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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. 1998*a*). As summarized by Craighead and Mitchell (1982) and Waits et al. (1998*a*), 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. 1998*a*). 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; 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. 1998*a*). 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. (1998*a*: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 subspecies 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 additional genes,

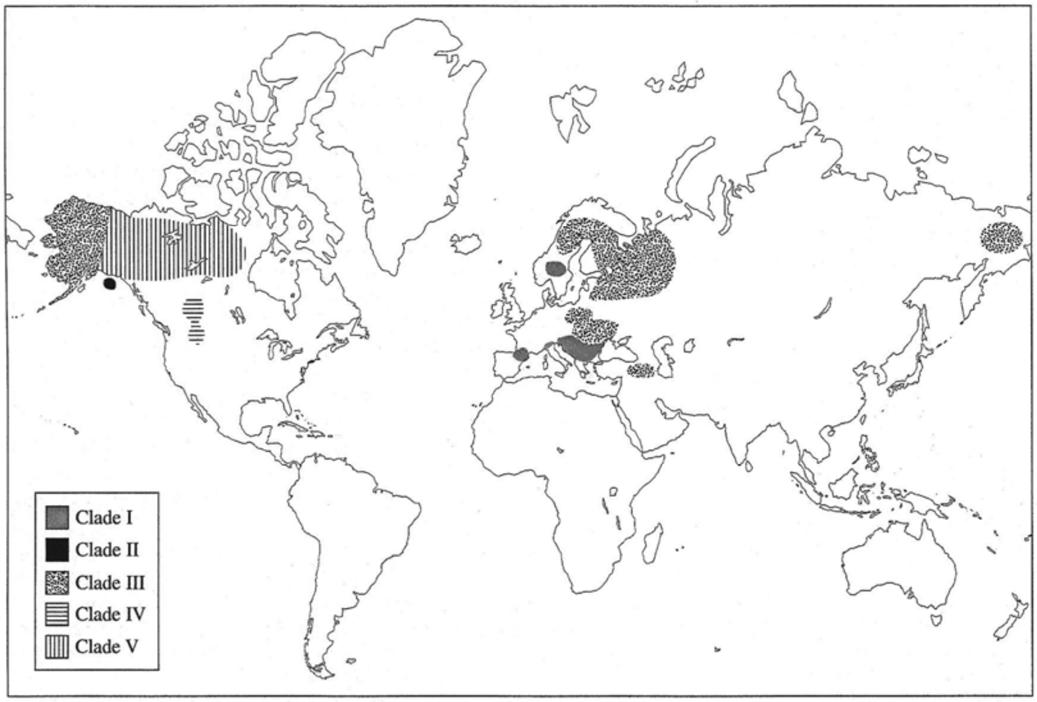

FIGURE 26.1. Worldwide geographic distribution of the five mitochondrial polyogenetic clades in the brown/grizzly bear. Source: Waits et al. (1999).

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

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

Historic 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; Schneider 1977; Craighead and Mitchell 1982). The distribution provided by Rausch (1963) seems to be the most

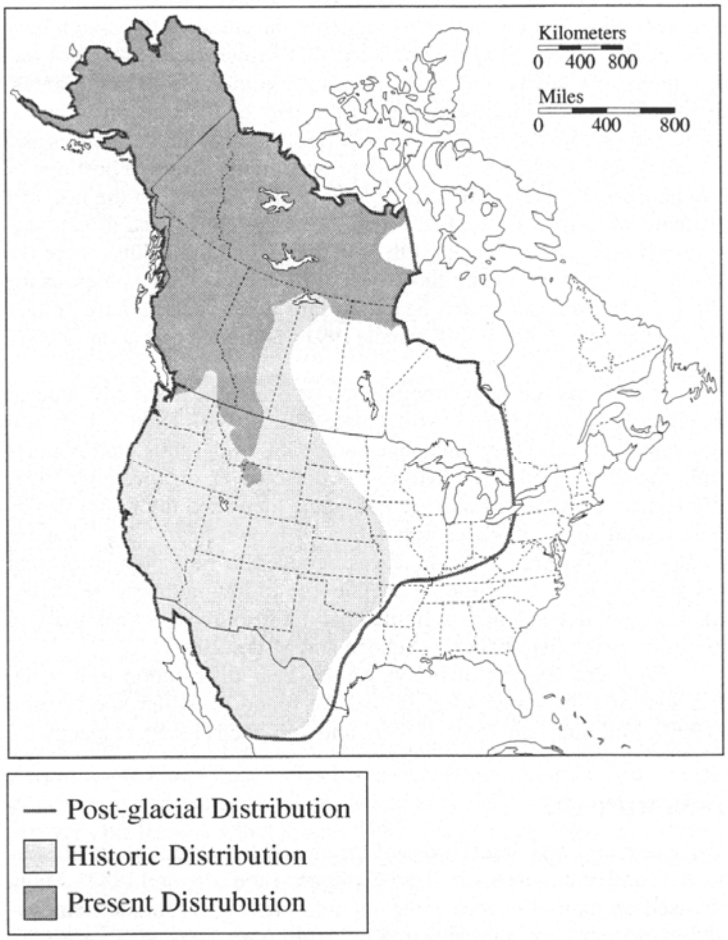

FIGURE 26.2. Postglacial, historical, and current distribution of the brown/grizzly bear. Source: Data from Rausch (1963); Martinka (1976), Servheen et al. (1999).

commonly accepted and we use it here (Fig. 26.2) with additional detail from Herrero (1972). According to MacPherson (1965), the eastern extent of the barren-grounds grizzly was near the Thelon, Back, Dubawnt, and Kazan Rivers in Northwest Territories. In the southwestern extreme of the range in the grassland and chaparral of California, the grizzly probably was numerous, extending to the coast (Herrero 1972). In interior North America, grizzlies used riparian bottoms of the Great Plains. The range extended eastward to the great bend of the Missouri River in North Dakota, southward to the Moreau River in South Dakota, and possibly to the Red River region of Texas (Stebler 1972). The southern extent reached into Mexico.

Current Range. With the advent of European settlement of the North American continent, grizzly bear range was drastically reduced (Mattson et al. 1995). These reductions were greatest in the southern and eastern parts of the range. In the lower 48 states, grizzly bears were eliminated from 98% of their historical range during a 100-year period (Mattson et al. 1995). Grizzlies were extirpated throughout much of their range in the 1920s and 1930s. Thirty-one of 37 bear populations present in 1922 were eliminated by 1975 (Servheen 1999), when the species was declared threatened (USFWS 1993). Currently there are 5 recognized populations south of 49°N, but 3 populations contain <35 individuals each (Servheen 1999). The Yellowstone and Northern Continental Divide populations each contain >350 individuals. Servheen (1999) estimated 800-1020 bears reside in the United States south of Canada. Some people contend that grizzly bears still occupy the Bitterroot Mountains of central Idaho and western Montana, but there is no evidence supporting this belief (Melquist 1985, Groves 1987, Servheen et al. 1990, Kunkel et al. 1991)

Macey (1979) and more recently Banci (1991), Banci et al. (1994), and McLellan and Banci (1999) reviewed the status of the brown bear in Canada. Macey (1979) concluded that brown bears were not endangered in Canada, but were extremely vulnerable in some areas. Brown bears have been extirpated from part of their historical range in Manitoba, Saskatchewan, and Alberta, primarily in the prairies and boreal plains. Densities are most depressed in the southern portions of Canada, particularly in British Columbia and Alberta. In the hot, dry plateaus of British Columbia, brown bears are considered threatened. In inhospitable areas of the north or in the rugged mountains, there are limited human settlements and brown bears are relatively numerous for the habitat, whereas brown bears are rare where people have settled (McLellan and Banci 1999). Banci (1991) estimated that about 25,000 brown bears live in Canada.

Alaska has the largest population of brown bears of any state or province in North America (Miller and Schoen 1999). Their distribution has remained relatively unchanged since the mid-1700s, and populations are considered stable (Miller 1993). However, in November 1998, the Alaska Department of Fish and Game identified the Kenai Peninsula (south of Anchorage) population of brown bears as a "Species of Special Concern" because it was believed to be a population that "…is vulnerable to a significant decline due to low numbers, restricted distribution, dependence on limited habitat resources, or sensitivity to environmental disturbance." (Shoen and Miller 2002).

Excellent reviews of brown/grizzly bear distribution in Alaska, Canada, and the lower 48 states can be found in Miller and Schoen (1999), McLellan and Banci (1999), and Servheen (1999), respectively.

DESCRIPTION

Early accounts and descriptions of the grizzly bear are superficial, subjective, and often sensationalized at best (Craighead and Mitchell 1982). Many focused on natural history, behavior, and hunting techniques emphasizing extremes in body size and strength, with little attention to the typical. The earliest scientific descriptions of the grizzly bear based on adequate sample size were those of Swainson, Baird, and Elliot from the arctic, western United States, and British Columbia, respectively (Storer and Tevis 1955). With the advent of immobilization drugs, our knowledge of individual bear populations has advanced considerably (LeFranc et al. 1987).

General Morphology and Structure. The brown/grizzly bear varies greatly in size and shape throughout the range in North America. However, certain characteristics are consistent. The skeletal structure of the brown bear is larger and heavier than that of most other ursids, but the axial and appendicular skeleton is similar to that of the American black bear (*Ursus americanus*). Brown bears are tetrapedal, with legs of approximately equal length, tapering to large plantigrade feet (Craighead and Mitchell 1982). Each foot has 5 toes ending with a relatively long claw. Foreclaws can reach 8 cm in length and are much larger than on black or polar bears. Claws of *U. arctos* evolved as tools for digging (Herrero 1972) rather than tree climbing or capturing and holding prey as in *U. maritimus*. They walk with a heavy shuffling gait (Pasitschniak-Arts 1993). Features that distinguish the species include a large hump of muscle overlying the scapulae, characteristic skull and dental structure, and in some individuals, color and appearance of the pelage (Craighead and Mitchell 1982).

Size and Weight. Size varies greatly across the North American range, among sex and age classes of bears, and seasonally. Body masses from various populations are reviewed in the Interagency Grizzly Bear compendium (LeFranc et al. 1987) and supplemented with additional information (McLellan 1994). These records illustrate variation in body mass among populations (Table 26.1). Brown bears occupying coastal habitats of Alaska and British Columbia are the largest representative of the species in North America.

Bears from coastal Alaska with access to salmon are the heaviest. For example, males from the Alaska Peninsula (Miller and Sellers 1992) average 357 kg, whereas males from the Yukon (Pearson 1975) average 145 kg. Females from the same areas average 226 and 98 kg, respectively.

Popular literature often sensationalizes the "1000-pound bear." Although brown bears have been documented to reach and exceed this weight (Craighead and Mitchell 1982), most are smaller. Mass in bears is related to diet (Hilderbrand et al. 1999*a*). Bear populations with better nutrition from consuming large quantities of animal flesh (salmon and ungulates) tend to be larger (Fig. 26.3). Bears consuming principally vegetal diets are smaller.

Brown bears are sexually dimorphic, with males about 1.2-2.2 times larger than females (LeFranc et al. 1987; Stringham 1990; Hilderbrand et al. 1999*a*). Differences in body mass between males and females are influenced by age at sexual maturity, samples from within the population, season of sampling, reproductive status, and differential mortality. Any or all of these factors can contribute to a slightly different ratio. Dimorphism begins early in life and is apparent between ages 2 and 4 years (Troyer and Hensel 1969; Pearson 1975, Blanchard 1987). Dimorphism is believed to be related to dominance competition among males during the breeding season.

Body mass is dynamic in brown bears. During late summer and fall, brown bears gain weight rapidly, primarily as fat (Troyer and Hensel 1969; Pearson 1975; Craighead and Mitchell 1982; Kingsley et al. 1983; Nagy et al. 1983*a*, 1983*b;* Blanchard 1987; Hilderbrand et al. 2000) when they feed intensively before denning (Nelson 1980; Nelson et al. 1983*a*). Because bears rely solely on their stored energy reserves during hibernation, this predenning weight gain is essential for reproduction and survival. Peak body mass generally occurs in fall just prior to hibernation. Bears metabolize fat and muscle during the denning period (Hellgren 1998; Hilderbrand et al. 2000).

Weight loss during the denning season depends upon condition of the bear when entering the den (Atkinson and Ramsay 1995; Atkinson et al. 1996; Hilderbrand et al. 1999*a*), length of the denning season, and reproductive status (Hilderbrand et al. 1999*a*). Bears in poor body condition use more muscle mass relative to fat compared to fatter individuals (Figure 1 in Hilderbrand et al. 2000). Daily loss of mass in 6 adult female Alaskan brown bears was

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 populations									
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
MacKenize Mountains	1.2	1.8 (6)	3.8 (5)	---	148 (20)	110 (28)	---	---	Yes
Glacier 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 populations									
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 study period due to intensive harvests.

352 ± 136 g/day over a 208 ± 19-day period (Hilderbrand et al. 2000). Over the course of the winter, 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. 1983*b*). 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.

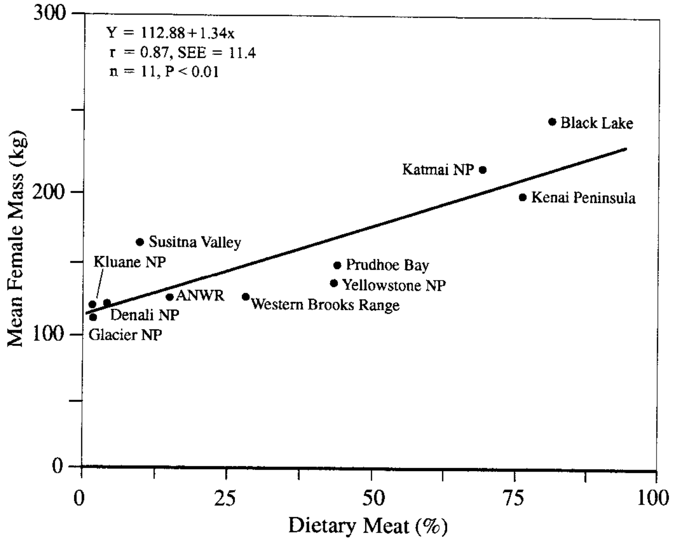

Figure 26.3. Body mass of adult female brown bears and the amount of meat in the diet. Source: Data from Hilderbrand et al. (1999*a*).

Depending upon availability and quality of spring forage, bears can continue to loose 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 onwards. 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 brown with a natal ring of whitish hair around the neck and

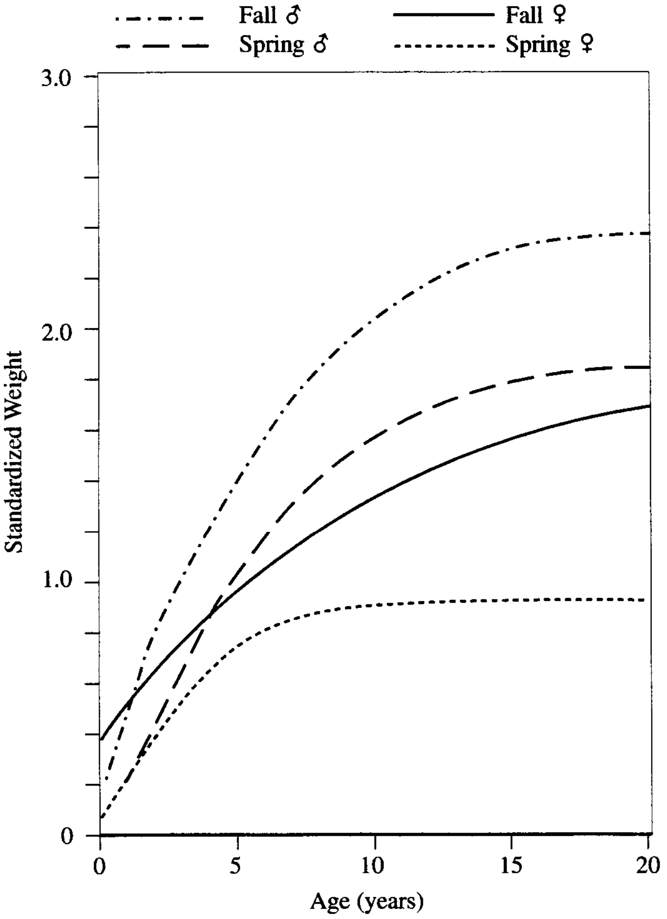

FIGURE 26.4. Growth curves depicting typical growth patterns in brown bears. Curves fitted to spring and fall weights; differences between spring and fall represents summer weight gain. SOURCE: Data from Kingsley et al. (1988) for northern Canadian grizzly bears.

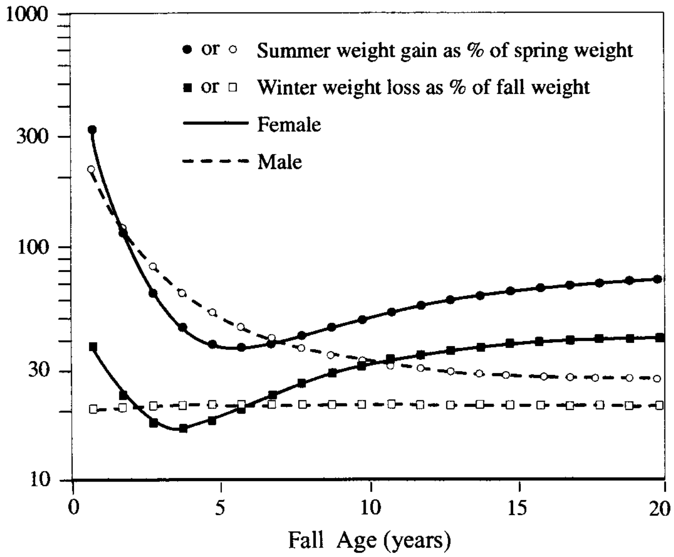

FIGURE 26.5. Annual weight gain and loss in grizzly bears as percentages (y axis), respectively, of spring and fall weight with respect to bear age. SOURCE: After Kingsley et al. (1988).

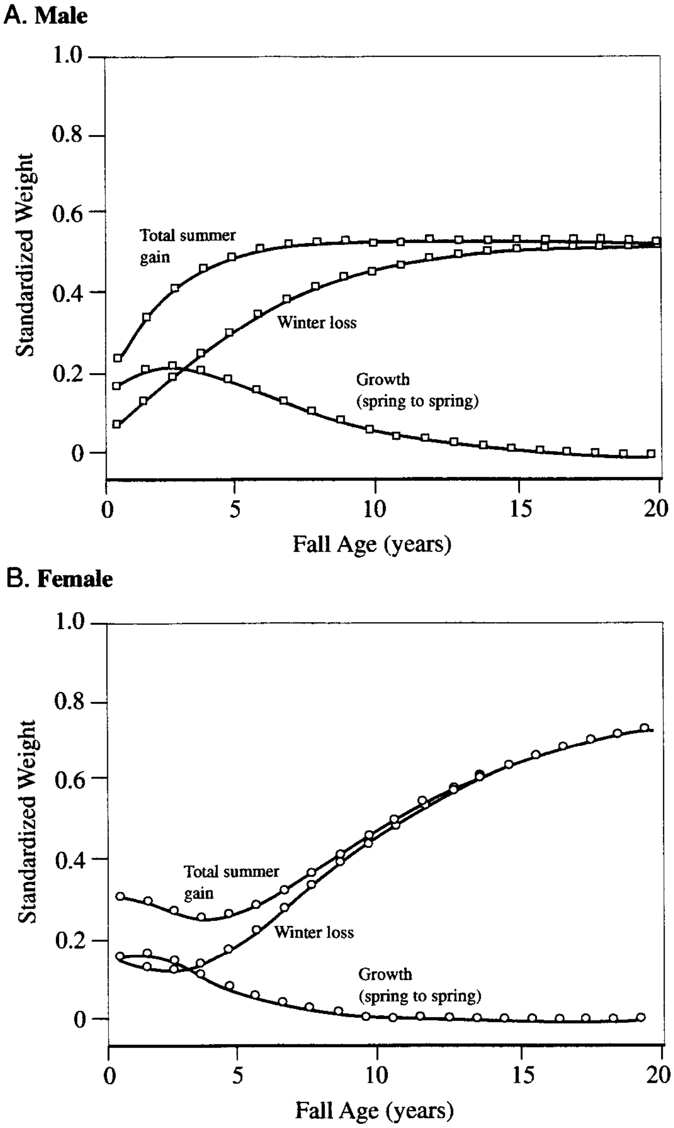

FIGURE 26.6. Magnitude and allocation of summer weight gain in (A) grizzly bear males and (B) females. SOURCE: After Kingsley et al. (1988).

on the chest. The shade of color of a bear varies according to the direction from which light strikes it relative to the position of the viewer. The bear appears darker when facing away from the light because of reduced reflection (Murie 1981).

Reynolds (1987) reported that color in Alaskan brown bears varies regionally and may be related to habitat use. Although all colors from blond to dark brown were found in most populations, lighter colors were more prevalent in open tundra habitats of the Arctic and interior Alaska. In areas where bears used darker, more forested habitats, grizzled, brown, and dark brown pelage was more frequent. Rausch (1953), Erickson (1965), and Quimby and Snarski (1974) supported his generalization. In central and arctic areas of Alaska, the general pattern is a light-colored head and shoulders, dark back, sides, and belly, and darker legs and feet. This color phase is sometimes called Toklat, after the Toklat River in Denali National Park. Overall, color varies from pale-yellow to black. In coastal areas, such as the Alaska Peninsula and Kodiak Island, most bears are uniformly dark brown but exceptions are common.

In the boreal forests of Canada, LeFranc et al. (1987) note that northern Alberta bears are mostly brown. Some have brown underfur 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. 1983*a*). 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. 1983*a*). 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 cm 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) presents 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 = 42 (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 *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 upon 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*.

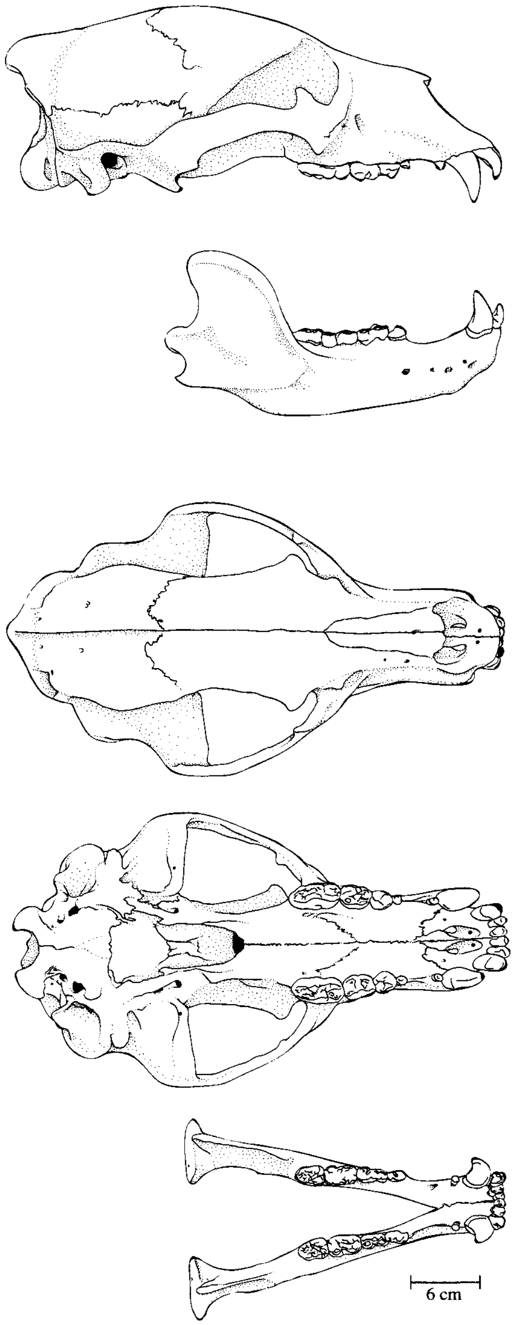

FIGURE 26.7. Skull of the brown/grizzly bear (*Ursus arctos*). From top to bottom: lateral view of cranium, lateral view of mandible, dorsal view of cranium, ventral view of cranium, dorsal view of mandible.

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 74 diploid chromosomes (Ewer 1973; Waits et al. 1999). These consist of 72 autosomes (60 acrocentric and 12 metacentric or submetacentric) and 2 sex chromosomes, a large metacentric X and small acrocentric Y (Pasitschniak-Arts 1993). According to Pasitschniak-Arts (1993) crosses between *U. arctos* and *U. maritimus* in zoos have produced fertile offspring (Davis 1950); hybrids of brown and black bears have been recorded, but the young died when just a few weeks old (Gray 1954).

PHYSIOLOGY

In general, bears exhibit the basic systemic physiology common to other carnivorous mammals (Bielanska-Osuchowska and Szankowska 1970). The digestive system of the grizzly bear is similar in form and function to that of canids and other ursids (Davis 1964). They possess a single stomach (monogastric), which constitutes about half of the total digestive capacity (Jaczewski et al. 1960). The intestines are short and nondifferentiated and are 5.1-7.7 times the total body length (Jaczewski et al. 1960; Bielanska-Osuchowska and Szankowska 1970). The cecum is either absent (Ewer 1973; Mealey 1975) or quite small (Jaczewski et al. 1960). Because bears are noncecal monogastrics, they cannot digest fiber efficiently (Bunnell and Hamilton 1983). Likewise, they cannot significantly increase fat reserves on foliage alone (Poelker and Hartwell 1973; Bunnell and Hamilton 1983; Eagle and Pelton 1983). Highly digestible, high-calorie foods are essential to their diet (Pritchard and Robbins 1990; Welch et al. 1997; Hilderbrand et al. 1999*a*). Foods pass through the digestive system rapidly, with meat, for example, taking about 13 hr and clover (*Trifolium* spp.) only 7 hr (Pritchard and Robbins 1990). Brown bears are unlikely to attain large body size consuming vegetable diets (Welch et al. 1997; Hilderbrand et al. 1999*a*; Jacoby et al. 1999; Rode 1999).

We know very little about the sensory system of the brown bear. The most acute sense is smell, but hearing and eyesight facilitate foraging and predatory behaviors (Pruitt and Burghardt 1977; LeFranc et al. 1987). The popular myth that bears do not see well is contradicted by our personal observations of grizzly bears observing other bears or humans from distances of 1-2 km.

Body temperature in the brown bear ranges from 36.5ºC to 38.5ºC when active, but declines 4-5ºC during hibernation (Irving and Krog 1954; Folk et al. 1968, 1972, 1976; Nelson 1973; Follman et al. 1979; LeFranc et al. 1987). Resting heart rate is 40-50 beats/min in summer and declines to 8-12 beats/min during hibernation (Folk 1967; Folk et al. 1972, 1976). Metabolic rate (51 kcal/kg$^{0.75}$/day) (Farley and Robbins 1995) during the denning period is approximately 68-73% (Watts and Cuyler 1988; Watts and Jonkel 1988; Farley and Robbins 1995) of the interspecific basal rate for active mammals (70 kcal/kg$^{0.75}$/day) (Kleiber 1947); no measurements of metabolic rates are available for the non-denning season.

The most noticeable physiological difference between bears and other carnivores is their state of winter dormancy. Based upon nearly 30 years of research, G.E. Folk, Jr., R.A. Nelson, and others, investigators have unequivocally stated that hibernation is the fitting term for the dormant or torpid state of bears during denning (Hellgren 1998). Nelson (1980) argued that bear hibernation represents the most refined response to starvation of any mammal. Bears exhibit continuous dormancy for up to 7 months without eating, drinking, defecating, or urinating (Craighead and Craighead 1972; Folk et al. 1972). However, others (Watts et al. 1981; Lyman et al. 1982; Pasitschniak-Arts 1993) do not consider winter denning in the bear to be deep hibernation because body temperature does not go below 15ºC. Body temperature in small mammals considered deep hibernators (see Lyman et al. [1982:2] for definitions) decreases from around 39ºC to below 10ºC (Lyman et al. 1982), whereas the bear's body temperature only declines to 31-35ºC. However, as demonstrated in simulations by Guppy (1986), the difference may be related to surface area:volume ratios. Bears depress metabolic rate to the same level as ground squirrels, but are not faced with problems of hypothermia. Bears likely have a more efficient torpor metabolism than the ground squirrel (Guppy 1986).

Female bears produce young during the denning period and face additional energetic costs of gestation and lactation during their winter fast. Ramsay and Dunbrack (1986:735) propose that bears produce small neonates relative to their body size when compared to other large mammals to conserve maternal proteins. Brown bear cubs are born during January–March; they are altricial and generally weigh about 0.5 kg (Pasitschniak-Arts 1993).

Lactation is the most energetically costly mammalian process (Thompson 1992; Robbins 1993). Though lactation in many species occurs when food resources are abundant, brown bear cubs are born in winter when the female is fasting. Farley and Robbins (1995) examined milk composition, lactation characteristics, cub growth, and maternal mass changes for grizzly bears during the denning season. Composition of various constituents in milk varies through time, but when averaged over the lactation period, grizzly bear milk contains 1.3% ash, 33% dry matter, 18% lipids, and 2.3 kcal/g of energy. Grizzly bear milk is more concentrated than that of most terrestrial carnivores. It is similar in protein content to that of the polar bear and the black bear. Brown bear milk contains about half the fat and total energy of polar bear milk. Cubs consume relatively small amounts of milk (353 g/day) during the denning period; milk consumption increases rapidly after den emergence, peaks at midsummer (1350 g/day), and ceases by hibernation. The mass of milk consumed throughout lactation averages 224 kg/cub (Farley and Robbins 1995).

Lactating females loose body mass throughout hibernation. Mass loss for lactating females averages about 500 g/day, and is about 95% higher than for nonlactating grizzly bears of the same mass. Each kilogram of tissue lost by the lactating mother above normal hibernating costs results in 0.7 kg gained by the cub (Farley and Robbins 1995).

Most of the physiological studies of hibernation have been conducted with black bears. Where comparable data are available, it appears that the mechanisms are similar in the grizzly. For a detailed review, see Hellgren (1998).

Nelson et al. (1983*a*) described four behavioral and biochemical patterns in bears. Stage I, hibernation has been described above. Stage II, walking hibernation, occurs after den emergence and lasts 10-14 days in the brown bear. During this period, bears are active, yet anorexic, with low intake of water and limited urine output, suggesting the biochemical stage of hibernation persists in part or in full after denning. Stage III, normal activity, lasts from May-September (this may be shorter for some populations; see Mattson et al. 1991*a*, 1994; Mattson 1997). During this period, bears cannot duplicate the hibernation phase. If deprived of food or water, they burn muscle tissue, suffer dehydration, and become uremic. Body mass increases during this phase, with most (78% in adult female Alaskan bears) as lean tissue (Hilderbrand et al. 1999*a*). Stage IV, hyperphagia, is the period of fat accumulation. Food intake rates increase and animals gain significant body mass, primarily as fat (81% in adult female Alaskan bears) (Hilderbrand et al. 1999*a*).

REPRODUCTION

Reproductive biology of the brown/grizzly bear is similar to that of the black bear (J.J. Craighead et al. 1995). Breeding occurs in late spring. The fertilized ova develop to the blastocyst stage and then arrest development. Implantation occurs in late November, followed by a 6- to 8-week gestation period and birth (Pasitschniak-Arts 1993). On average, females reach sexual maturity sometime between 4 and 7 years of age, and give birth to one to three cubs about every 3 years (Craighead and Mitchell 1982). Offspring remain with the female for 2-4 years before weaning.

There is some confusion in the technical literature regarding to the term *cub*. Some use the term broadly to refer to all dependent young, whereas others use it narrowly referring only to offspring <1 year old. Here we use the term *cub(s)* in the narrow sense, with age calculated from an assumed February birth date. Bears >1 but <2 years old are yearlings; bears >2 but <3 years old are referred to as 2-year-olds. Age at first reproduction, litter size, and interbirth interval vary among populations. These factors are linked to body size which depends on nutrition (Stringham 1990; Hilderbrand et al. 1999*a*). 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 upon 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.

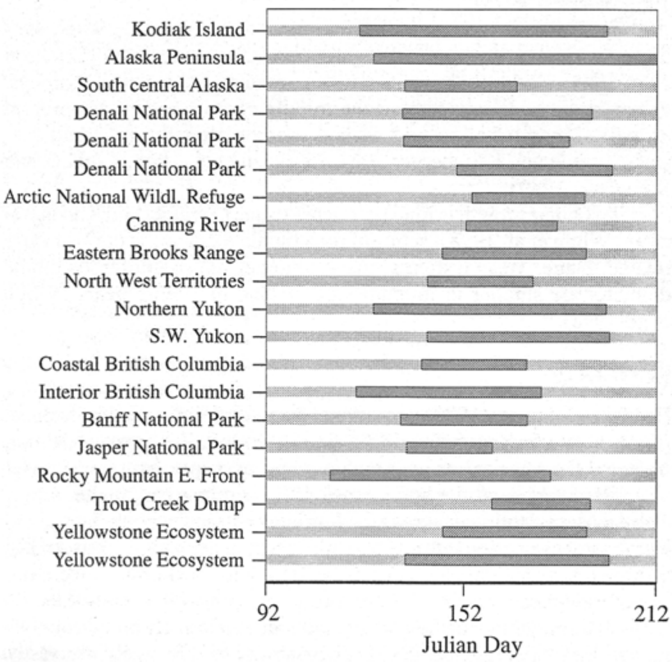

FIGURE 26.8. The period of male-female association, breeding plus postcopulatory association, for grizzly bear populations. Julian days 92 and 213 are the first day of April and last day of July, respectively. SOURCE: Data from LeFranc et al. (1987), Table 7.

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 <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. 1999*a*) (Table 26.1). Nagy and Haroldson (1990), however, caution 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 upon 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. 1999*a*); 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 young and old females producing fewer cubs per litter than prime-age adults (J.J. Craighead et al. 1974, 1995*a*; Sellers and Aumiller 1994). Reported mean litter sizes (Table 26.1) range from 1.7 and 2.5 cubs/litter across North America (Blanchard 1987; LeFranc et al. 1987; Stringham 1990; McLellan 1994), although smaller or larger means have been reported within a year or age class (Sellers and Aumiller 1994; Pac and Dood 1998). Litter size typically averages close to 2, and has less demographic significance than age at first parturition, interbirth interval, and cub survivorship.

Interbirth Interval. The interval between production of cubs is related to maternal nutrition and litter loss before weaning, but is generally ≥3 years in North America (Table 26.1). Females that lose either cub or yearling litters can have shorter interbirth intervals, but from a demographic standpoint this statistic may be misleading. Females that wean offspring as yearlings (Craighead and Mitchell 1982) can rebreed and produce their next litters at a shorter interval (2 years) which is demographically meaningful if the offspring survive to adulthood. For most females that successfully rear their offspring to weaning, the interval between litters is 3 years, but can extend up to 6 years (Craighead and Mitchell 1982; Stringham 1990; McLellan 1994; Miller 1997). Most cubs remain with their mother for 2.5 years but some are weaned at 1.5 years (this is rare in North America) or remain as long 4.5 years (Reynolds 1976; McLellan 1994).

Method of calculation can influence the reproductive interval statistic. Inclusion of only females completing a reproductive cycle (litter to litter) results in an estimate that is biased low. This is because longer cycles are more likely to be missed because some animals die or have radiocollar failure prior to their next successful litter production. Interweaning interval, the time between successful weaning of offspring, is a more informative statistic from a demographic perspective, but is very difficult to quantify because of the number of years required to monitor each female. Inclusion or exclusion of incomplete intervals also influences calculation of this statistic. Miller (1997) calculated interweaning interval in Alaska at 3.2 years when including only complete intervals. The same statistic including only incomplete or both complete and incomplete was 5.0 and 3.5 years, respectively.

Depending on maternal body condition, age, and other factors, adult females may or may not produce their next cub litter the year following loss or weaning of offspring. In rich environments, females may be more likely to produce a litter in the year following litter loss or weaning, whereas in poor environments, they may require additional year(s) to replenish body reserves (Reynolds 1976; Reynolds and Hechtel 1980, 1984; Nagy et al. 1983*b*; Case and Buckland 1998).

Reproductive Rates. Natality can be expressed in various ways, but for large mammals it is common to express it as birth rate per unit of time or per female per unit time (Odum 1959). Natality can be used synonymously with maternity, although the latter generally expresses the number of offspring produced by an adult female in a given breeding season (Akcakaya et al. 1999). Natality is derived from litter size and interbirth interval, and so it varies among brown bear populations. Natality (cubs/female/year) varies from a low of 0.42 to as high as 1.07 (Stringham 1990), although the upper value was based on only four litters. A more recent review (Case and Buckland 1998) presents an upper value of 0.87.

Population ecologists are interested in the number of female offspring produced per reproductive female per year. Most assume an equal sex ratio at birth (Eberhardt 1990), although there are data suggesting a slight predominance of male cubs (55-59%) born in some populations (Craighead et al. 1974; Craighead and Mitchell 1982; Knight and Eberhardt 1985, 1987). The sex for 1326 cubs born in zoos was 51% male (U.S.Fish and Wildlife Service 1993:Appendix C).

Reproductive Longevity. Craighead and Mitchell (1982) and Pasitschniak-Arts (1993) indicate that reproductive longevity approximates physical longevity. A recent study, which compiled data from 20 geographically distinct areas across North America and Sweden, clearly demonstrates that reproductive senescence in brown bears occurs before physical senescence (Schwartz et al. 2003). Maximum per capita litter production occurred at age 8.7 years and reproductive performance remained relatively high between about 8 and 25 years of age. Thereafter, productivity declined rapidly, with the rate of decline peaking around age 28 years.

Delayed Implantation. Grizzly bears exhibit obligate delayed implantation or embryonic diapause (Renfree and Calaby 1981). Studies in brown bears describe the presence of unimplanted embryos in the uterus several months after mating season (Craighead et al. 1969; Tsubota and Kanagawa 1993). Implantation is assumed to occur in late November to early December as based on changes in serum progesterone concentrations and fetal growth (Tsubota et al. 1987). For more information on delayed implantation in bears, see Chapter 25.

Male Reproductive Characteristics. White et al. (1998) provide an excellent review of the reproductive characteristics of male grizzly bears. Based upon presence or absence of spermatozoa in the lumen of the seminiferous tubules, mean age of sexual maturity in a sample 20 grizzly bears from the continental Unites States was 5.5 years (White et al. 1998). The youngest bear with fully-formed spermatozoa was 3.5 years old and killed in July. Only 1 of 11 bears that were ≤4.5 years of age had spermatozoa, whereas 8 of 9 bears ≥5.5 years of age did (White et al. 1998). Erickson et al. (1968) reported spermatozoa in seminiferous tubules of brown bears in Alaska at 4.5 years of age, whereas Pearson (1975) reported them in bears 5-7 years of age. In Hokkaido, Tsubota and Kanagawa (1991) concluded that sexual maturity in captive brown bears was reached between 2 and 5 years of age. As with females, sexual maturity in males is probably related to nutrition; variation among populations is expected.

Testicular mass is greatest during the breeding season, regresses by September, and is smallest by mid- to late October. By late September, sperm are no longer produced, although they may be present in the epididymides (Erickson et al. 1964, 1968; Pearson 1975). By mid- to late October, or early November, testicular regression is nearly complete; by mid-November the testicles are infiltrated by adipose tissue and loose fibrous connective tissue (Erickson et al. 1964; Pearson 1975; Tsubota and Kanagawa 1989). Testicular weights in early winter are the lowest found in mature bears through the year (Erickson et al. 1964, 1968; Pearson 1975).

Testicular recrudescence begins prior to den emergence, when seminiferous tubules enlarge and Leydig cell activity increases (Erickson et al. 1964). Spermatogenesis, with spermatozoa in the epididymides, occurs in bears in late May to the middle of July. Sperm are present at least 1 month before and several months after the breeding season (Dittrich and Kronberger 1963; Erickson et al. 1968; Tsubota and Kanagawa 1989).

Testicular growth is linearly related to age (Tsubota and Kanagawa 1991; White et al. 1998); seminiferous tubule diameter is curvilinearly related to age. Mean testicular mass, volume, and seminiferous tubule diameter are smaller in immature bears than in mature bears (White et al. 1998).

ECOLOGY

Habitat. Johnson (1980) considered habitat selection a hierarchical process, with four spatial scales, defined as orders. First-order selection included the physical or geographic range of a species; second-order selection operates at the home range scale within a geographic range. Third-order selection occurs at feeding sites within the home range, and forth-order refers to specific foraging decisions. Most studies of brown bear habitat use focus on second- and third-order selection.

Brown bears currently occupy a variety of primary habitats (first-order selection) throughout North America, indicating relatively broad environmental limits (Craighead 1998). Their ability to effectively use vastly different landscapes can be attributed to their omnivorous generalist lifestyle and intelligence, which in effect translate to adaptability. Because the active season for brown bears is compressed to 5-7 months, during which bears must gain sufficient weight to supply their energetic 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. 1983*b*; 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) spring/early-summer preberry period, when bears forage on a variety of locally available graminoids, forbs, and roots; and (2) summer/early-fall berry-producing period when bears fatten on locally available berry crops (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. 1999*a*). Use of ungulates abates during summer as bears use habitats that supply a variety of graminoids, forbs, and root crops (Mattson et al. 1991*a*). 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. 1991*a*) and army cutworm moths (*Euxoa auxiliaris*) at insect aggregation sites (Mattson et al. 1991*b*; 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 defines 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 among 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 to 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. 1983*b*), are usually more variable where key fall foraging opportunities are temporally and spatially unpredictable.

Table 26.2. Estimated mean home ranges of grizzly bears in North America

	Females		Males	
Study Area	Range (km^2)	*n*	Range (km^2)	*n*
Admiralty Island (Hawk Inlet), Alaska	24	12	115	6
Khutzeymateen River Valley, BC[a]	52	13	130	4
Kodiak Island, Alaska	71	33	185	6
Kluane National Park, Yukon	86	8	287	5
Revelstoke, BC	89	14	318	23
South Fork Flathead, Montana	99	2	286	5
Alaska Range	132	11	710	6
Mission Mountains, Montana	133	2	1398	3
Ivvavik National Park, Yukon[a]	149	15	447	8
Copper River Delta, Alaska[b]	174	4	295	2
Kananaskis, Alberta	179	5	1198	4
Akamina-Kishinena/Flathead, BC	200	5	446	5
Northern Yukon[c]	210	8	645	6
Western Brooks Range, Alaska	225	35	872	14
East Front Montana	226	3	747	5
Eastern Brooks Range, Alaska[c, d]	230	8	702	5
MacKenzie Mountains, NWT	265	6	---	---
Yellowstone National Park, Wyoming	281	48	874	28
Alaska Peninsula	293	30	262	4
Jasper National Park, Alberta[a]	331	6	948	6
West-central Alberta[e]	364	---	1918	17
Selkirk Mountains, Idaho	402	2	---	---
Upper Susitna River Basin, Alaska[c]	408	13	769	10
Tuktoyaktuk Peninsula, NWT[e]	670	---	1154	7
Noatak River, Alaska	993	33	1437	15
Anderson-Horton Rivers, NWT	1182	14	433	7
Central Northwest Territories	2434	35	8171	19

Source: After McLoughlin et al. (1999).

Note: Ranges are primarily adult annual home ranges calculated using the minimum convex polygon approach unless otherwise indicated; weighted means were calculated if ranges were estimated with small or variable numbers of locations. Ordered on female home range size.

[a] Weighted means calculated from data presented.

[b] Cited in LeFranc et al. (1987:28-30).

[c] Estimate contains some multiannual ranges (Woods et al. 1997).

[d] Ranges calculated using the modified exclusive boundary technique.

[e] Weighted means cited in Nagy and Haroldson (1990). For females, data are presented as the midpoint between the mean for females with and without young, except for the northern Yukon, where the mean is only for females without young.

Except for subadult bears that may not have established permanent home ranges, female brown bears exhibit a high degree of range fidelity, especially during spring (Nagy et al. 1983*a,* 1983*b*; Aune and Kasworm 1989; Blanchard and Knight 1991). Fidelity to fall ranges is more variable due to unpredictability in abundance and location of fall foods. If key fall foods fail in areas where traditional use has occurred, bears must search out alternative food. During failure of key natural food items, the search for alternative foods often results in an increased number of bear-human conflicts and an increase in human-caused bear mortality (Blanchard 1990; Riley et al. 1994; Blanchard and Knight 1995).

At natural feeding sites (salmon streams) and unnatural sites (garbage dumps) where bears congregate, spacing is effected through intraspecific aggression and formation of dominance hierarchies (Hornocker 1962; Stonorov and Stokes 1972). Aggression arguably forms the basis for social organization in all bears and also probably functions to affect spacing among individuals not aggregated at concentrated food resources (Lindzey and Meslow 1977). Classical territorialism (Burt 1943; Brown and Orians 1970) has not been found in brown bear populations (Mace and Waller 1997); but this may be a difference in degree rather than kind of sociality, as both hierarchies and territories are manifestations of aggressiveness within a species (Fisler 1969).

Natal philopatry (Waser and Jones 1983) may be viewed as an extension of maternal care past the age of independence. Rogers (1977) postulated that by residing within maternal ranges, yearling black bears are buffered from social conflicts while they continue to mature. The same may be true for newly independent grizzly bears that continue to reside within their maternal range. Philopatry beyond 3 years of age in brown bears is sexually biased toward females. Dispersal of subadult males is common, whereas female dispersal is rare in these age classes (Glenn and Miller 1980; Blanchard and Knight 1991). Waser and Jones (1983) commented that sex-biased philopatry tends to be stronger in long-lived species whose adults are iteroparous. This trend is consistent with the views that sex-biases reflect selection against inbreeding or that reproductive competition with parents discourages philopatry in one sex or the other (Waser and Jones 1983). Both views appear valid for differential dispersal among subadult brown bears. However, intrinsic rather than extrinsic factors probably influence male dispersal. Philopatric female offspring have the selective advantage of range familiarity (Waser and Jones 1983) and can occupy vacancies that may occur in adjacent habitats. Having close kin as neighbors may also decrease the cost of mutual tolerance (Waser and Jones 1983) and account in part for the considerable home range overlap observed among females (Mace and Waller 1997; Holms 1998).

Denning. Denning behavior in bears has been described as an elaborate bedding process that probably evolved as a result of adverse environmental conditions, primarily seasonal lack of food and unfavorable weather (Mystrud 1983). Nelson and Beck (1984) separated the physiological from the behavioral aspects of denning in black bears. They characterized denning as the physical act of reducing mobility and presumably conserving energy by entering a

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	Jun
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.

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. (1983*a*) report that the physiological condition is not readily and/or intermittently attained in response to fluctuating weather and suggest 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. 1983*b*). Hellgren (1998) provides 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. 1983*b*).

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 (1990*a*) 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 the selection and construction. Habitats used for denning vary from open tundra to forested sites, depending upon availability to local populations (Harding 1976; Vroom et al. 1977; Judd et al. 1986; Schoen et al. 1987; Van Daele et al. 1990).

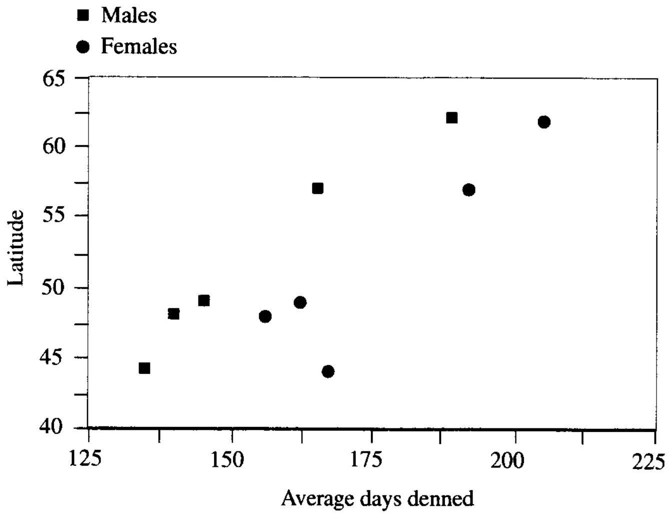

FIGURE 26.9. Average days denned relative to latitude for five interior brown bear study areas. SOURCE: Data from Aune et al. (1986), Judd et al. (1986), Schoen et al. (1987), Miller (1990*a*), Mace and Waller (1997).

TABLE 26.4. Topographic and habitat characteristics [mean(range)] and den construction type of brown bear dens in North America

		Slope Use	Elevation (m)		Den Construction (%)[a]				Habitat Type (%)[b]				
Location	°N	(deg)	Used	Available	*n*	Exc	Cave	Sn	*n*	Tun	For	Eco	Alp
N Yukon	70	40 (20-80)	---	---	24	96	---	4	24	100	---	---	---
N Alaska	70	54	816	---	29	93	7	---	29	---	---	10	90
N Alaska	70	---	1063	---	49	70	30	---	---	---	---	---	---
NW Alaska	68	>30	500	0-1200	86	100	---	---	---	---	---	---	---
N Alaska	68	--- (20-35)	---	---	52	75	25	---	---	---	---	---	---
Central Alaska	62	32 (11-60)	1200 (320-1626)	---	96	99	1	---	102	---	---	48	52
SW Yukon	62	35 (30-40)	1250	---	10	100	---	---	---	---	---	---	---
SE Alaska[c]	57	35 (5-75)	640 (6-1190)	1-1400	38	29	63	8	38	---	52	22	13
Kodiak Island (2 sites)	57	>45	450 (128-915) 665 (91-1189)	0-1000 0-1300	135	82	13	5	320	---	1	43	56
SW Alaska	57	40 (0-60)	450 (30-1000)	0-1200	30	96	---	4	30	---	---	50	50
Rocky Mts.	53	57	2147	---	60	93	7	---	60	---	---	100	---
Rocky Mts.	53	26	2057	---	---	---	---	---	24	---	42	8	50
Jasper NP	53	27 (15-40)	2236	---	10	90	10	---	---	---	---	---	---
Banff NP	53	33 (21-35)	2200 (2050-2300)	1300-3500	47	100	---	---	38	---	71	29	---
NW Montana	48	30 (21-35)	2124 (2050-2500)	850-3000	15	100	---	---	---	---	---	---	---
NW Montana	48	57 (51-62)	2166	1280-2800	---	---	---	---	---	---	---	---	---
Yellowstone NP	44	45 (30-60)	2470 (2000-3050)	1500-4200	33	91	6	3	55	---	100	---	---
Yellowstone NP	44	---	---	---	11	100	---	---	---	---	---	---	---

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

[a] Exc, Excavated; Cave, natural cave or cavity; Sn, snow den.

[b] Tun, Tundra/muskeg; For, forest/swamp forest and shrub; Eco, forest/alpine ecotone; Alp, alpine meadows.

[c] Habitat type does not include rock.

Selection of den sites with a steep slope relative to available slopes was a consistent pattern among studied populations. Aspect and elevation of den sites were much more variable within and among study areas. Female brown bear generally exhibit greater fidelity to den-areas than do males (Linnell et al. 2000).

Security at den sites appears to be an important factor, especially if human disturbance occurs near the time of den entry. Craighead and Craighead (1972) observed that bears disturbed by their approach were more likely to abandon dens shortly after entry than they were during midwinter. Reynolds et al. (1986) observed increases in activity, heart rate, and one instance of possible den abandonment by brown bears that were likely due to activities of seismic crews working near den sites. However, they concluded that the effects of these activities on denned bears were probably minimal. Mace and Waller (1997) did not observe any overt effects of snowmobiles within 2 km of dens in western Montana. They believed the greatest potential impact on bears was during spring when females with cubs were still confined to the vicinity of the den, and also after bears had moved to gentler terrain more suitable to use by snow machines. Predictable denning chronology and the behavioral plasticity bears exhibit toward den and den site characteristics suggest potential human impacts on denning brown bears may be mitigated by careful consideration when implementing strategies for human activity.

FEEDING HABITS

As a group, bear species deviate from most other meat-eating members of the Carnivora by the volume and variety of vegetative foods in their diets. Comparing the three North American bear species, feeding habits of brown bears fall somewhere between those of the largely herbivorous black bear and the primarily carnivorous polar bear. Brown bears are opportunistic omnivores; few taxa, from insects to vertebrates and fungi to angiosperms, are overlooked as potential foods. Evolutionarily, brown bears have developed several adaptations for herbivory, including expansion of molar chewing surfaces and longer claws for digging. Nevertheless, they have maintained an unspecialized digestive system capable of digesting protein with efficiency equal to that of obligate carnivores (Bunnell and Hamilton 1983).

Most commonly, brown bear feeding habits have been quantified by analysis of scat contents. However, because of the Differential digestibility of foods, contents of fecal residue are rarely equivalent to amounts of foods ingested by bears. The resulting underestimation of highly digestible foods is most pronounced for meat and fish diets (Hewitt and Robbins 1996). Fecal correction factors have been developed to convert results of scat analyses to actual volume of foods consumed, however, high variability in residues relative to methods of feeding reduces their utility (Hewitt and Robbins 1996). Recently, analyses of stable isotopes in hair and bone samples have been used to assess the relative importance of terrestrial animal, marine fish, and plant matter to brown bear populations (Hilderbrand et al. 1999*a*; Jacoby et al. 1999).

Major foods consumed by brown bears (LeFranc et al. 1987) can be grouped a variety of ways. Major categories, characterized by taxonomic group and method of acquisition, include (1) vegetative matter readily available by grazing, including graminoids, horsetails (*Equisetum* spp.), and forbs; (2) roots, corms, and bulbs acquired by digging, including hedysarum (*Hedysarum* spp.), biscuitroot (*Lomatium* spp.), glacier lily (*Erythronium* spp.), and yampa (*Perideridia* spp.); (3) fruits harvested from shrubs, including huckleberries/blueberries (*Vaccinium* spp.), buffaloberry (*Shepherdia* spp.), bearberry (*Arctostaphylos* spp.), and American devil's club (*Oplopanax horridus*); (4) whitebark pine nuts excavated from red squirrel (*Tamiasciurus hudsonicus*) middens; (5) insects harvested from nests or aggregation sites, including ants (Formicidae), wasps (Vespidae), army cutworm moths, and ladybird beetles (*Hippodamia casey*); (6) mammals and birds, acquired through predation or scavenging, including ungulates and rodents; and (7) fish acquired through predation or scavenging, including salmon and trout (*Oncorhynchus* spp.).

Grizzly bears commonly consume herbaceous vegetation during spring and early summer in many ecosystems. Even in areas with abundant meat or fish resources, grasses, forbs, and sedges can make up the majority of the diet in spring and early summer (LeFranc et al. 1987). In the northern Rocky Mountains (McLellan and Hovey 1995) and in captive feeding studies (Rode et al. 2001), brown bears selected forbs over grasses. This is likely because forbs retain more of their nutritional value longer than grasses with advancing phenology (McLellan and Hovey 1995). In captive feeding trials, small brown bears met their nutritional needs and gained weight on herbaceous diets. Very large bears had difficulty meeting their energy requirements on vegetation 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. 1999*a*).

Due to high digestibility and energy content, animal matter is arguably a highly valuable bear food (Welch et al. 1997; Hilderbrand et al. 1999*a*). 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. 1983*b*; 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. 1991*b*; 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. 1991*a*; 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. 1999*a*). 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. (1999*a*) 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 (see 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 1990*b*). Age of males and females in harvested populations are younger and older, respectively, with intensive harvest (Miller 1990*b*), 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 26.5. Age and sex composition of selected grizzly bear populations in North America with multiple years of study

Location	Years of Study	Cubs (%)	Yearlings (%)	Subadults (%)	Adults (%) (age, years)	M:F Adult Sex Ratio	Hunted?	Reference
Alaska Peninsula	5	25.0	15.0	34.3	25.6 (>4)	15:85	Yes	Glenn (1975)
Northwest Territories	3	15.0	8.0	18.0	59.0 (>4)	37:63	Yes	Clarkson and Liepins (1994)
Northwest Territories	4	15.6	13.3	34.6	36.5 (>6)	31:69	Yes	Nagy et al. (1983*b*)
Southeast British Columbia	8	21.5	17.5	26.5	34.5 (>5)	38:62	Yes	McLellan (1989*a*)
Swan Mountains, Montana	7	16.9	10.5	27.2	48.2 (>4)	32:68	No	Mace and Waller (1998)
Yellowstone National Park	9	18.7	13	25.1	43.2 (>4)	46:54	No	J.J. Craighead et al. (1995)

males have a lower survival rate. Differential mortality is apparent between the genders following weaning. These differences are due to gender-linked behavioral characteristics including dispersal, denning chronology, home range size, and vulnerability to harvest (Bunnell and Tait 1980). Sex ratio of the adult population is skewed toward females (Tables 26.1 and 26.5) in heavily harvested populations such as the Black Lake area on the Alaska Peninsula (Glenn 1975) and nearly equal in unharvested populations as in Yellowstone National Park (J.J. Craighead et al. 1995). Variation in sex ratio and age structure among populations is primarily driven by differential mortality among the various gender-age classes and is discussed below.

Survival. Survival in bears is estimated in various ways. In some studies, a simple ratio of animals dead to alive at the end of a study or year is used. If a sample of animals is marked at the start of a period of interest, calculation of survival and cause-specific mortality rates as simple percentages is appropriate (Hessler et al. 1970). More often, animals are radio-marked at different times or even tracked during periods for which survival rates differ; simple ratios applied to such sampling lead to serious biases (Heisey and Fuller 1985). As a consequence, more sophisticated analytical techniques have been developed to correct such biases (White and Garrott 1990). One commonly applied method is the Kaplan-Meier or product limit estimator (Kaplan and Meier 1958). The Kaplan-Meier approach is simple and flexible and allows for staggered entry of newly tagged animals. Although this approach is widely used to estimate survival, it is not uniquely the best in all circumstances (Pollock et al. 1989).

Many estimates of survival rates in grizzly bears are generated with the Kaplan-Meier approach, making it easier for comparisons among populations. A sample of recent studies (Table 26.6) indicates that annual survival of adult females is usually quite high (≥0.90%). Survival of adult males varies among populations, but is generally lower in hunted populations (Tables 26.1 and 26.6). Subadult female survival is also high, normally equal to or slightly less than adult female survival. Subadult male survival can be quite variable, but tends to be lower than that of the other independent bears. Survival of dependent young is lower than adults; yearling survival is usually greater than that of cubs.

Cub survival is generally estimated by tracking the fate of cubs of radio-marked females. Because cubs are seldom collared, actual causes of mortality are difficult to document. Cub mortality is highly variable (Tables 26.1 and 26.6) and can be as low as 13% or as high as 44%. Modafferi (1984) reported 31% mortality for cubs on the Alaskan Peninsula between the ages of 0.5 and 1.5 years. From 1978 to 1991, 31% of observed cubs at McNeil River Bear Sanctuary disappeared between 0.5 and 1.5 years of age (Sellers and Aumiller 1994). Where litters were typically observed shortly after den emergence in Alaska, reported cub mortality was 33% in south-central Alaska (Miller 1988), 29% in the north-central Alaska Range (Reynolds 1993), and 37% on Kodiak Island (Smith and Van Daele 1991). Cub mortality was estimated at 9% in the Northern Continental Divide ecosystem (Aune et al. 1994).

Management agencies often resort to translocation to reduce human-caused mortality associated with problem bears. Relocating grizzly bears from human-bear conflict situations is often a short-term solution to an immediate crisis because many bears return to the conflict site (Judd and Knight 1980; Miller and Ballard 1982). Blanchard and Knight (1995) found that survival rate of transported

TABLE 26.6. Kaplan-Meier survival estimates for several North American grizzly bear populations

Location	Adult Male	Adult female	Subadult Male	Subadult female	Yearling	Cub	Age of Adults (years)	Reference
Noatak, AK	0.91	0.94	---	0.89[a]	0.89[a]	0.87	≥5	Ballard et al. (1991)
Nelchina, AK	0.80	0.92	---	---	---	0.69	≥5	Miller (1990*c*, 1997)
McNeil River, AK	0.94	0.93	---	---	0.89[b]	0.67[b]	≥5	Sellers and Aumiller (1994)
Mountain Parks, Canada[c]	0.89	0.91	0.74	0.95	---	---	≥6	McLellan et al. (1999)
Flathead River, British Columbia	0.92	0.94	0.91	0.94	0.88	0.82	>5	McLellan (1989*b*)
Blackfeet-Waterton[d]	0.62	0.92	0.80	0.86	---	---	≥6	McLellan et al. (1999)
Selkirk-Yaak[e]	0.84	0.95	0.81	0.93	---	---	≥6	McLellan et al. (1999)
North Fork Flathead, MT	0.89	0.96	0.78	0.94	---	---	≥6	McLellan et al. (1999)
South Fork Flathead, MT	0.89	0.89	0.78	0.87	---	---	≥6	McLellan et al. (1999)
Swan Mountains, MT	0.87	0.90	0.83	0.83	0.90	0.77	≥5	Mace and Waller (1998)
Rocky Mountain East Front, MT	0.811	0.94	0.66	0.92	0.82[f]	0.82[f]	≥5	Aune and Kasworm (1989)
Greater Yellowstone Ecosystem	---	0.94	---	0.80[g]	---[g]	0.84	≥5	Eberhardt (1995)

NOTE: Survival generally was estimated from radio-collared bears; cub and yearling survival was estimated for most studies by observing marked females with offspring.

[a] Calculations of survival for yearlings combined males and females.

[b] Early survival prior to arrival at the sanctuary not recorded. Estimate is high relative to survival estimated from den emergence to den entrance in other studies.

[c] Includes Jasper, Cascade Valley, Eastern Slope, Upper Columbia, Yoho-Kootenay, and Kananaskis areas that are Canadian national and provincial parks.

[d] Waterton and the Blackfeet Indian Reservation are adjacent and some bears move between study areas; they were pooled.

[e] The Cabinet-Yaak Ecosystem and Selkirk Mountains encompass ecosystems in both the continental United States and Canada. Although geographically distinct, their management goals were similar and were combined to improve sample size.

[f] Cubs included with yearlings.

[g] Yearlings included with subadults.

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 (1989*b*)
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.

bears was 83%; survival for nontransported 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. 1983*b*). Cubs and yearlings are killed by conspecifics, although the cause of mortality in dependent young is often unknown because few are radio-collared; 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 1990*b*). On Chichagof Island in south-eastern 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 1990*c*, 1990*d*). 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 1990*c*; Garshelis 1994; McLellan 1994) caution against density-dependent interpretation until the effects of nutrition and other confounding factors can be distinguished.

The second theory proposes that conspecific killing of unrelated cubs by adult male bears may increase male fitness if females that lose their offspring are subsequently impregnated by the male doing the killing (Hausfater and Hrdy 1984). The sexually selective infanticide hypothesis predicts that survival of cubs would decline after a resident adult male was killed due to immigration of nonresident males (Swenson et al. 1997). No study has been specifically designed to test this theory. However, data by Swenson et al. (1997) support the theory, but are inadequate to draw strong conclusions.

Janson and Van Schaik (2000) and Boyce et al. (1999) cited Swenson et al. (1997) as an example illustrating that an increased rate of infanticide might be a consequence of male based hunting in mammal populations. Boyce et al. (2001) cited the studies in Scandinavia (Swenson et al. 1997) and southern Canada (Wielgus 1993) studies as illustrating possible relationships meriting consideration in management of bear hunting. In contrast, a panel of 6 scientists reviewed brown bear hunt management in British Columbia and concluded that presently available data on the effects of selective removal of males by hunting are equivocal, and therefore hunting-related changes in density or social structure should not be incorporated into the British Columbia harvest management program (Peek et al. 2003).

Hunting. Legal hunting seasons for brown/grizzly bears exist in Alaska and all Canadian provinces that have grizzly bears. In the United States south of Canada, there are no hunting seasons; the species is protected as "threatened" under the Endangered Species Act.

During 1989/90-1998/99, an average of 1600 bears were annually harvested by recreational hunters in North America (Table 26.8). Most of these were taken in Alaska (73%) and British Columbia (18%), with the remaining 9% from the more eastern Canadian provinces, where bear densities are lower (Table 26.8). An average annual total of 1825 known human-caused moralities occurred in North America (Table 26.8). This documented total included control actions, illegal kills, and defense-of-life and property kills of bears. Such nonsport kills ranged from a low of 5% of total human-caused mortalities in Alaska (Miller and Tutterrow 1999) to 48-50% in areas of northern Canada, where bears are sparse and hunting quotas are low (Table 26.8). In the contiguous United States, all human-caused mortalities were from defense-of-life, incidental, and control kills (Table 26.8).

Grizzly bear hunting is highly valued by participants. In an Alaska study, nonresident bear hunters reported trip expenditures of $10,677 compared to $1247 for resident hunters (Miller et al. 1998). The estimated cumulative annual value of bear-viewing trips ($29.1 million) was higher than for bear-hunting trips taken by nonresidents ($17.05 million) or resident hunters ($4.15 million) (Miller et al. 1998).

Access to brown/grizzly bear hunting opportunities varies in different geographic regions. Where bears are relatively abundant, as in Alaska, residents and nonresidents can hunt them in some areas, and hunter participation is unlimited. Lotteries are used to limit hunting intensity in areas where bear populations are sparse (such as in northern Canada and Alberta) or where bears are abundant but potential hunting intensity is especially high (such as on Kodiak Island, Alaska, and in British Columbia). On the Alaska Peninsula, where brown bear hunting is very popular, hunter participation is limited by closing the season in alternate years rather than by limiting the number of hunters through a lottery.

Like any renewable resource, brown bear populations can sustain a certain level of mortality without declining. Sustainable harvest in most areas is derived from estimates of population size and reproduction data (Miller 1990*e*). Because brown bears can sustain only very low mortality rates (a maximum of 5.7% was estimated by Miller [1990*e*]), most managers adopt conservative regulations to avoid overharvests. The Canadian provinces and settlement areas have quotas on total human-caused mortality designed to avoid population declines. In different areas, these quotas are 2-6% of conservative estimates of population size. The 2% figure applies to areas with lower reproductive rates, the 6% quota to areas with higher reproductive rates. In British Columbia, conservative estimates of population size are assured by subtracting one standard deviation from point estimates of population size before calculating quota size (Province of British Columbia 1999). In Canada, as well as on the Kenai Peninsula in Alaska, mortalities by control actions or defense-of-life or property kills are the first to be counted against the quota, with any remainder available to be taken by hunters. In Yukon Territory, resident sport hunters receive a priority in harvest allocations over nonresidents guided by big game outfitters. On the Kenai Peninsula in Alaska, brown bear numbers have been reduced by large numbers of control, defense-of-life and property kills combined with habitat deterioration from road building and increased human presence. This situation on the Kenai Peninsula demonstrates that even Alaska is not immune from the decimating factors that have caused dramatic declines in grizzly bear abundance in southern Canada and the lower 48 states.

In areas of North America where bears are hunted, the principle of "sustainable yield" is practiced except in portions of interior Alaska. In 1994, the Alaska legislature passed an "intensive management" law intended to assure maintenance of high levels of human harvest of moose and caribou through control of predators like bears and wolves (Alaska Statutes 16.05.255). In several portions of interior Alaska, this law has been implemented in attempts to reduce grizzly bear numbers by killing in excess of sustainable rates. This was done regardless of analyses indicating that increased hunting of grizzly bears did not benefit moose or caribou in one of these areas (Miller and Ballard 1992) and the

TABLE 26.8. Number of brown bears taken in sport harvests and defense-of-life or property (DLP) circumstances in North America

		Hunter-Killed				Annual Average Number of Control and DLP Kills
Location	Period	Male	Female	Sex Unknown	Annual Average	
Alaska	1989/1990-1998/1999	7883	3872	119	1187	92.1
Yukon	1989-1998	522	289	0	81	15
Northwest Territories and Nunavut	1989-1998	81	17	10	11	10
Gwich'in Settlement Area	1990-1999	35	6	12	5	2.6[a]
Inuvialuit Settlement Area	1990-1999	176	46	29	25	5.7[a]
British Columbia	1990-1999	1878	1018	12	291	53
Alberta	1990-1999	109	52	7	17	6.7[b]
Northern Continental Divide Ecosystem	1990-1999	---	---	---	0	13
Greater Yellowstone Ecosystem	1992-1998	---	---	---	0	6
Total		10,684	5300	189	1617	204.1

NOTE: Ordered north to south.

[a] These kills are included in the hunter-killed data.

[b] "Nonhunter" kills.

absence of data indicating it would be beneficial in other areas where intensive bear management was adopted.

Hunting impacts population composition in different ways and regulations can impact the composition of harvests (Miller 1990*e*; 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 1990*a*). In the fall, females represented 53% of the kill during the first week of September but <43% of the kill during October (Miller 1990*a*). 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 1995*a*). 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 (1990*b*) 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 1990*b*). 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 40-60%. 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. 1999*a*). 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. 1999*b*).

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 1995*b*; 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

TABLE 26.9. Density estimates (bears/1000 km^2) of brown/grizzly bear populations based on bears of all ages in different North American study areas

Study Area	Density	Reference
Interior populations		
Tuktoyaktuk Peninsula, and northern Yukon[a]	3-4	Nagy et al. (1983*a*, 1983*b*)
Arctic National Wildlife Refuge coastal plain, Alaska	4	Reynolds (1976)
West-central Alberta	4-5	Nagy and Haroldson (1990)
Eastern Brooks Range, Alaska	7	Reynolds and Garner (1987)
East Front, Montana[b]	7	Aune and Kasworm (1989); Aune and Brannon (1987)
Jasper National Park, Alberta	10-12	Nagy and Haroldson (1990)
South-central Alaska Range	10-15[b]	Miller et al. (1997)
South-central Alaska	11-41[b, c]	Miller et al. (1987, 1997); Miller (1995*a*); Testa et al. (1998)
MacKenzie Mountains	12	Miller et al. (1982)
Yellowstone Ecosystem	14-18	Calculated based on data in Servheen (1999)
Southwest Alberta (Waterton Lakes)	15[b]	Mowat and Strobeck (2000)
Arctic National Wildlife Refuge, Alaska	16	Reynolds and Garner (1987)
East-central Alaska Range	16	Boertje et al. (1987); Gasaway et al. (1992)
Northern Continental Divide Ecosystem, Montana	17-22	Calculated based on data in Servheen (1999)
Seward Peninsula, Alaska	18[b]	Miller et al. (1997)
Northern British Columbia, Prophet River	21[b]	Boulanger and McLellan (2001)
Northern Yukon Territory[a]	26-30	Nagy and Haroldson (1990)
Southeastern British Columbia (Selkirks)	27[b]	Mowat and Strobeck (2000)
Western Brooks Range, Alaska	30[b]	Miller et al. (1997)
Denali National Park, Alaska	34[b]	Dean (1987)
Kluane National Park, Yukon Territory	37	Pearson (1975)
Glacier National Park and adjacent National Forest, Montana	47[b]	K. Kendall, U.S. Geological Survey, pers. commun., 1998, hair snare results
Glacier National Park, Montana	47	Martinka (1974)
Glacier National Park, Montana	79[b]	K. Kendall, U.S. Geological Survey, pers. commun., 1998, hair snare results
Flathead River, Montana	80	McLellan (1989*a*, 1989*b*, 1989*c*); British Columbia Forest Service, unpublished data
Coastal populations		
Alaska Peninsula, Black Lake	191[b]	Miller and Sellers (1992); Miller et al. (1997)
Chichagof Island, SE Alaska	318[b]	Miller et al. (1997)
Kodiak Island, Alaska	323-342[b, c]	Miller et al. (1997)
Admiralty Island	399-440[b, c]	Schoen and Beier (1990); Miller et al. (1997)
Alaska Peninsula, Katmai National Park	551[b]	Miller et al. (1997)

SOURCE: Adapted from McLellan (1994).

NOTE: Ordered by increasing density.

[a] Currently Inuvialuit Settlement Region.

[b] Technique used included estimate of precision; other approaches had no estimates of precision, and due to a variety of methods used in their derivation, comparisons must be done cautiously.

[c] Range reflects different study areas or different times in the same study area.

and DNA analysis. Although her research is in progress, she has identified a minimum number of different individuals (>200) in Glacier National Park and vicinity that is larger than previously suspected (K. Kendall, pers. commun., 2000).

Estimates of density frequently have problems associated with differential inclusion of age or gender groups. Because newborn cubs have high mortality rates, estimates made early in the year will be larger than estimates made later in the year for the same population. Closure problems may result in overestimation of males, the more mobile sex, in a density estimation area. With DNA hair-snaring techniques, efforts are made to exclude cubs by setting the barbed wire too high to snag their hair. Nonetheless, some cubs leave hair samples behind and some bears >1 year old may be able to go under the barbed wire without leaving hair. The age of a bear is not revealed by DNA analyses. The Alaska capture-mark-resight technique avoids most of these problems, but estimates of precision may be exaggerated by tabulating each member of a family group as a separate individual (Miller et al. 1997). Biologists attempting to estimate bear density need to be aware of these sources of potential bias and specify which sex and age groups occur in their density estimates.

Demographic Modeling. Models are useful tools in evaluating hypotheses about grizzly bears because they integrate large amounts of information. They are also useful when incorporating uncertainties in available data by bounding input parameters within feasible ranges. Demographic models are used to guide the management decision process for wild populations of grizzly bears.

Although modeling efforts can take various forms, a common application to threatened or endangered populations is termed population viability analysis (PVA). A PVA estimates the likelihood of persistence of a population over time and is most frequently employed in endangered species or small population management. There are many different concepts of what composes a PVA, from simple, deterministic models for estimating population change to complex, spatially explicit individual-based models of landscape and population dynamics (Beissinger and Westphal 1998). Single deterministic models are among the simplest analyses and demand the least amount of data (Beissinger and Westphal 1998). Demographic vigor of a population can be measured by its survival-fecundity rate of increase (Caughley 1977). This intrinsic rate of increase (r_s) is the exponential rate at which a population with a stable age distribution changes when resources are not limiting.

As reviewed by Hovey and McLellan (1996), several researchers have estimated r_s or its antilogarithm, the finite rate of increase ($\lambda = e^{r_s}$) to assess status of grizzly bears. A $\lambda > 1.0$ indicates an increasing population, whereas $\lambda < 1.0$ indicates a declining population; $\lambda = 1.0$ suggests a stable population. Most published estimates of λ for grizzly bear populations are derived with the Lotka model (Lotka 1907) as proposed by Eberhardt (1985); many lack confidence intervals. The highest published rate of increase (1.085 ± 0.026) was derived by Hovey and McLellan (1996) in the North Fork of the Flathead River in

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) express 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. 2000) 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 to 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 upon 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 historic 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 proportion of BMUs within which females with offspring must be observed (70%, 82%, 89%, and 91% in the Selkirk, Cabinet/Yaak, GYE, and NCDE, respectively). These occupancy rates must be obtained during a 6-year sum of sightings during which no two adjacent BMUs can remain unoccupied.

The U.S. Grizzly Bear Recovery Plan also recognizes that there are areas of acceptable habitat where grizzly bears have been eliminated and should be restored. Foremost among these is the Selway-Bitterroot in central Idaho and western Montana where two designated wilderness areas of 14,983 km^2 (5785 mi^2) form the core recovery area for a 65,100-km^2 (25,140-mi^2) experimental population area that includes the wilderness areas and surrounding national forests. The plan for restoring grizzly bears was developed by a coalition of advocates for the grizzly bear (the National Wildlife Federation and the Defenders of Wildlife) and representatives of timber and labor groups (Resource Organization on Timber Supply and the Intermountain Forest Association). Their plan was adopted by the U.S. Fish and Wildlife Service as its preferred alternative for restoring grizzly bears into the largest area of acceptable habitat (without grizzly bears) south of Canada. In this area, grizzly bears appear to have been extirpated >50 years earlier (U.S. Fish and Wildlife Service 2000).

A key element of the plan was that bears would be reintroduced as an “experimental nonessential” population under Section 10(j) of the Endangered Species Act. The designation as experimental allows more flexibility in managing the reintroduced population and the “nonessential” designation means that the population is unnecessary to avoid extinction of the species. Another element of the plan is that the reintroduced population would be managed by a local citizens management committee (CMC). The CMC is composed of nominees from the governors of Idaho and Montana plus representatives from the U.S. Fish and Wildlife Service, the U.S. Forest Service, and the Nez Perce Tribe. The CMC is an effort to reassure local citizens who are currently using these areas that their concerns about the way the reintroduced bears are managed will be heard. If the decisions of the CMC do not lead toward recovery goals, then the plan calls for mediation. If this is unsuccessful, it allows the U.S. Secretary of Interior to assume management authority over the reintroduced population. Estimates of carrying capacity in the core recovery area suggest the wilderness areas alone can support nearly 250 bears; more can be supported in the national forest lands surrounding the wilderness areas (Boyce and Waller 2000).

The Record of Decision to implement the Bitterroot reintroduction was published in the Federal Register in November, 2000. Shortly thereafter, the State of Idaho filed suit to block implementation and the Secretary of Interior of the newly elected Bush Administration entered into negotiations. In February 2001, the Secretary of Interior proposed to substitute a “no action” alternative for the published Record of Decision and announced a 60-day comment period. During this period, 98% of the public comments received opposed substituting a “no action” alternative for the previously adopted reintroduction decision; opposition included 98% of comments from Idaho and 93% from Montana (Schoen and Miller 2002). In addition, 8 prominent professional organizations of scientists and biologists wrote letters in opposition to the proposed change (Schoen and Miller 2003). Perhaps because of this negative response, no new record of decision has been announced and the existing decision remains in place although no funding to implement it has been provided by the Department of Interior putting the reintroduction into limbo.

Reasons for the decline of brown/grizzly bears in North America are excessive human-caused mortality and habitat loss (Storer and Tevis 1955; Brown 1985; Servheen 1999). Habitat loss results from conversion of native vegetation to agriculture, depletion of preferred food resources (i.e., salmon and whitebark pine), disturbance, displacement from human developments and activities (roads, mines, subdivisions), and fragmentation of habitat into increasingly smaller blocks inadequate to maintain viable populations. Until the 1950s, brown/grizzly bears were considered dangerous to humans and livestock, and consequently, excessive mortality was intentional and sanctioned by government agencies. Currently, in most areas where human-caused mortality is excessive, it results from the same motives despite government efforts to limit mortality.

Management. Radiotelemetry studies have identified roads as significant factors in habitat deterioration and increased mortality of brown/grizzly bears (Archibald et al. 1987; Mattson et al. 1987; Peak et al. 1987; McLellan and Shackleton 1988; Schoen 1990; Mace et al. 1996, 1999; Mace and Waller 1997; Claar et al. 1999). Areas of adult female displacement by roads and developments totaled about 16% of available habitat in Yellowstone National Park (Mattson et al. 1987). In southeastern British Columbia, McLellan and Shackleton (1988) estimated that brown bear habitat loss from roads totaled 8.7% of their entire study area. The percentage of habitat loss as a consequence of behavioral displacement from roads is a function of road density. Percentage is higher in areas having higher road density regardless of the distance at which roads affect bear behavior.

The distance at which bears appear to be displaced by roads varies in different areas and seasons. In Yellowstone National Park, bears avoided areas within 500 m from roads during spring and summer. During summer, daytime disruption of foraging was observed out to 2 km from roads (Mattson et al. 1987). In southeastern British Columbia, bears used areas within 100 m of roads significantly less than expected (McLellan and Shackleton 1988). Habitat use was 58% less than expected within 100 m from roads and 7% less than expected 101-250 m from roads (McLellan and Shackleton 1988). Displacement of grizzlies from habitats near roads may extend up to 3 km for primary roads and 1.5 km for secondary roads (Kasworm and Manley 1990). Roads are typically constructed along streams in riparian areas most intensively used by bears early in the spring following emergence from dens. Correspondingly, the impact of roads on displacement from preferred habitats is greatest in spring (Mace et al. 1996, 1999). During fall, bears tend to move to higher elevations to forage. At this time they select habitats that are typically more distant from existing roads. Consequently, the importance of disturbance displacement by roads is less evident during fall than during spring (Mace et al. 1996, 1999).

Level of traffic appears to influence degree of bear avoidance of roads. Buffer zones of 500 m around roads with no traffic or with use by ≤10 vehicles/day received positive or neutral selection. In contrast, bears avoided buffers surrounding roads having >10 vehicles/day (Mace et al. 1996). In another analysis, radio-marked bears significantly avoided roads with even low levels of human use (<1 vehicle/day) as well as roads with moderate (1-10), and high (>10) levels of use (Mace et al. 1999).

In southeastern British Columbia, areas near roads were used less than expected by adult males and more than expected by weaned yearlings and adult females (McLellan and Shackleton 1988). This pattern may result from selection by female and subadults, the classes most vulnerable to intraspecific predation, of the roadside areas avoided by adult males (Mattson et al. 1987; McLellan and Shackleton 1988; Mattson 1990). Bears living near roads have higher probability of human-caused mortality as a consequence of being mistakenly identified as a black bear by hunters, by illegal shooting, and by control actions influenced by attraction to unnatural food sources (Mattson 1990; McLellan 1990; Mace et al. 1996).

In Montana’s Flathead National Forest, Amendment 19 to the forest plan recognizes the impact of roads to grizzly bear habitat security based on research in the northern Swan Mountains of Montana (Mace and Manley 1993; Mace et al. 1996; Mace and Waller 1997). This plan divided the grizzly bear habitat into three categories and specified the maximum road density in each category for each BMU:

1. At least 68% had to be roadless core area (classified as >0.5 km from any roads) at least 1012 ha (2500 acres) in size.
2. No more than 19% of the grizzly bear habitat in each BMU could have a road density >2.0 mi/mi^2 (“roads” were defined as any driveable road or trail).
3. No more than 19% of the grizzly bear habitat could have >1 mi/mi^2 of open roads (defined as roads or trails used more than six times/week by motorized vehicles).

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 St., 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. 1999*b*). 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. 1999*b*). 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 require that agencies proposing to conduct telemetry studies on grizzly bears or other rare animals must seek and incorporate review of their proposed research from biologists outside their agency before studies are initiated.

However, properly executed telemetry studies remain critical to improving our ability to manage grizzly bear populations and habitats. With modern drugs, competently conducted capture efforts should have a mortality rate of handled bears <1%. Only collars that are designed to drop off without the need to recapture an individual should be used on bears. This reduces risk that collars will injure growing animals or that animals will wear the collar longer than necessary to complete the project.

More recent advances in satellite telemetry employ global positioning system technology (Schwartz and Arthur 1999) and are providing insight into bear movements, home range analyses, habitat use, and other spatial statistics not obtainable via conventional telemetry (Arthur and Schwartz 1999). Satellite telemetry enables the collection of thousands of locations during the life of a transmitter, thus reducing the need to put collars on numerous individuals. It also allows for continuous 24-hr sampling, which is independent of personnel, weather, terrain, and other factors that limit conventional tracking. In designing telemetry studies, it is essential that the information obtained result in sufficient gains in improved management to offset the costs to bear populations associated with handling.

Humans have the greatest influence on brown/grizzly bear distribution and abundance in North America. Understanding, mitigating, and managing human impacts on bears and their habitats are the greatest challenges facing resource managers, wildlife and conservation biologists, politicians, and the general public. Much of the research needs now and in the future must address these issues.

Improved population abundance estimation and trend assessment remain critical research needs. Today's techniques are expensive and labor intensive. Also, some population estimation techniques are subjective, have no estimate of precision, and cannot be replicated in a systematic manner. Some techniques require radio-marking large numbers of individuals (i.e., Reynolds and Boudreau 1992; Miller et al. 1997), which may not be feasible in some environments. These techniques also typically provide density estimates in only small portions of the area inhabited by the entire population of interest to bear managers. Hair snaring and DNA analysis techniques (Woods et al. 1996, 1999; Mowat and Strobeck 2000; K. Kendall, unpublished data) have potential to become a standardized and objective approach to abundance estimation without the need to handle and radio-collar individual bears. However, these techniques are currently expensive and have problems with demographic and geographic closure, potential capture biases, and standardization of experimental design. Design issues include grid size and scent lure rotation frequency, sample collection frequency, and mathematical techniques for data analysis. On Kodiak Island, Alaska, the bear population may be too homozygous (Waits et al. 1998*a*, 1998*b*) to distinguish between individuals based on DNA. Techniques based on visual observations of unduplicated adult females accompanied by newborn cubs (Knight et al. 1995) have been used to estimate minimum population size and establish mortality quotas for bears in the Yellowstone Ecosystem, but extrapolation to a total population number or population density remain problematic (Boyce et al. 2001). Observational techniques using double-count procedures are under investigation in Alaska (E. Becker, Alaska Department of Fish and Game, pers. commun., 2000).

Brown bears are hunted in all jurisdictions north of the border between the United States and Canada. However, methods of assessing the impacts of hunting on populations are poorly developed (Miller 1990*e*). Better means of assessing impacts of hunting are needed because brown/grizzly bears have the lowest reproductive rates among North American game mammals. Without such techniques, appropriate hunting opportunities may be needlessly curtailed or populations may be overharvested.

Especially in the lower 48 states, better means of assessing the biological carrying capacity of actual or potential grizzly bear habitats are needed. Early assessment efforts were pioneered by Craighead et al. (1982). Boyce and McDonald (1999), Hogg et al. (1999), and Merrill et al. (1999) have proposed other approaches. Such assessments are important to insure restoration efforts for grizzly bears are successful in areas where they have been extirpated or to adapt management policy to environmental change to ensure long-term persistence in extant habitats.

Further research is also needed on the importance of anthropogenic impacts on bear habitats. As documented elsewhere in this section, roads, commercial activities (mining, logging), livestock grazing, suburban sprawl, and recreational uses impact (i.e., snowmachining, off-road vehicles) the ability of bear populations to persist in an area (e.g., Mattson et al. 1987; McLellan and Shackleton 1988; McLellan 1989*a*, 1990; Mace et al. 1996, 1999). More intensive research is needed on threshold levels at which these impacts become significant and possible ways to mitigate adverse human impacts on brown/grizzly bear populations. Similarly, it is important to find ways to identify threshold levels of tolerance for adverse impacts of grizzly bears on humans.

Efforts to restore grizzly bears also require better information on economic costs and benefits of bears and social attitudes towards bears. Swanson et al. (1994), Bath (1998), Duda et al. (1998), and Miller et al. (1998) present such analyses. Among other reasons, such information is needed to demonstrate the value of preserving wildlife corridors among fragmented islands of habitat that characterize grizzly bear habitat in the continental United States and southern Canada (Noss and Harris 1986; Craighead and Vyse 1996). Additional research is required to document the impacts of introduced exotics on grizzly bears including blister rust, lake trout (*Salvelinus namaycush*), and brucellosis, to name a few (Reinhart et al. 2001).

There are still some basic biological issues still unresolved. Hellgren (1998) identified aspects of the hibernation physiology in bears where our knowledge is lacking. We do not clearly understand the role of intraspecific killing as it relates to bear behavior, male density, and hunting. Furthermore, our understanding of density dependence is still unclear.

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