzly bear recovery in the Bitterroot Ecosystem, final environmental impact statement. U.S. Fish and Wildlife Service.

Boyce, M. S., B. M. Blanchard, R. R. Knight, and C. Servheen. 2001. Population viability for grizzly bears: A critical review (Monograph Series No. 4). International Association for Bear Research and Management.

Brady, K. S., and D. Hamer. 1992. Use of summit mating area by a pair of courting grizzly bears, *Ursus arctos*, in Waterton Lakes National Park, Alberta. Canadian Field-Naturalist 106:519–20.

Brown, D. E. 1985. The grizzly in the southwest, documentary of an extinction. University of Oklahoma Press, Norman.

Brown, J. L., and G. H. Orians. 1970. Spacing patterns in mobile animals. Annual Review of Ecological Systematics 1:239–62.

Bunnell, F. L., and T. Hamilton. 1983. Forage digestibility and fitness in grizzly bears. International Conference on Bear Research and Management 5:179–85.

Bunnell, F. L., and D. E. N. Tait. 1980. Bears in models and reality: Implications to management. International Conference on Bear Research and Management 3:15–23.

Bunnell, F. L., and D. E. N. Tait. 1981. Population dynamics of bears: Implications. Pages 75–98 *in* C. W. Fowler and T. D. Smith, eds. Dynamics of large mammal populations. John Wiley, New York.

Bunnell, F. L., and D. E. N. Tait. 1985. Mortality rates of North American bears. Arctic 38:316–23.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346–352.

Byers, C. R., and G. A. Bettas. 1999. Records of North American big game, 11th ed. Boone and Crockett Club, Missoula, MT.

Carr, H. D. 1989. Distribution, numbers, and mortality of grizzly bears in and around Kananaskis Country, Alberta (Wildlife Research Series No. 3). Alberta Forest Lands and Wildlife.

Carrel, W. K. 1992. Reproductive history in dental cementum of female black bears. International Conference on Bear Research and Management 9(1):205–12.

Carroll, C., P. C. Paquet, and R. F. Noss. 1999. Modeling carnivore habitat in the Rocky Mountain region: A literature review and suggested strategy. World Wildlife Fund-Canada, Toronto.

Case, R. L., and L. Buckland. 1998. Reproductive characteristics of grizzly bears in the Kugluktuk area, Northwest Territories, Canada. Ursus 10:41–47.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley, New York.

Claar, J. J., N. Anderson, D. Boyd, B. Conard, G. Hickman, R. Hompesch, G. Olson, H. I. Pac, T. Wittinger, and H. Youmans. 1999. Carnivores. Pages 7.1–7.61 *in* G. Joslin and H. Youmans, coords. Effects of recreation on Rocky Mountain wildlife: A review for Montana. Committee on Effects of Recreation on Wildlife, Montana Chapter of the Wildlife Society, Missoula.

Clark, W. K. 1957. Seasonal food habits of the Kodiak bear. Transactions of the North American Wildlife Conference 22:145–51.

Clarkson, P. L., and I. S. Liepins. 1994. Grizzly bear population estimate and characteristics in the Anderson and Horton Rivers area, Northwest Territories. International Conference on Bear Research and Management 9(1):213–21.

Coy, P. L., and D. L. Garshelis. 1992. Reconstructing reproductive histories of black bears from the incremental layering in dental cementum. Canadian Journal of Zoology 70:2150–60.

Cracraft, J. 1983. Species concepts and speciation analysis. Current Ornithology 1:159–87.

Craighead, D. J. 1998. An integrated satellite technique to evaluate grizzly bear habitat use. Ursus 10:187–201.

Craighead, F. C., Jr. 1976. Grizzly bear ranges and movement as determined by radiotracking. International Conference on Bear Research and Management 3:97–109.

Craighead, F. C., Jr., and J. J. Craighead. 1972. Grizzly bear prehibernation and denning activities as determined by radiotracking. Wildlife Monograph 32:1–35.

Craighead, F. L., and E. Vyse. 1996. Brown/grizzly bear metapopulations. Pages 325–51 *in* D. McCullough, ed. Metapopulations and wildlife conservation management. Island Press, Washington, DC.

Craighead, F. C., Jr., J. J. Craighead, and R. S. Davies. 1963. Radiotracking of grizzly bears. Pages 133–48 *in* L. E. Slater, ed. Biotelemetry: The use of telemetry in animal behavior and physiology in relation to ecological problems. Macmillan, New York.

Craighead, F. L., D. Paetkau, H. V. Reynolds, E. R. Vyse, and C. Strobeck. 1995. Microsatellite analysis of paternity and reproduction in arctic grizzly bears. Journal of Heredity 86:255–61.

Craighead, F. L., D. Paetkau, H. V. Reynolds, C. Strobeck, and E. R. Vyse. 1998. Use of microsatellite DNA analysis to infer breeding behavior and demographic processes in an arctic grizzly bear population. Ursus 10:323–27.

Gordon, K. R. 1977. Molar measurements as a taxonomic tool in *Ursus*. Journal of Mammalogy 58:247–48.

Gray, A. P. 1954. Mammalian hybrids. A check list with bibliography. Commonwealth Bureau of Animal Breeding and Genetics, Edinburgh Technical Communications 10:1–144.

Green, G. 1994. Use of spring carrion by bears in Yellowstone National Park. M.S. Thesis, University of Idaho, Moscow.

Green, G. I., D. J. Mattson, and J. M. Peek. 1997. Spring feeding on ungulate carcasses by grizzly bears in Yellowstone National Park. Journal of Wildlife Management 6:1040–55.

Grinnell, J., J. S. Dixon, and J. Linsdale. 1937. Fur-bearing mammals of California, their natural history, systematic status, and relations to man. University of California Press, Berkeley.

Groves, C. 1987. A compilation of grizzly bear reports from central and northern Idaho (Endangered Species Projects E-III, E-IV). Idaho Department of Fish and Game, Boise.

Guilday, J. E. 1968. Grizzly bears from eastern North America. American Midland Naturalist 79:247–50.

Gunther, K. A., and R. A. Renkin. 1990. Grizzly bear predation on elk calves and other fauna of Yellowstone National Park. International Conference on Bear Research and Management 8:329–34.

Guppy, M. 1986. The hibernating bear: Why is it so hot, and why does it cycle urea through the gut? Trends in Biochemical Science 11:274–76.

Gustafson, K. A., and L. B. Fox. 1983. A comprehensive interactive computer program for calculating and plotting home ranges and distributions. Pages 299–317 *in* D. G. Pincock, ed. Fourth international conference on wildlife biotelemetry. Applied Microelectronics Institute and Technology, University of Nova Scotia, Halifax, Canada.

Hall, E. R. 1984. Geographic variation among brown and grizzly bears (*Ursus arctos*) in North America (Special Publication 13). Museum of Natural History, University of Kansas, Lawrence.

Hamer, D., and S. Herrero. 1987. Grizzly bear food and habitat in the Front Ranges of Banff National Park, Alberta. International Conference on Bear Research and Management 7:199–213.

Hamer, D., and S. Herrero. 1990. Courtship and use of mating areas by grizzly bears in the Front Ranges of Banff National Park, Alberta. Canadian Journal of Zoology 68:2695–97.

Hamer, D., and S. Herrero. 1991. Elk, *Cervus elaphus*, calves as food for grizzly bears, *Ursus arctos*, in Banff National Park, Alberta. Canadian Field-Naturalist 105:101–3.

Harding, L. 1976. Den-site selection of arctic coastal grizzly bears (*Ursus arctos* L.) on Richards Island, Northwest Territories, Canada. Canadian Journal of Zoology 54:1357–63.

Harestad, A. S., and F. L. Bunnell. 1979. Home range and body weight: A reevaluation. Ecology 60:389–402.

Hausfater, G., and S. B. Hrdy, eds. 1984. Infanticide: Comparative and evolutionary perspectives. Aldine, New York.

Hechtel, J. L. 1985. Activity and food habits of barren-ground grizzly bears in Arctic Alaska. M.S. Thesis, University of Montana, Missoula.

Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668–74.

Hellgren, E. C. 1998. Physiology of hibernation in bears. Ursus 10:467–77.

Hensel, R. J., W. A. Troyer, and A. W. Erickson. 1969. Reproduction in the female brown bear. Journal of Wildlife Management 33:357–65.

Herrero, S. 1972. Aspects of evolution and adaptation in American black bears (*Ursus americanus* Pallas) and brown and grizzly bears (*Ursus arctos* Linné) of North America. International Conference on Bear Research and Management 2:221–31.

Herrero, S. 1985. Bear attacks: Their causes and avoidance. Lyons and Burford, New York.

Herrero, S., and D. Hamer. 1977. Courtship and copulation of a pair of grizzly bears, with comments on reproductive plasticity and strategy. Journal of Mammalogy 58:441–44.

Herrero, S., P. S. Miller, and U. S. Seal, eds. 2000. Population and habitat viability assessment for the grizzly bear of the Central Rockies Ecosystem (*Ursus arctos*). Eastern Slopes Grizzly Bear Project, University of Calgary, Calgary, Canada, and Conservation Breeding Specialist Group, Apple Valley, MN.

Hessing, P., and L. Aumiller. 1994. Observations of conspecific predation by brown bears, *Ursus arctos*, in Alaska. Canadian Field-Naturalist 108:332–36.

Hessler, E., J. R. Tester, D. B. Siniff, and M. M. Nelson. 1970. A biotelemetry study of survival of pen-reared pheasants released in selected habitats. Journal of Wildlife Management 34:267–74.

Hewitt, D. G., and C. T. Robbins. 1996. Estimating grizzly bear food habits from fecal analysis. Wildlife Society Bulletin 24:547–50.

Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, M. E. Jacoby, T. A. Hanley, S. M. Arthur, and C. Servheen. 1999a. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Canadian Journal of Zoology 77:132–38.

Hilderbrand, G. V., T. A. Hanley, C. T. Robbins, and C. C. Schwartz. 1999b. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. Oecologia 121:546–50.

Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, and T. A. Hanley. 2000. Effect of hibernation and reproductive status on body mass and condition of coastal brown bears. Journal of Wildlife Management 64:178–83.

Hogg, J. T., N. S. Weaver, J. J. Craighead, M. L. Pokorny, B. M. Steele, R. L. Redmond, and F. B. Fisher. 1999. Abundance and spatial distribution of grizzly bear plant-food groups in the Salmon–Selway Ecosystem: A preliminary analysis and report. Craighead Wildlife-Wildlands Institute, Missoula, MT [Excerpt in Appendix 21D, Pages 6-247–6-270 *in* Grizzly bear recovery in the Bitterroot Ecosystem (Final Environmental Impact Statement). U.S. Department of the Interior, U.S. Fish and Wildlife Service (March 2000)].

Holms, G. W. 1998. Interactions of sympatric black and grizzly bears in northwest Wyoming. M.S. Thesis, University of Wyoming, Laramie.

Hornocker, M. G. 1962. Population characteristics and social and reproductive behavior of the grizzly bear in Yellowstone National Park. M.S. Thesis, University of Montana, Missoula.

Hovey, F. W., and B. N. McLellan. 1996. Estimating population growth of grizzly bears from the Flathead River drainage using computer simulations of reproduction and survival rates. Canadian Journal of Zoology 74:1409–16.

Irving, L., and J. Krog. 1954. Body temperatures of arctic and subarctic birds and mammals. Journal of Applied Physiology 6:667–80.

Jacoby, M. E., G. V. Hilderbrand, C. Servheen, C. C. Schwartz, S. M. Arthur, T. A. Hanley, C. C. Robbins, and R. Michener. 1999. Trophic relations of brown and black bears in several western North American ecosystems. Journal of Wildlife Management 63:921–29.

Jaczewski, Z., J. Gill, and S. Kozniewski. 1960. Capacity of the different parts of the digestive tract in the brown bear. Transactions of the International Union of Game Biologists 4:146–54.

Janson, C. H., and C. P. Van Schaik. 2000. The behavioral ecology of infanticide by males. Pages 469–94 *in* C. P. Van Schaik and C. H. Janson, eds. Infanticide by males and its implications. Cambridge University Press, New York, New York. USA.

Johnson, D. H. 1980. The comparisons of usage and availability measurements for evaluations of resource preference. Ecology 61:65–71.

Judd, S., and R. R. Knight. 1980. Movements of radio-instrumented grizzly bears within the Yellowstone transport area. International Conference on Bear Research and Management 4:359–67.

Judd, S. L., R. R. Knight, and B. M. Blanchard. 1986. Denning of grizzly bear in the Yellowstone National Park Area. International Conference on Bear Research and Management 6:111–17.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457–81.

Kasworm, W. F., and T. L. Manley. 1990. Road and trail influences on grizzly bears and black bears in northwest Montana. International Conference on Bear Research and Management 8:79–84.

Kendall, K. C., and S. F. Arno. 1990. Whitebark pine—An important but endangered wildlife resource. Pages 264–73 *in* W. C. Schmidt and K. J. McDonald, comps. Proceedings of symposium on whitebark pine ecosystems: Ecology and management of a high mountain resource (General Technical Report INT-270). U.S. Department of Agriculture, Forest Service, Ogden, UT.

Kevan, P. G., and D. M. Kendall. 1997. Liquid assets for fat bankers: Summer nectarivory by migratory moths in the Rocky Mountains, Colorado, U.S.A. Arctic and Alpine Research 29:478–82.

Kingsley, M. C. S., J. A. Nagy, and R. H. Russell. 1983. Patterns of weight gain and loss for grizzly bears in northern Canada. International Conference on Bear Research and Management 5:174–78.

Kingsley, M. C. S., J. A. Nagy, and H. V. Reynolds. 1988. Growth in length and weight of northern brown bears: Differences between sexes and populations. Canadian Journal of Zoology 66:981–86.

Kitchener, A. C. 1994. A review of the evolution, systematics, functional morphology, distribution, and status of the Ursidae. International Zoo News 242:4–24.

Klaver, R. W., J. J. Claar, D. B. Rockwell, H. R. Mays, and C. F. Acevedo. 1986. Grizzly bears, insects, and people: Bear management in the McDonald Peak region, Montana. Pages 204–11 *in* G. Contreras and K. Evans, comps.

Alberta, Montana, Washington, and Idaho. Journal of Wildlife Management 63:911–20.

McLoughlin, P. D. 2000. The spatial organization and habitat selection patterns of barren-ground grizzly bears in the central Arctic. Ph.D. Dissertation, University of Saskatchewan, Saskatoon, Canada.

McLoughlin, P. D., R. L. Case, R. J. Gau, S. H. Ferguson, and F. Messier. 1999. Annual and seasonal movement patterns of barren-ground grizzly bears in the central Northwest Territories. Ursus 11:79–86.

Meagher, M., and J. R. Phillips. 1983. Restoration of natural populations of grizzly and black bear in Yellowstone National Park. International Conference on Bear Research and Management 5:152–58.

Mealey, S. P. 1975. The natural food habits of free ranging grizzly bears in Yellowstone National Park, 1973–1974. M.S. Thesis, Montana State University, Bozeman.

Mealey, S. P. 1980. The natural food habits of grizzly bears in Yellowstone National Park, 1973–74. International Conference on Bear Research and Management 4:281–92.

Melquist, W. 1985. A preliminary survey to determine the status of grizzly bears (*Ursus arctos horribilis*) in the Clearwater National Forest of Idaho. Idaho Cooperative Fish and Wildlife Research Unit, University of Idaho, Moscow.

Merriam, C. H. 1918. Review of the grizzly and big brown bears of North America (genus *Ursus*) with the description of a new genus, *Vetularctos*. North American Fauna 41:1–136.

Merrill, T., D. J. Mattson, R. G. Wright, and H. B. Quigley. 1999. Defining landscapes suitable for restoration of grizzly bears *Ursus arctos* in Idaho. Biological Conservation 87:231–48.

Miller, S. D. 1988. Impacts of increased hunting pressure on the density, structure, and dynamics of brown bear populations in Alaska's Management Unit 13 (Federal Aid in Wildlife Restoration Final Report, Project W-22-6, Job 4.21). Alaska Department of Fish and Game, Juneau.

Miller, S. D. 1990a. Denning ecology of brown bears in southcentral Alaska and comparisons with sympatric black bear populations. International Conference on Bear Research and Management 8:279–87.

Miller, S. D. 1990b. Detection of differences in brown bear density and population composition caused by hunting. International Conference on Bear Research and Management 8:393–404.

Miller, S. D. 1990c. Impact of increased bear hunting on survivorship of young bears. Wildlife Society Bulletin 18:462–67.

Miller, S. D. 1990d. Impacts of increased hunting pressure on the density, structure, and dynamics of brown bear populations in Alaska's Game Management Unit 13 (Project. W-23-3). Alaska Department of Fish and Game, Juneau.

Miller, S. D. 1990e. Population management of bears in North America. International Conference on Bear Research and Management 8:357–73.

Miller, S. D. 1993. Brown bears in Alaska: A statewide management overview (Wildlife Technical Bulletin 11). Alaska Department of Fish and Game, Juneau.

Miller, S. D. 1995a. Impacts of heavy hunting pressure on the density and demographics of brown bear populations in southcentral Alaska (Federal Aid in Wildlife Restoration Progress Report W-24-3, Study 4.26). Alaska Department of Fish and Game, Juneau.

Miller, S. D. 1995b. Impacts of increased hunting pressure on the density, structure, and dynamics of brown bear populations in Alaska's Game Management Unit 13 (Federal Aid in Wildlife Restoration Progress Report W-24-3, Study 4.21). Alaska Department Fish and Game, Juneau.

Miller, S. D. 1997. Impacts of heavy hunting pressure on the density and demographics of brown bear populations in southcentral Alaska (Federal Aid in Wildlife Restoration, Final Report W-24-2, W-24-3, and W-24-4, Study 4.26). Alaska Department of Fish and Game, Juneau.

Miller, S. D., and W. B. Ballard. 1982. Homing of transported Alaskan brown bears. Journal of Wildlife Management 46:869–76.

Miller, S. D., and W. B. Ballard. 1992. Analysis of an effort to increase moose calf survivorship by increased hunting of brown bears in southcentral Alaska. Wildlife Society Bulletin 20:445–54.

Miller, S. D., and J. Schoen. 1999. Status and management of the brown bear in Alaska. Pages 40–46 *in* C. Servheen, S. Herrero, and B. Peyton, comps. Bears: Status survey and conservation action Plan. IUCN/SSC Bear and Polar Bear Specialist Groups, IUCN, Gland, Switzerland, and Cambridge, UK.

Miller, S. D., and R. A. Sellers. 1992. Brown bear density on the Alaska Peninsula at Black Lake, Alaska. Final report on completion of density estimation objectives of cooperative interagency brown bear studies on the Alaska Peninsula. Alaska Department of Fish and Game, Juneau.

Miller, S. D., and V. L. Tutterrow. 1999. Characteristics of nonsport mortalities to brown and black bears and human injuries from bears in Alaska. Ursus 11:235–48.

Miller, S. D., E. F. Becker, and W. B. Ballard. 1987. Black and brown bear density estimates using modified capture–recapture techniques in Alaska. International Conference on Bear Research and Management 7:23–35.

Miller, S. D., G. C. White, R. A. Sellers, H. V. Reynolds, J. W. Schoen, K. Titus, V. G. Barnes, Jr., R. B. Smith, R. R. Nelson, W. B. Ballard, and C. C. Schwartz. 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. Wildlife Monograph 133:1–55.

Miller, S. J., N. Barichello, and D. Tait. 1982. The grizzly bears of the MacKenzie Mountains, Northwest Territories (Completion Report 3). Northwest Territories Wildlife Service, Yellowknife, Canada.

Miller, S. M., S. D. Miller, and D. W. McCollum. 1998. Attitudes toward and relative value of Alaskan brown and black bears to resident voters, resident hunters, and nonresident hunters. Ursus 10:357–76.

Modafferi, R. D. 1984. Review of Alaska Peninsula brown bear investigations (Federal Aid in Wildlife Restoration Final Report Project W-17-10, W17-11, W-21-1, W-21-2, and W-22-1, Job 4.12R). Alaska Department of Fish and Game, Juneau.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223–49.

Mowat, G., and C. Strobeck. 2000. Estimating population size of grizzly bears using hair capture, DNA profiling, and mark–recapture analysis. Journal of Wildlife Management 64:183–93.

Mundy, K. R. D., and W. A. Fuller. 1964. Age determination in the grizzly bear. Journal of Wildlife Management 28:863–66.

Murie, A. 1944. The wolves of Mount McKinley (National Park Service, Fauna Series No. 5). U.S. Government Printing Office, Washington, DC.

Murie, A. 1981. The grizzlies of Mount McKinley (Scientific Monograph Series No. 14). U.S. Department of the Interior, National Park Service, Washington, DC.

Mystrud, I. 1983. Characteristics of summer beds of European brown bears in Norway. International Conference on Bear Research and Management 5:208–22.

Nagy, J. A., and M. A. Haroldson. 1990. Comparisons of some home range and population parameters among four grizzly bear populations in Canada. International Conference on Bear Research and Management 8:227–35.

Nagy, J. A., R. H. Russell, A. M. Pearson, M. C. Kingsley, and B. C. Goski. 1983a. Ecological studies of the grizzly bear in arctic mountains, northern Yukon Territories, 1972 to 1975. Canadian Wildlife Service, Edmonton, Alberta.

Nagy, J. A., R. H. Russell, A. M. Pearson, M. C. Kingsley, and C. B. Larsen. 1983b. A study of grizzly bears on the barren grounds of Tuktoyaktuk Peninsula and Richards Island, Northwest Territories, 1974–1978. Canadian Wildlife Service Report, Edmonton, Alberta.

Nagy, J. A., M. C. S. Kingsley, R. H. Russell, and A. M. Pearson. 1984. Relationship of weight to chest girth in the grizzly bear. Journal of Wildlife Management 48:1439–40.

Nelson, R. A. 1973. Winter sleep in the black bear: A physiologic and metabolic marvel. Mayo Clinic Proceedings 48:733–37.

Nelson, R. A. 1980. Protein and fat metabolism in hibernating bears. Federal Proceedings 39:2955–58.

Nelson, R. A., and T. D. I. Beck. 1984. Hibernation adaptation in the black bear. Implications for management. Proceedings Eastern Workshop on Black Bear Research and Management 7:48–53.

Nelson, R. A., D. L. Steiger, and T. D. I. Beck. 1983a. Neuroendrocine and metabolic interactions in the hibernating black bear. Acta Zoologica Fennica 174:137–41.

Nelson, R. A., G. E. Folk, Jr., E. W. Pfeiffer, J. J. Craighead, C. J. Jonkel, and D. L. Steiger. 1983b. Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. International Conference on Bear Research and Management 5:284–90.

Noss, R. F., and L. D. Harris. 1986. Nodes, networks, and MUMs: Preserving diversity at all scales. Environmental Management 10:299–309.

O'Brien, S. L., and F. G. Lindzey. 1998. Aerial sightability and classification of grizzly bears at moth aggregation sites in the Absaroka Mountain, Wyoming. International Conference on Bear Research and Management 10:427–35.

Odum, E. P. 1959. Fundamentals of ecology, 2nd ed. W. B. Saunders, Philadelphia, PA.

Onoyama, K., and R. Haga. 1982. New record of four fetuses in a litter of Yeso brown bears (*Ursus arctos yesoensis*) Lydekker with mention of prenatal growth and development. Journal of the Mammal Society of Japan 9:1–8.

Schoen, J. W., R. W. Flynn, L. H. Suring, K. Titus, and L. R. Beier. 1994. Habitat-capability model for brown bear in southeast Alaska. International Conference on Bear Research and Management 9(1):327–37.

Schwartz, C. C., and S. M. Arthur. 1999. Radio-tracking large wilderness mammals: Integration of GPS and Argos technology. Ursus 11:261–74.

Schwartz, C. C., K. A. Keating, H. V. Reynolds, III., V. G. Barnes, Jr., R. A. Sellers, J. E. Swenson, S. D. Miller, B. N. McLellan, J. Keay, R. McCann, M. Gibeau, W. F. Wakkenin, R. D. Mace, W. Kasworm, and R. Smith. 2003. Reproductive maturation and senescence in the female brown/grizzly bear. Ursus 14(2) in press.

Sellers, R. D., and L. D. Aumiller. 1994. Brown bear population characteristics at McNeil River, Alaska. International Conference on Bear Research and Management 9(1):283–93.

Servheen, C. 1998. The grizzly bear recovery program: Current status and future considerations. Ursus 10:591–96.

Servheen, C. 1999. Status and management of the grizzly bear in the lower 48 United States. Pages 50–54 *in* C. Servheen, S. Herrero, and B. Peyton, comps. Bears: Status survey and conservation action plan. IUCN/SSC Bear and Polar Bear Specialist Groups, IUCN, Gland, Switzerland, and Cambridge, UK.

Servheen, C., J. Waller, and P. Sandstrom. 2001. Identification and Management of linkage zones for grizzly bears between the large blocks of public land in the Northern Rocky Mountains. Pages 161–98 *in* Proceedings of the 2001. International Conference on Ecology and transportation. September, 2001.

Servheen, G., A. Hamilton, R. Knight, and B. McLellan. 1990. Report of the technical review team: Evaluation of the Bitterroot and North Cascades to sustain viable grizzly bear populations (Report to the Interagency Grizzly Bear Committee). U.S. Fish and Wildlife Service, Boise, ID.

Servheen, C., S. Herrero, and B. Peyton, comps. 1999. Bears: Status survey and conservation action Plan. IUCN/SSC Bear and Polar Bear Specialist Groups, IUCN, Gland, Switzerland, and Cambridge, UK.

Shaffer, M. L. 1978. Determining minimum viable population size: A case study of the grizzly bear (*Ursus arctos* L.). Ph.D. Dissertation, Duke University, Durham, NC.

Shaffer, M. L. 1983. Determining minimum viable population size for the grizzly bear. International Conference on Bear Research and Management 5:133–39.

Shaffer, M. L. 1992. Keeping the grizzly bear in the American West: A strategy for real recovery. Wilderness Society, Washington DC.

Shields, G. F., D. Adams, G. Garner, M. Labelle, J. Pietsch, M. Ramsay, C. Schwartz, K. Titus, and S. Williamson. 2000. Phylogeography of mitochondrial DNA variation in brown bears and polar bears. Molecular Phylogenetics and Evolution 15:319–26.

Simberloff, D. 1999. Biodiversity and bears: A conservation paradigm shift. Ursus 11:25–31.

Smith, J., and J. Hoffman. 1998. Status of white pine blister rust in Intermountain Region white pines (Forest Health Protection Report No. R4-98-02). U.S. Forest Service Intermountain Region, State and Private Forestry.

Smith, R. B., and L. J. Van Daele. 1991. Terror Lake hydroelectric project, Kodiak Island, Alaska. Final report 1. Brown bear studies (1982–86). Alaska Department of Fish and Game and Alaska Power Authority.

Soulé, M. E., 1987. Viable populations for conservation. Cambridge University Press, Cambridge.

Speiss, A. 1976. Labrador grizzly (*Ursus arctos* L.): First skeletal evidence. Journal of Mammalogy 57:787–90.

Speiss, A., and S. Cox. 1977. Discovery of the skull of a grizzly bear in Labrador. Arctic 29:194–200.

Stebler, A. M. 1972. Conservation of the grizzly: Ecologic and cultural considerations. International Conference on Bear Research and Management 2:297–303.

Stonorov, D., and A. W. Stokes. 1972. Social behavior of the Alaska brown bears. International Conference on Bear Research and Management 2:232–42.

Storer, T. I., and L. P. Tevis. 1955. California grizzly. University of California Press, Berkeley.

Stringham, S. F. 1983. Roles of adult males in grizzly bear population biology. International Conference on Bear Research and Management 5:140–51.

Stringham, S. F. 1984. Responses by grizzly bear population dynamics to certain environmental and biosocial factors. Ph.D. Dissertation, University of Tennessee, Knoxville.

Stringham, S. F. 1986. Effects of climate, dump closure, and other factors on Yellowstone grizzly bear litter size. International Conference on Bear Research and Management 6:33–39.

Stringham, S. F. 1990. Grizzly bear reproductive rate relative to body size. International Conference on Bear Research and Management 8:433–43.

Suchy, W., L. L. McDonald, M. D. Strickland, and S. H. Anderson. 1985. New estimates of minimum viable population size for grizzly bears of the Yellowstone ecosystem. Wildlife Society Bulletin 13:223–28.

Suring, L. H., K. R. Barber, C. C. Schwartz, T. N. Bailey, W. C. Shuster, and M. D. Tetreau. 1998. Analysis of cumulative effects on brown bears on the Kenai Peninsula, southcentral Alaska. Ursus 10:107–17.

Swanson, C. S., D. W. McCollum, and M. Maj. 1994. Insights into the economic value of grizzly bears in the Yellowstone recovery area. International Conference on Bear Research and Management 9:575–82.

Swenson, J. E., F. Sandegren, A. Söderberg, A. Bjärvall, R. Franzén, and P. Wabakken. 1997. Infanticide caused by hunting of male bears. Nature 386:450–52.

Taberlet, P., and J. Bouvet. 1994. Mitrochondrial DNA polymorphism phylogeography, and conservation genetics of the brown bear *Ursus arctos* in Europe. Proceedings of the Royal Society London, Series B 255:195–200.

Taberlet, P., J. E. Swenson, F. Sandegren, and A. Bjarvall. 1995. Localization of a contact zone between two highly divergent mitrochondrial DNA lineages of brown bear (*Ursus arctos*) in Scandinavia. Conservation Biology 9:1255–61.

Tabor, G. M. 1996. Yellowstone to Yukon (Y2Y). Report to the Kendall Foundation, Boston, MA.

Tabor, G. M., and M. E. Soulé. 1999. Yellowstone to Yukon (Y2Y). Report to the Wilburforce Foundation, Seattle, WA.

Talbot, S. L., and G. F. Shields. 1996. A phylogeny of the bears (Ursidae) inferred from complete sequences of three mitochondria genes. Molecular Phylogenetics and Evolution 5:567–75.

Taylor, M. K., D. DeMaster, F. L. Bunnell, and R. Schweinsburg. 1987. Modeling the sustainable harvest of female polar bears. Journal of Wildlife Management 51:811–20.

Testa, J. W., W. P. Taylor, and S. D. Miller. 1998. Impacts of increased hunting pressure on the density and dynamics of brown bear populations in southcentral Alaska (Federal Aid in Wildlife Restoration Progress Report, W-27-1, Study 4.28). Alaska Department of Fish and Game, Juneau.

Thenius, E. 1959. Ursidenphylogenese und biostratigraphie. Zeitschrift für Säugertierkunde 24:78–84.

Thomas, D. C. 1977. Metachromatic staining of dental cementum for mammalian age determination. Journal of Wildlife Management 41:207–10.

Thompson, S. D. 1992. Energetics of gestation and lactation in small mammals: Basal metabolic rate and the limits of energy use and reproduction. Pages 213–25 *in* T. Tomasi and T. Horton, eds. Mammalian energetics: Interdisciplinary views of metabolism and reproduction. Cornell University Press, Ithaca, NY.

Titus, K., and L. Beier. 1991. Population and habitat ecology of brown bears on Admiralty and Chichagof Islands (Federal Aid in Wildlife Restoration Project Progress Report W-23-4). Alaska Department of Fish and Game, Juneau.

Titus, K., and J. W. Schoen. 1992. A plan for maintaining viable and well-distributed brown bear populations in southeast Alaska. Pages 171–205 *in* L. H. Suring, D. C. Crocker-Bedford, R. W. Flynn, C. S. Hale, G. C. Iverson, M. D. Kirchhoff, T. E. Schenck, II, L. C. Shea, and K. Titus, eds. A proposed strategy for maintaining well-distributed, viable populations of wildlife associated with old-growth forests in southeast Alaska. Unpublished report. U.S. Department Agriculture Forest Service, Alaska Region, Juneau.

Troyer, W. A., and R. J. Hensel. 1969. The brown bear of Kodiak Island. U.S. Department of the Interior, Bureau of Sport Fish and Wildlife, Branch of Wildlife Refuges, Kodiak, AK.

Tsubota, T., and H. Kanagawa. 1989. Annual changes in serum testosterone levels and spermatogenesis in Hokkaido brown bear, *Ursus arctos yesoensis*. Journal of the Mammalogy Society of Japan 14:11–17.

Tsubota, T., and H. Kanagawa. 1991. Sexual maturity of the Hokkaido brown bear. Asiatic Bear Conference 1:1–9.

Tsubota, T., and H. Kanagawa. 1993. Morphological characteristics of the ovary, uterus and embryo during the delayed implantation period in the Hokkaido brown bear (*Ursus arctos yesoensis*). Journal of Reproductive Development 39:325–31.

Tsubota, T., Y. Takahashi, and H. Kanagawa. 1987. Changes in serum progesterone levels and growth of fetuses in Hokkaido brown bear, *Ursus arctos yesoensis*. International Conference on Bear Research and Management 7:355–58.

U.S. Fish and Wildlife Service. 1982. Grizzly bear recovery plan. U.S. Fish and Wildlife Service, Denver, CO.

U.S. Fish and Wildlife Service. 1993. Grizzly bear recovery plan. Missoula, MT.

U.S. Fish and Wildlife Service. 2000. Grizzly bear recovery in the Bitterroot Ecosystem. Final environmental impact statement. U.S. Department of the Interior, Washington DC.