GRIZZLY BEAR

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Grizzly Bear

Ursus arctos

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John A. Mitchell

COMMON NAMES. Grizzly bear, grisly bear, range bear, roach-back, smut-face, griz, Old Ephraim, Moccasin Joe, great white bear, silvertip, white bear
SCIENTIFIC NAME. *Ursus arctos*

The species is distributed widely throughout the Palearctic and Nearctic across a variety of habitats. Local variations in body size, skull structure, pelage color, and other morphological characteristics were utilized by early taxonomists as specific and subspecific classification criteria. This resulted in early taxonomic schemes that have defied accurate interpretation. The most noteworthy early effort to classify the brown and grizzly bears of North America was that of C. Hart Merriam. His work, produced over a period of about 20 years, culminated in a comprehensive taxonomy of brown and grizzly bears embracing 87 different species in North America alone (Merriam 1918). Although accepted as authoritative by Hall and Kelson (1955), Merriam's classification has been largely discarded in favor of the single holarctic species concept established by the works of Couterier (1954), Rausch (1953, 1963), and Kurtén (1968).

SUBSPECIES. Rausch (1953, 1963), on the basis of skull structure, body size, and coloration, suggested that *Ursus arctos* on the North American continent and its adjacent islands is comprised of three subspecies: *U. a. horribilis* Ord, to include all brown and grizzly bears of continental North America; *U. a. middendorffi* Merriam, to include brown bears of the Alaskan Islands of Kodiak, Afognak, and Shuyak; and *U. a. gyas* Merriam, to include brown bears confined to the Alaskan peninsula.

Although *U. a. gyas* is no longer considered a distinct subspecies (Rausch 1963), the taxa *U. a. horribilis* and *U. a. middendorffi* are recognized by most current workers. The grizzly bear is considered a genetically strong variant of the classical brown bear phenotype of *U. a. horribilis*.

The family Ursidae originated in Europe early in the Miocene epoch as a derivative of the Miacidae, a family of small, carnivorous, tree-climbing mammals (Simpson 1945). Subsequent phylogenetic develop-
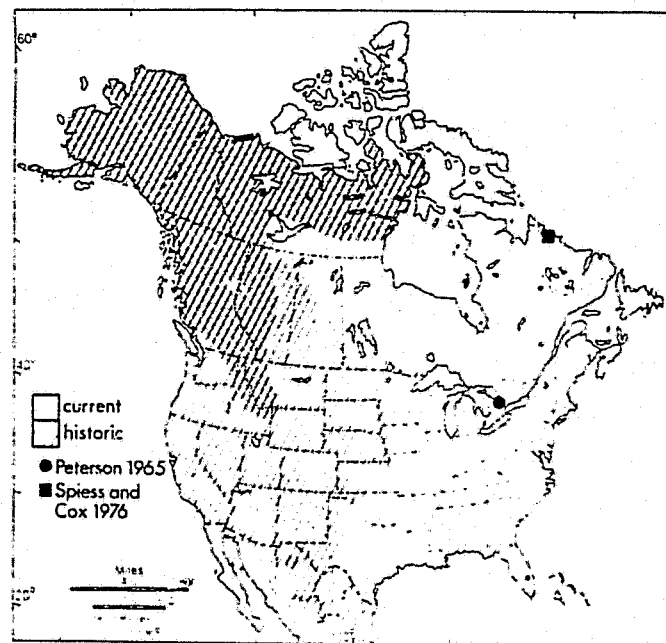

FIGURE 25.1. Present and past distribution of the grizzly bear (*Ursus arctos*). After Rausch 1963.

ment of the ursids has been well documented in the works of Thenius (1959) and Kurtén (1968). A thorough review of bear evolution that relates environmental selective pressures in postglacial North America with behavioral, ecological, morphological, and physiological adaptations that, today, constitute distinct differences between black bears and grizzly/brown bears was done by Herrero (1972). Also, Martinka (1976) briefly reviewed the phylogeny of bears.

At least three distinct evolutionary lines emerged from the earliest ursid progenitors. Of these, only one was of major importance in the origin of modern day bears. Divergence of this major evolutionary line during the early Pliocene gave rise to forms considered representative of the two extant genera of bears, *Ursus* and *Tremarctos*.

The Auvergne bear, *Ursus minimus* Devèze and Bouillet, has been identified from remains in Europe dating to the latter phases of the Pliocene some 4 to 6 million years ago. Among the most primitive of fossil *Ursus* spp., it was relatively small and similar in struc-

ture to the modern Asiatic black bear. The bear was a forest dweller and, despite persisting relatively unchanged into the Pleistocene, provided the early progenitors to the Etruscan bear, *Ursus etruscus* Cuvier.

The Etruscan bear was well established in Europe and Asia by the early Pleistocene 2 to 3 million years ago. The repeated cycles of continental glaciation that shaped the Northern Hemisphere throughout the time of the mid-Pleistocene provided selective pressures that spurred adaptive radiation in the Etruscan bear population nucleus. All extant species of *Ursus* had been derived by the late Pleistocene, with the polar bear, *Ursus maritimus* (*Thalarctos maritimus*), being most recently derived as an offshoot of the basic grizzly bear stock (*U. arctos*).

The grizzly/brown bear group, the black bear group, and the great cave bears (*U. spelaeus*) all were derived from Etruscan bear stock in Asia. The cave bears of Europe were extinct by recent times. The black bear group, now represented in Asia by *U. thiebetanus*, had radiated via the Aleutian land bridge into North America by the middle of the Pleistocene to provide the black bear (*U. americanus*) lineage. The grizzly/brown bear group did not cross into North America until the end of the Pleistocene epoch and appears to have been confined to the northern reaches of Alaska until the withdrawal of the continental ice flows. *Ursus arctos* then expanded its range southward to inhabit land area from the northern limits of North America well into Mexico.

DISTRIBUTION

Historical Range. From early records and paleontological finds, it is clear that *Ursus arctos horribilis* was once native to a far more extensive area of North America than it now inhabits (Roosevelt 1907; Wright 1909; Dobie 1950; Storer and Tevis 1955; Stebler 1972; Schneider 1977). The historical distribution of the bear was best summarized by Rausch (1963), although many other workers provided similar descriptions compiled from the literature (figure 25.1). It should be noted that, according to current documentation, the historical distribution described by Rausch is more accurate than that reported in Hall and Kelson (1959). However, discoveries of skulls in southern Ontario (Peterson 1965) and on the northern coast of Labrador (Spiess 1976; Spiess and Cox 1977) suggest that the range historically may have extended across the breadth of North America (figure 25.1). Guilday (1968) documented the presence of *U. a. horribilis* in the vicinity of what is now Ohio and Kentucky.

From the beginning of the European invasion of North America, the continental range of the grizzly bear receded, especially from the south and east. Bears were killed out of fear, for food, or to protect livestock. The natural habitat over which grizzlies ranged widely was often eliminated. The early and rapid extinction of populations from most of Mexico and from the central and southwestern United States and California suggests that many were weak populations dynamically, and of marginal status in the community structure.

Current Range. Grizzly bears are present, and even common, throughout much of the current range (figure 25.1). Populations continue to thrive in the remote, largely unsettled areas of Alaska and northwestern Canada (Pearson 1972, 1975, 1976; Reynolds 1979; Reynolds et al. 1976; Hamer et al. 1977, 1978, 1979). Within the contiguous 48 states populations are more sporadic, particularly at the western extremes of the range. Populations in the Yellowstone ecosystem have declined in recent years (Craighead et al. 1974; Craighead 1980b); various population units in the vicinity of the continental divide and north through Montana appear to be stable or declining slowly. Sightings of grizzlies in the Selway-Bitterroot drainages separating Idaho and Montana indicate only the presence of isolated animals. Layser (1978) presented evidence that grizzlies survive, although probably marginally, in the Selkirk Mountains of northern Idaho and northeastern Washington. A small, but probably viable, population inhabits the Cabinet Range, the Yaak River area, and adjoining forests in eastern Idaho and northwestern Montana. There is also a remote possibility that a small remnant population survives far to the south in the San Juan Wilderness of Colorado.

Because the grizzly bear requires large areas for its natural ranging habits, continued human competition will undoubtedly further reduce its range. It is important to note that much of the habitat that supported the grizzly bear in its historic range still exists and that the range of the animal could easily be extended by transplantation. The technology necessary for range extension is available, but the socioeconomic and sociopolitical conditions necessary for support of such a venture are not.

DESCRIPTION

A considerable mystique has long been associated with the grizzly bear. This, combined with the confused state of early taxonomic distinctions, provided for many early descriptions of the bear of only incidental scientific value (Allen 1814; James 1823; Fremont 1843; Coues 1893; Roosevelt 1907; Wright 1909; Mills 1919; Holzworth 1930; Dobie 1950; Hubbard 1960; Haynes and Haynes 1966). Observations on the morphology were superficial, subjective, and often sensationalized. Most natural history and behavioral descriptions were oriented toward hunting techniques, Indian mythology, or the bear's vaunted aggressive tendencies. Nevertheless, the early writings concerning the grizzly bear are enjoyable reading and have contributed to popular legends that endure even today.

Although well known to the American Indians and most probably encountered by the 1540 Coronado expedition to the seven cities of Cibola (now west-central New Mexico), the first known record of the grizzly bear is that of Sebastian Vizcaino (Storer and Tevis 1955). In 1602 while camped at the site of

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Monterey, he observed bears feeding on the carcass of a beached whale. Because black bears were not native to that area, these could only have been grizzlies. The next record of a grizzly bear was that of Henry Kelsey, an Englishman employed by the Hudson Bay Company in Canada, when he wrote on 20 August 1691 of encountering a "silver hair'd" bear (Schneider 1977). Although bears undoubtedly were observed by other travelers moving west of the Mississippi River, it was not until the mounting of the Lewis and Clark expedition more than a century later that data of some value were collected. The first type-specimen was collected, as were occasional feet, claws, teeth, and skulls. Measurements and general morphological descriptions of specimens killed or observed were often recorded. The explorers killed at least 43 grizzly bears (Burroughs 1961), a number that journals of the expedition do not correlate clearly with a need for food (Allen 1814; Coues 1893; DeVoto 1953).

George Ord, credited with the first scientific naming of the grizzly bear (*Ursus horribilis* Ord) in Guthrie (1815), actually had little first-hand knowledge of the bears (Storer and Tevis 1955). His species description was obtained indirectly from information of the Lewis and Clark expedition published by Brackenridge (1814).

The earliest scientific descriptions of the grizzly bear based on adequate specimen numbers were those of Swainson, Baird, and Elliot from the arctic, western United States, and British Columbia, respectively (Storer and Tevis 1955). C. Hart Merriam (1918) was the next important contributor to a scientific description of the grizzly bear. As discussed earlier, his efforts were comprehensive, but eventually were of limited systematic value.

Description of the grizzly bear must be approached with the understanding that it is a genetic variant within a subspecies with the large brown bears. Moreover, any description must account for considerable variations in size, color, and morphology between populations.

General Morphology and Structure. Members of *Ursus arctos horribilis* are larger and more heavily built than most other ursids, with relatively short tails and ears, and with the four limbs of approximately equal length tapering to large feet structured for plantigrade locomotion. Features that distinguish the subspecies include a large hump of muscle overlying the scapulae, unusually long foreclaws, characteristic skull and dental structure, and, at least in some specimens, the color and appearance of the pelage (figure 25.2).

The feet of the grizzly bear are cushioned by heavy plantar and digital pads of fibrous connective tissue covered by cornified epidermis (Storer and Tevis 1955; Ewer 1973). The major plantar pad of the forefoot is somewhat rectangular and is wider than it is long. The distal extremity of the pisiformis serves as the "heel" of the forefoot and is capped by an oval pad. Each of the five digits of the forefoot also has a small oval pad. The plantar surface of the hindfoot is comprised of a single, triangular pad that extends posteriad over the calcaneus to form the heel. A small oval pad surfaces each of the five digits. While there are minor differences in pad conformations (Wright 1909; Holzworth 1930), the feet of grizzly bears do not differ substantially from those of black bears except for being larger and lacking interpedal hair. The claws, however, differ considerably and are the feature that often permits distinction of bear tracks.

The foreclaws of grizzly bears are heavier, longer, broader, and straighter than those of black bears. Measurements along the external curvature of claws from four grizzly bear skins yielded value extremes for the claws of the forefeet ranging from 62 to 83 mm and for claws of the hindfeet ranging from 25 to 59 mm (Storer and Tevis 1955). Foreclaws of black bears seldom exceed 51 mm in length and usually do not produce track markings, as those of grizzlies routinely do.

The pelage of grizzly bears consists of an underfur of very fine hairs overlaid with coarse, long guard hairs that are more densely distributed in some bodily regions than in others. Often the bears have a full, thick mane, or roach, of guard hairs from the skull to the shoulders. Vibrissae appear to be present only vestigially. Most of the underfur is shed during the late spring and summer and replaced between August and October, depending on the climate of the locale (Holzworth 1930; Ewer 1973). Scholander et al. (1950) found that grizzly bear winter fur was an excellent insulator. When compared with the winter furs of seven other North American mammals, its insulating capacity was exceeded only by the pelts of the arctic fox (*Alopex lagopus*) and timber wolf (*Canis lupus*).

The colors of the grizzly bear pelage are extremely variable, but not so much, perhaps, as they were prior to the virtual extinction of the animal south of Yellowstone Park, Wyoming. The journals of the Lewis and Clark expedition (Allen 1814), as well as many other sources (Roosevelt 1907; Wright 1909; Holzworth 1930; Dobie 1950; Storer and Tevis 1955), note specimens with pelages of white, black, gray, or various shades of brown, tan, yellow, cream, or red. These specimens also often had the silvering or "frosting" of the guard hairs characteristic of the "grizzly" grizzly bear. In general, grizzly bears are colored a dark to blondish brown and may have silver- or blond-tipped guard hairs. Some specimens may even appear to be broadly striped dorsally or laterally. Color appears to be partially related to age and to annual replacement of pelage; old males are normally dark brown to red brown with few silver-tipped guard hairs. As in many large mammals, the new pelage is darker and richer in color than the old pelage. Some cubs and yearlings may exhibit a white or cream neck V-patch that disappears with age.

The axial and appendicular skeleton of the grizzly bear is similar to that of the black bear except, perhaps, that the hind legs are longer relative to the forelegs in the grizzly. The bone structure of both species is relatively massive and there is no fusion of leg bones as in

FIGURE 25.2. Female grizzly bear (*Ursus arctos*) and two one-year-old offspring.

some other carnivores. An interesting anatomical adaptation for climbing is the large flangelike postscapular fossae on the upper part of the posterior scapular margins (Ewer 1973). The subscapulares minor arise from the lateral and mesial surfaces of these flanges and insert on the heads of the humeri. These muscles play a direct role in resisting the pull of the humeri away from their glenoid articulations when a bear pulls its body up by its forelimbs. Despite having evolved foreclaws adapted to digging rather than to climbing, the grizzly bear retains this skeletomuscular arrangement in common with the black bear.

Size and Weight. Much of the early American natural history and adventure literature already cited includes reports of bears of gargantuan proportions. Some may have been Alaskan brown bears, while others may have been subjectively inflated by the observer. Few reliable records of grizzly bear measurements from specimens taken prior to the 20th century survive. It has been suggested that the race now extinct in California (designated *Ursus arctos californicus* currently and *U. magister* by Merriam 1918) was somewhat larger than other races south of Alaska (Storer and Tevis 1955). Leopold (1959) described a race of brown bears from the mountains of northern Mexico that, according to Rausch (1963), qualifies as the smallest form of *U. a. horribilis* in North America. In general, size and weight of adult grizzly bears are highly variable between populations (Rausch 1953, 1963). Within populations, adults are found to vary over a wide range of dimensions and weight relative to genotypic expression, gender, age, circumstances of habitat, and season of year.

Commonly referenced sources of information on mammals do not agree on any range of measurements for grizzly bears. In part, this is because of the paucity of verifiable data and the failure of systematics adequately to define the heterogeneity of the species. Weights and dimensions obtained from animals kept in captivity usually are not representative of their free-ranging counterparts. Such animals commonly are relatively inactive and obese.

Burt and Grossenheider (1964) list the following parameters for the grizzly bear: length of head and body 1.8-2.2 m, height at shoulders 0.9-1.1 m, weight 147-386 kg. Walker et al. (1964) refer to a maximum weight of almost 363 kg and a maximum length of more than 2.5 m. Storer and Tevis (1955) included reports for California grizzlies, many of dubious reliability, estimating total length to be 3.2 m and weight in excess of 544 kg.

Reliable data on measurements of grizzly bears exist for populations in the Brooks Range of Alaska (Rausch 1963), the Yukon Territory (Pearson 1975), and the Yellowstone ecosystem (Craighead and Craighead 1973b). Weights of large adult animals from the Yellowstone ecosystem ranged from 158 to

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TABLE 25.1. Mean weights and measurements of grizzly bears

| Sex and Age | Weight | Foot Dimensions (cm) | | | | Length (cm) | Claw Base (cm) | | Neck Circumference (cm) | Interocular Length (cm) | Nose to eye Length (cm) | Ear Length (cm) |
		Right Front	Left Front	Right Rear	Left Rear		Left	Right				
Males												
under 9 mos.	(34)	(31)	(30)	(30)	(31)	(29)	(23)	(23)	(27)	(30)	(30)	(28)
	31.6	7.9 × 8.8	7.9 × 8.8	14.4 × 8.3	14.2 × 8.2	99.3	1.43	1.44	38.1	6.5	10.0	8.9
17–21 mos.	(39)	(37)	(22)	(22)	(22)	(22)	(18)	(18)	(19)	(19)	(20)	(18)
	68.0	10.6 × 11.5	10.1 × 11.5	19.0 × 11.0	18.9 × 10.7	131.8	1.82	1.85	51.2	7.9	13.4	11.4
29–33 mos.	(16)	(14)	(14)	(14)	(14)	(12)	(8)	(8)	(13)	(13)	(13)	(13)
	110.8	11.7 × 12.8	11.7 × 13.0	21.3 × 12.1	21.3 × 12.2	159.0	1.84	1.85	61.9	8.7	15.2	12.2
41–45 mos.	(16)	(10)	(10)	(10)	(10)	(10)	(6)	(6)	(8)	(9)	(9)	(9)
	124.6	12.1 × 13.8	11.9 × 13.7	23.0 × 13.0	22.7 × 13.1	165.2	2.04	2.07	65.9	9.6	16.6	11.9
53–57 mos.	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)
	152.7	12.0 × 14.0	12.4 × 13.9	23.8 × 12.9	23.0 × 12.8	177.2	2.11	2.12	69.3	9.3	16.9	12.5
65 + mos.	(33)	(25)	(25)	(28)	(28)	(24)	(15)	(15)	(19)	(18)	(19)	(19)
	245.0	13.8 × 15.4	13.8 × 15.1	25.0 × 14.6	24.7 × 14.5	195.4	2.29	2.31	85.3	11.0	17.7	12.8
Females												
under 9 mos.	(17)	(17)	(17)	(17)	(17)	(16)	(15)	(14)	(14)	(15)	(15)	(15)
	26.9	8.0 × 8.5	7.8 × 8.4	13.8 × 8.0	13.9 × 8.0	94.7	1.40	1.35	38.0	6.4	9.6	9.1
17–21 mos.	(19)	(18)	(18)	(18)	(18)	(15)	(13)	(13)	(15)	(15)	(15)	(15)
	57.6	9.8 × 10.7	10.0 × 10.6	18.2 × 10.1	18.0 × 10.0	128.1	1.74	1.74	49.9	7.5	12.6	10.7
29–33 mos.	(22)	(19)	(19)	(19)	(19)	(16)	(11)	(12)	(13)	(13)	(14)	(13)
	83.8	11.1 × 11.7	11.1 × 11.6	19.8 × 11.2	19.8 × 11.2	144.6	1.75	1.73	57.4	8.3	13.6	10.9
41–45 mos.	(7)	(6)	(6)	(6)	(6)	(6)	(5)	(5)	(6)	(6)	(6)	(6)
	125.4	11.4 × 12.5	11.0 × 12.8	21.0 × 11.9	20.8 × 11.7	162.1	1.90	1.94	63.5	8.7	15.1	10.4
53–57 mos.	(4)	(4)	(4)	(4)	(4)	(4)	(3)	(3)	(4)	(4)	(4)	(4)
	132.4	11.4 × 12.8	11.4 × 12.8	20.5 × 12.2	20.3 × 11.6	160.4	1.88	1.85	66.7	9.0	15.1	12.0
65 + mos.	(72)	(42)	(42)	(45)	(45)	(41)	(19)	(19)	(34)	(35)	(36)	(34)
	152.0	11.8 × 13.0	11.7 × 12.9	21.2 × 12.0	21.3 × 12.0	172.2	2.05	2.05	69.4	9.2	15.6	12.9

NOTE: The size of the sample for each category is given in parentheses.

204 kg for females, and from 363 to 500 kg for males. Average weights and physical dimensions by age classes of Yellowstone grizzly bears are given in table 25.1 (J. J. Craighead unpublished data).

Skull and Dentition. The skull of the grizzly bear is highly variable in its size and configuration. Rausch (1953, 1963) presented an intensive evaluation of 357 skulls from 26 regions of North America, which served as the basis for his distinction of subspecies *U. a. horribilis* and *U. a. middendorffi*. The structure of the skull is characteristically massive (figure 25.3). However, tremendous variations exist within and between *U. a. horribilis* populations in such commonly evaluated paramenters as condylobasal length, zygomatic width, frontal profile, rostral length, sagittal crest development, length and width of palate, length and form of mandibular ramus, and length of maxillary tooth row. Variations in mean condylobasal length were reported by Rausch (1963) to exist on a clinal gradient, mean lengths increasing from south to northwest. Zavatsky (1976), in an attempt to correlate age with general skull development and morphology, carefully described a skull series from 43 Russian brown bears of age classes assigned according to tooth cementum layers. The specific skull characteristics used to distinguish the 11 age classes would not seem to apply well to the heterogeneous *U. arctos* of North America.

The dental structure of *U. a. horribilis* is generally distinguishable from that of *U. americanus*. For both species, the dental formula is 3/3, 1/1, 4/4, 2/3 = 42. However, the length of the third upper molar of the adult grizzly bear is seldom less than 38 mm, while that of the adult black bear does not attain 31 mm (Storer and Tevis 1955). If teeth are badly worn or fractured, differentiation often is not easy.

Karyotype. All ursids, with the exception of *Tremarctos* sp., have a diploid chromosome number of 74 (Ewer 1973). If centric fusion of chromosomes has accompanied evolution of the families of carnivores from their miacid progenitors, then this number, and the chromosome numbers of some canid species, are primitive to most other carnivores (Wurster and Benirschke 1968). If, as Todd (1970) suggested, karyotypic fission is characteristic of evolutionarily progressive species, the majority of carnivores have retained the primitive condition and the ursids and canids are advanced.

PHYSIOLOGY

In general, bears exhibit the basic systemic physiology common to most mammals. Few studies have defined physiological characteristics specific to *Ursus arctos horribilis*. Jenness et al. (1972) presented a comparative analysis of total solids, fats, lactose, casein, whey proteins, and various minerals and vitamins found in the milk of four bear species. Milk specimens analyzed from eight wild grizzly females differed greatly from the milk of two females confined to zoos and, to a lesser degree, from milk specimens of *U. americanus*,
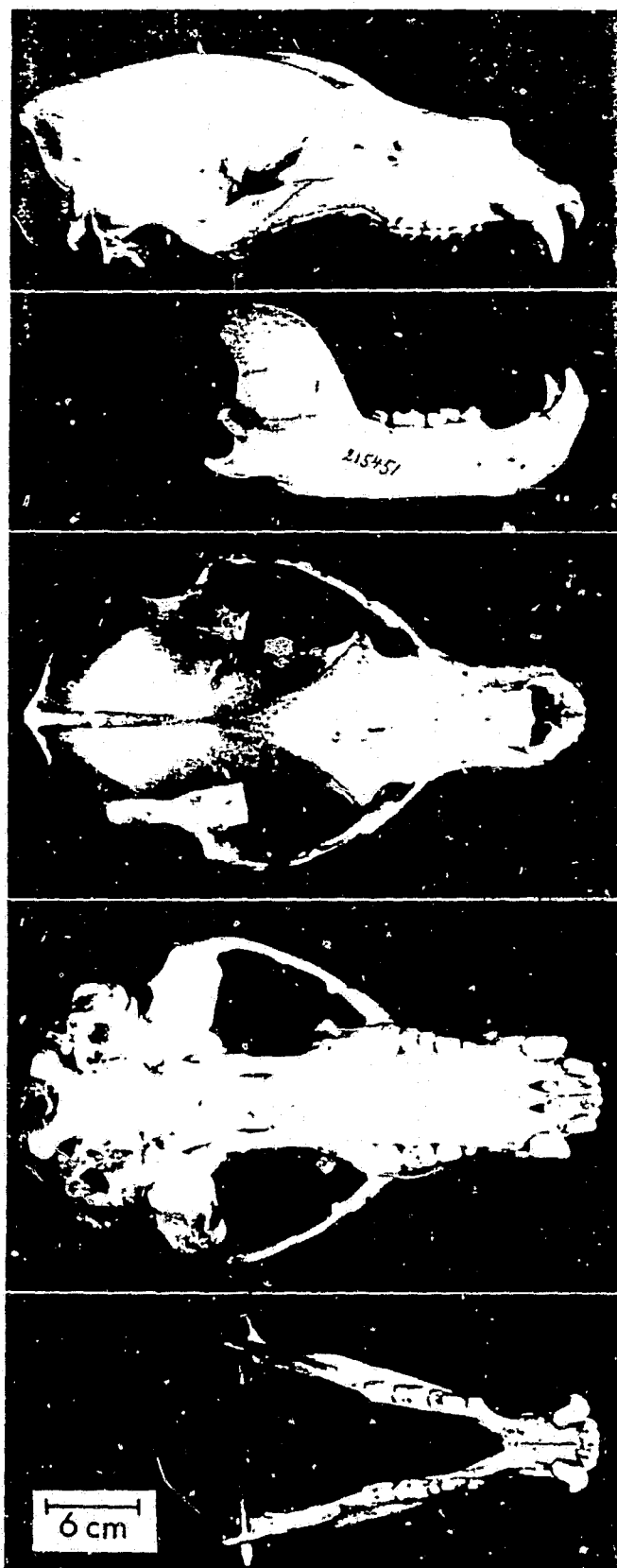

FIGURE 25.3. Skull of the grizzly bear (*Ursus arctos*). From top to bottom: lateral view of cranium, lateral view of mandible, dorsal view of cranium, ventral view of cranium, dorsal view of mandible.

U. maritimus, and other *U. arctos* subspecies. Gel electrophoresis of milk caseins revealed differences in protein composition between samples from the different bear species. There was inadequate resolution for determining if differences were species related or

)ear (*Ursus arctos*). From
m. lateral view of mandi-
.l view of cranium, dorsal

arctos subspecies. Gel
revealed differences in
samples from the dif-
s inadequate resolution
were species related or

simply due to polymorphism within a species, how-ever.

Pearson and Halloran (1972) reported consistent anisocytosis of erythrocytes in blood samples from 22 *U. arctos* of southwestern Yukon Territory. On re-peated sampling, they documented statistically signifi-cant decreases in erythrocyte count and increases in basic erythrocyte indices from spring to summer, with some evidence of trend reversal in autumn. They speculated that a relationship existed with the hiberna-tion cycle, but the adaptive value of such a relationship is not obvious.

Studies of hibernation physiology and related cy-clic phenomena comprise the bulk of literature treating bear physiology. Nelson et al. (1980) presented a thorough review of current literature. Folk et al. (1967, 1972, 1976) have studied intensively the cardiac cycle of *U. a. horribilis* in Alaska. They found that bears required at least two weeks to enter deep "winter sleep" and, unless disturbed, did not normally waken until spontaneously aroused in the spring. Body tem-perature did not decrease appreciably (no more than 5° C on the average) as in many other hibernators. A very distinct bradycardia was observed—25–43 percent of normal summer heart rates—but correlative data on respiratory rate, blood pressure, and cardiac output were not obtained. Folk et al. (1972) postulated that the bradycardia is associated with circulatory shunting, which transforms the bears into "heart-lung-brain" preparations and provides other organ systems only marginal support.

Grizzly bears generally do not feed, urinate, or defecate during "winter sleep." According to Folk et al. (1976), this qualifies as a true state of "hiberna-tion" more highly evolved than that observed in small mammals. The latter exhibit bouts of hypothermic torpor periodically interrupted by arousal for imbibition, feed-ing, and excretion.

The reduction in cardiac rate is paralleled in black bears by a reduction in oxygen consumption (Hock 1960). The lowered oxygen consumption is reflected in the relatively low respiratory quotient values of 0.7–0.85 for bears during cold exposure (Folk et al. 1972). Such respiratory quotients are quite appropriate for energy metabolism based primarily on fats (South and House 1967). Although grizzlies are known to develop extensive fat deposits prior to winter denning, the exact sites and mechanics of deposition and relative quan-tities have not been well documented. Attempts to measure fat utilization by weighing animals before and after hibernation are often invalid because of unmea-sured variations in water weight.

Most work on hibernation metabolism has been on black bears (Brown et al. 1971; Nelson et al. 1971, 1973, 1975). Black bears maintain constant fluid levels in the blood and tissues by retaining the metabolic water of fat catabolism. Blood levels of total protein, urea, and uric acid remain relatively constant, but creatinine concentrations increase. Urea is formed by normal pathways during hibernation. The deamination of amino acids for energy is reduced in favor of lipid utilization. Any urea resulting is recycled via a deami-nation and recombination with glycerol from lipolysis to form alanine. Thus, lean body weight is preserved and uremia avoided (Nelson et al. 1980). It is assumed that metabolic processes in the hibernating grizzly bear are very similar to those of the black bear. Folk et al. (1976) presented data comparing urine volumes and compositions from a grizzly bear during and following hibernation, which compare well with blood and urine analyses from the black bear.

REPRODUCTION

Relatively little was known about the reproductive biology of grizzly bears prior to the development and use of immobilizing drugs to capture, individually color mark, and radio-instrument specific animals for study over extended periods of time (Craighead et al. 1960, 1963; Craighead and Craighead 1969, 1972, 1973a).

Prior to the use of the definitive field techniques, the bulk of information on ursine reproductive biology concerned the European brown bear (*U. a. arctos*), the polar bear, and the American black bear. Studies by Rausch (1961), Wimsatt (1963), and Erickson et al. (1964) contributed greatly to knowledge of the reproductive biology of the American black bear. Dittrich and Kronberger (1962) reviewed the re-productive biology of the European brown bear.

Murie (1944) reported on breeding dates for grizzly bears in Alaska. Erickson et al. (1968) and Hensel et al. (1969) described breeding biology and discussed reproduction in the Alaskan brown bear.

In the past two decades intensive research has focused on all aspects of the grizzly bear's reproduc-tive biology. Early work was focused on the southern interior ecotype of brown bear inhabiting Wyoming, Montana, and Canada (Craighead et al. 1960, 1961, 1963; Craighead and Craighead 1967, 1969; Hor-nocker 1962). Knight (1975) and Servheen and Lee (1979) have current investigations under way. Repro-ductive biology for the ecotype inhabiting northern British Columbia, Yukon, Northwest Territory, and Alaska was treated by Pearson (1975), while that for the ecotype found at the northern extreme of the range on the north slope of the Brooks Range, Alaska, was well documented by Reynolds (1979). Reproduction in brown bears of coastal Alaska was described by Glenn et al. (1976).

The reproductive tract of the female grizzly bear is similar to that of the black bear (Erickson et al. 1964; Kordek and Lindzey 1980). Pearson (1975) described the gross anatomy of reproductive tracts of male and female grizzlies. The size of the uterus varies with the stage of the reproductive cycle and age of the animal. Changes in gross anatomy of the testes also occur.

In the Yellowstone ecosystem, the mating season may begin as early as mid-May and terminate in mid-July. As the season progresses, the vulva enlarges twofold or more, retracting to nonbreeding size in July. Ovaries increase in size with attainment of sexual

maturity. Placental scars are present and readily visible in properly prepared specimens. Placental scars, as well as size and coloration of mammae, are indicative of postreproductive history.

Young female grizzly bears mate in Yellowstone National Park from 26 May to 9 July, a period of 45 days (Craighead et al. 1969). The earliest mating recorded was a 7.5-year-old female that copulated twice in one afternoon. Three females were seen to mate on 28 May. The latest mating was recorded on 9 July; other late mating dates were 1 July and 6 July. Records covering a 6-year period showed that during seasons in which mating began early, it terminated early, and vice versa. The periods over which copulation annually occurred proved remarkably similar, averaging 26 days per mating season (figure 25.4).

Precopulatory and postcopulatory behavior were noted as early as 14 May and as late as 15 July, respectively. A period of estrous behavior persisted for approximately 62 days. Dittrich and Kronberger (1962) reported a mating season of approximately 72 days (end of April to mid-July) for captive European brown bears.

From 1962 to 1967, 49 copulations were observed in Yellowstone (table 25.2). They show that 80 percent of all copulations occurred in June, with a preponderance during the first two weeks. Twelve percent occurred in late May and 8 percent in early July.

Copulation. Copulation by grizzly bears is vigorous and prolonged. The copulatory act and related overt behavior vary considerably with the age of the female, her responsiveness, and the number of males vying for her (table 25.3). Several females were observed to copulate more than once in a single day.

The length of a successful copulation varies greatly. Normally a minimum of 10 minutes is required; the maximum time recorded was 60 minutes. The breeding histories clearly show that the female grizzly will mate with a number of males (table 25.3). It is not uncommon for females to accept two males in

TABLE 25.2. Frequency of copulations occurring between 26 May and 9 July (1961-67)

Date of Breeding	Number of Copulations	Percentage of Copulations
26-31 May	6	12.2
1-15 June	23	46.9
16-30 June	16	32.7
1- 8 July	4	8.2
Total	49	100.0

one day. During the period 13-15 June, female #29 copulated with four different males: female #200 showed similar behavior.

Grizzly bears in Yellowstone Park and vicinity are definitely polygamous. This is probably the case wherever they congregate or are sufficiently abundant to allow a female in estrus to meet more than one adult male. Pairing normally occurs only for short periods of time and the maintenance of this bond is dependent on the ability of the male to defend his female against contenders. A postestrous female quickly loses the attention of her mate if another estrous female appears. Although pairing was observed among the grizzlies in Yellowstone, it was not normally a partnership that lasted throughout the mating season. It may be a tenuous, short-term arrangement for the convenience of mating or, in a few instances, a partnership that persists throughout the period of estrus. Neither the male nor the female in these partnerships remains unresponsive to the sexual condition or sexual advances of other bears.

Duration of Estrus. Females in estrus are readily detected by the number and behavior of the male or males they attract. Preestrous and postestrous periods are characterized by complete lack of sexual interest by both male and female.
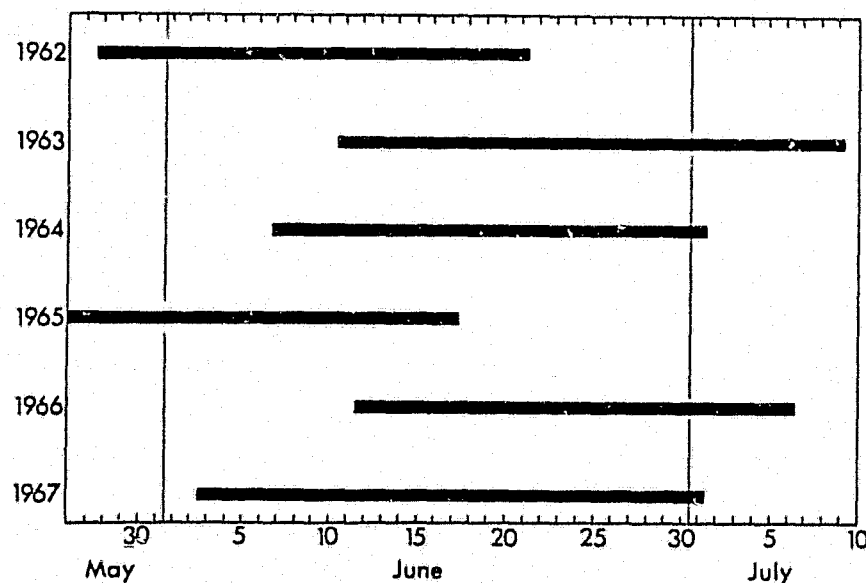
Some females may experience relatively brief es-

FIGURE 25.4. Duration of the mating season, defined by dates of first and last copulations of female grizzly bears (*Ursus arctos*).

TABLE 25.3. Copulation behavior of female grizzlies (1961–67)

Designation of Female	Total Number of Copulations Observed (All Seasons)	Number of Males Involved	Maximum Number of Copulations Observed during a Breeding Season	Number of Males Involved
40	13	11	6	5
29	7	5	7	5
200	7	5	4	3
101	5	3	5	3
109	5	4	4	3
81	4	3	2	2
6	2	2	2	2
15	2	2	1	1
10	2	2	1	1
96	1	1	1	1
187	1	1	1	1
Totals	49	39	34	27

trous periods. For example, in 1962 a female in Yellowstone, #6, was observed to be in estrus from 6 to 13 June (table 25.4). Her heat period, which lasted eight days, probably began on 6 June. She was then observed for eight consecutive days after 13 June, during which she attracted no males and exhibited no mating behavior. When observed again on 29 and 30 June and 2 and 4 July, she still attracted no males. This female was 3.5 years old and experiencing estrus for the first time.

Females #200 and #29, both entering first estrus

at the age of 3.5 years, had relatively short heat periods (see table 25.4). Female #40 exhibited a short estrous period in 1965 at the age of 7.5 years, but had considerably longer periods in 1963 and 1967.

In 1966, female #200 was in estrus over a period of 15 days. Because she was seen on only 6 days of the mating season and was observed to mate on 3 of these, it is quite probable that the estrous period exceeded that observed (see table 25.4). Female #29 was in estrus for 17 days in 1964 and, when first observed on 7 June, had attracted two large males that showed interest but

TABLE 25.4. Durations of estrus (1961–67)

Designation of Female	Age of Female	Inclusive Dates of Estrus	Observed Period of Estrus (Days)	Result of Breeding (Number of Cubs)
15	3½	6/28 1961	1	none
15	4½	6/11–6/13 1962	3	2
15	6½	6/26 1964	— (26)	none
15	9½	6/27 1967	1	
96	4½	5/28 1962	1	2
200	3½	6/10–6/13 1965	4	none
a 200	4½	6/22–7/6 1966	15	2
187	4½	6/20 1967	1	
29	3½	6/15–6/20 1962	6	none
a 29	5½	6/7–6/23 1964	17	2
a 40	5½	6/12–6/27 1963	16	2
a 40	7½	5/26–5/30 1965	5	2
a 40	9½	6/3–6/27 1967	25	
132	5½	6/21 1967	1	
a 6	3½	6/6–6/13 1962	8	none
6	5½	6/23–6/30 1964	did not come into estrus	none
a 101	8½	6/5–6/17 1965	13	1
109	4½	6/10 1965	1	none
109	5½	6/12 1966	1	none
a 109	6½	6/5–7/1 1967	27	
81	5½	5/28 1962	1	none
81	6½	6/11 1963	1	none
81	7½	6/22–6/30 1964	9	1
81	10½	6/9 1967	1	
10	6½	7/9 1963	1	none
10	7½	7/1 1964	1	none

aMost accurately established estrous periods

did not attempt to mate with her. That she was just entering estrus was confirmed 2 days later when she copulated, the first of six copulations. Female #40 exhibited estrous periods of 16, 5, and 25 days duration in 1963, 1965, and 1967, respectively (see table 25.4).

The longest estrous periods recorded were 26 and 27 days. With the exception of one, all females exhibiting long periods of estrus whelped cubs the following year. No 3.5 year olds showed estrous periods exceeding 8 days. Dittrich and Kronberger (1962) reported captive European brown bears in estrus for two to five weeks.

Age at Puberty. Female grizzlies under 3.5 years of age exhibited no heterosexual behavior. Some 3.5-year-old females copulated long, vigorously, and frequently. However, no 3.5-year-old females whelped following this mating activity.

The age at which female black bears become sexually mature is reported to vary with latitude and individual growth rates (Rausch 1961). Erickson et al. (1964, citing Baker 1912) and Rausch (1961) suggest 3.5 years for captive black bears.

Observations in Yellowstone show that female grizzlies produce a first litter at 5.5 years of age. However, some females may whelp for the first time considerably later than this. Among 15 females, 7 had their first litter at 5.5 years of age, 2 at 6.5, 4 at 7.5, and 1 each at 8.5 and 9.5 years of age. It is possible that the first observed litters were the result not of first pregnancies, but of later ones. Also, marked females whose first litters were born when the mothers were 6 to 9 years old may have been pregnant at an earlier age, and lost embryos before birth or cubs soon after it. This would mean that 53 percent of the females studied failed to produce offspring from conceptions occurring before the time they produced their first observed litter. This seems highly unlikely, but cannot be completely discounted.

Estrous and Anestrous Periods. Young females may breed in alternate years or every third year. Older bears often show greater intervals between breeding. The sequences, by years, when individual females either were in estrus or were anestrous were determined for seven bears (figure 25.5). The anestrous condition normally accompanies lactation, but it may occur at other times. Seven females showed continuous anestrous periods of one, two, or three years between their first active mating season and their first established pregnancy.

It is evident that there is much variability in the breeding pattern. Four out of seven females exhibited "false estrus" at 3.5 years, five exhibited anestrus with no mating at age 4.5, while two mated successfully for the first time at 4.5 years. Four females exhibited estrous periods, presumably without ovulation and characterized by unsuccessful breeding.

Wimsatt (1963) offered strong, but not conclusive, evidence that ovulation in the black bear may be coitus induced. There is evidence that the female grizzly is an induced ovulator, but conclusive histolog-

FIGURE 25.5. Estrous condition of seven female grizzly bears (*Ursus arctos*), observed in successive breeding seasons.

ical evidence is lacking. It is intriguing to consider the possibility that the mechanism for inducing ovulation by coital stimulus may develop slowly and, thus, may vary considerably with the age of the individual bear. This could explain effectively why some female grizzlies between the ages of 4.5 and 8.5 years apparently do not ovulate following mating.

Mating Interval and Estrous Cycle. Hansson (1947) provided strong quantitative evidence that the female mink (*Mustela vison*) has several estrous cycles during the same mating season. The female permits copulation at periods of follicular maturity. The time between development of mature follicles and subsequent matings was termed the *mating interval*. Dittrich and Kronberger (1962) studied the mating behavior of the European brown bear in the Zoological Gardens of Leipzig and found that the females allowed numerous copulations. The periods of copulation were followed by days without copulation, implying a mating interval similar to that described for mink. These pauses in the mating of the European brown bear might be short or long and occurred in the presence of males. Prell (cited by Rausch 1961) reported an interval of variable length between a "pseudoestrus" and true estrus in the brown bear and polar bear. Schneider (cited by Rausch 1961) concluded that "pseudoestrus does not occur in the polar bear, but rather a true estrus of long duration."

Observations suggest that the female grizzly has two estrous cycles during the same mating season (Craighead et al. 1969). A female comes in estrus and is receptive and attractive to males. Copulation occurs for a period of days (figure 25.6), after which the female is no longer receptive and the male is not attracted to her. Following a period varying from 4 to 18 days, the female again is receptive and once again attracts males. Thus, an interval exists during which mating does not occur and is probably coincident with follicular development following ovulation. It appears to be quite similar, if not identical, to the "mating interval" in mink described by Hansson (1947).

Collectively, data on durations of the two mating

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periods show that each probably does not exceed 10 days, and that there may be little or no difference between the duration of the two periods (figure 25.6). Each cycle begins and terminates rather abruptly, probably following ovulation induced by mating. It is of interest that the inclusive dates of the "mating interval" all occur within the month of June, when 80 percent of all copulations were recorded.

Delayed Implantation. Hamlett (1935) postulated the occurrence of delayed implantation in the black bear, European brown bear, grizzly bear, and polar bear. Dittrich and Kronberger (1962) later provided evidence for delayed implantation in the European brown bear and the Himalayan black bear (*Selenarctos thibetanus*) and Wimsatt (1963) provided conclusive proof of the phenomenon in the black bear.

There is clear evidence that discontinuous embryonic development also occurs in the grizzly bear (Craighead et al. 1969). A female mated during June 1965, at the age of 6.5 years, and was killed on 27 July of the same year. Free blastocysts were flushed from the uterine horns and fixed for future histological study. A second female mated on 18 June 1967, at the age of 14.5 years. When she was killed 50 days later, unimplanted blastocysts were recovered. The long interval between presumed time of ovulation and recovery of the unimplanted blastocysts is evidence of developmental arrest. Erickson et al. (1964) discounted the possibility of a delayed ovulation in the black bear because of the early formation of corpora lutea following mating. Wimsatt (1963) likewise ruled out this possibility for the black bear. Large corpora present in the ovaries of the female specimens mentioned above ruled out delayed ovulation in the grizzly bear as well. The period in years between the earliest recorded pregnancy (age 4.5) and the age at which a first pregnancy actually occurs in a bear is the prepregnancy period. Among 30 females with reproductive histories, this period ranged from 0 to 4 years.

Craighead et al. (1974) recorded the age at first

FIGURE 25.6. Observed duration of mating interval and estrous cycles of six female grizzly bears (*Ursus arctos*).

pregnancy for 16 of 30 marked females. Eleven of these (69 percent) first became pregnant at 4.5 years of age, 1 at 5.5, 3 at 6.5, and 1 at 8.5 years of age. Although younger females copulated, none became pregnant before she was 4.5 years old (Craighead et al. 1969). The average age of first pregnancy was 5.2 years for 16 females. The age at which female grizzlies attain sexual maturity varies widely in other bear populations. Age of sexual maturity ranged in the eastern Brooks Range, Alaska, from 6.5 to 12.5 years (Reynolds 1976) and in the Yukon Territory from 6.5 to 7.5 years (Pearson 1976). Brown bears on the Alaska Peninsula showed an age range of 3.5 to 6.5 years for first pregnancy (Glenn et al. 1976).

Reproductive Cycles. The chronology of events occurring in a reproductive cycle varies with the cycle length. The length of a cycle is dependent on when the female weans and how soon thereafter she comes into estrus.

In a two-year cycle, the female becomes pregnant in June or July, whelps the following February, suckles cubs through summer and winter, weans them as yearlings in the spring, and then comes into estrus, breeds, and becomes pregnant following weaning. In a three-year cycle, the female becomes pregnant, whelps cubs, attends them as yearlings, dens with them, weans them as two-year olds soon after leaving the den, and then comes into estrus and breeds to begin another cycle. In a four-year cycle, the female follows the three-year cycle, but after weaning two year olds, she either remains anestrous or comes into estrus and is not fertilized. She is bred the following year and becomes pregnant. In longer cycles, the female may remain anestrous or for various reasons fail to produce cubs.

Precise data on reproductive cycles require that marked animals be recognized and observed over a period of years. Reproductive cycles of 19 marked females were calculated from known pregnancies (Craighead et al. 1974). The number of cycles per female varied from 1 to 3 and totaled 33 for all 19 animals during a cumulative reproductive period of 99 years. The reproductive cycle varied from 2 to 5 years. Of the 33 cycles, 9 lasted 2 years; 16, 3 years; 7, 4 years; and 1, 5-years. Three-year cycles were more prevalent than 2-year cycles (64 to 36 percent). For some females, the reproductive period consisted of a single reproductive cycle, but for others it included 2 or more cycles.

An average reproductive cycle of 3.00 years was obtained when the total of reproductive periods in years for all 19 females (99) was divided by the total number of cycles (33). This parameter was then refined by including prepregnancy data. For example, among 19 females recorded, 5 were older than 4.5 years at first pregnancy. The average reproductive cycle of 3.00 was adjusted for the 11 years that these females were not pregnant. With this adjustment (99 years + 11 = 110/33 = 3.33), the average reproductive cycle becomes 3.33 years.

By assuming when each of 30 females would become pregnant following her last litter, it was possible

to use a larger number of cycles and reproductive years to compute reproductive rate. With longer reproductive histories to examine, changes occurred in average length of the reproductive cycle for individual females.

A sample of 30 marked females yielded 68 reproductive cycles, a cumulative reproductive period of 231 years, and an average reproductive cycle of 3.40 years. Data used to calculate average reproductive cycles for marked females in four data samples yielded values of 3.33, 3.21, 3.26, and 3.40 years, indicating the range occurring in this parameter with changes in sampling. They also indicate that a representative reproductive rate for a population of long-lived animals can be obtained only from a relatively large sample of animals over an extended period of time, because the accuracy of this biological parameter is dependent on an accurate measurement of cycle length.

Litter Sizes. Thirty marked females produced 68 litters. Among these, 9 were 1-cub litters, 38 were 2-cub litters, 18 were 3-cub litters, and 3 were 4-cub litters. Fifty-six and 26 percent were 2- and 3-cub litters, respectively. Reynolds (1979) reported litter sizes ranging from 1 to 3 per female with a mean litter size of 2.08, determined from 50 offspring of 17 marked females and 7 unmarked identifiable females in the Brooks Range, Alaska. Mean litter size probably reflects the nutritional quality of food available to bears in different regions. Average litter size in the Yellowstone ecosystem was 2.24 (Craighead et al. 1976a). A number of authors have reported mean litter size; the validity of the parameter in many instances is questionable because samples were small, yearling litters were included with cub litters, or data were not from marked animals.

Reproductive Rates. In a sample of 19 females, reproductive rates for individuals ranged from a low of 0.33 to a high of 1.50 (Craighead et al. 1974). The low represented two cubs produced in two cycles totaling six years, whereas the high resulted from six cubs produced in two cycles totaling four years. Of the 19 females, 4 exhibited reproductive rates of 1.00 or higher (table 25.5). The average rate for all 19 females was 0.70.

Individual bears showed highly variable reproductive cycles and reproductive rates. Because these biological parameters are so important for evaluating the status of a population and for computing reproductive rates for population units, more research effort should be directed toward isolating the factors causing such variability.

In a sample involving 30 females, a reproductive cycle of 3.40 years and a composite reproductive period of 231 years gave a reproductive rate of 0.66.

Maximum and minimum reproductive rates for individual females or a group of females are useful because they indicate the potential of a population to grow or to decline (table 25.6). A population exhibiting compensatory reproduction following a population decline should contain females with high reproductive rates. Similarly, a declining population under environmental stresses could be expected to have females with low reproductive rates.

Although the data indicate that one female exhibited a reproductive rate of 1.50 during a six-year

TABLE 25.5. Reproductive rates of 19 marked female grizzly bears (33 reproductive cycles), 1959–62

Bear Number	Age Marked	Number of Reproductive Cycles in Years				Total Cycles	Reproductive Period in Years	Date of Last Known Pregnancy	Number of Cubs	Reproductive Rates
		2	3	4	5					
5	1.5		1			1	3	1967	2	0.667
7	12.5		1	1		2	7	1965	6	0.857
10	2.5			1		1	4	1969	2	0.500
15	1.5		2			2	6	1968	3	0.500
34	14.5	1			1	2	7	1967	4	0.571
40	1.5	2				2	4	1967	4	1.000
42	5.5	1	2			3	8	1969	6	0.750
65	adult	2				2	4	1963	6	1.500
84	adult			1		1	4	1964	3	0.750
96	3.5		2			2	6	1968	6	1.000
101	4.5	1		1		2	6	1969	2	0.333
120	12.5			1		1	4	1964	2	0.500
125	5.5		3			3	9	1970	8	0.889
128	10.5	1	2			3	8	1969	10	1.250
144	0.5			1		1	4	1970	2	0.500
150	4.5			1		1	4	1966	3	0.750
172	11.5	1	1			2	5	1967	4	0.800
173	2.5		1			1	3	1969	2	0.667
175B	adult		1			1	3	1962	2	0.667
Totals		9	16	7	1	33	99		77	

Reproductive Rates
0.667
0.857
0.500
0.500
0.571
1.000
0.750
1.500
0.750
1.000
0.333
0.500
0.889
1.250
0.500
0.750
0.800
0.667
0.667

period, it is highly unlikely that she could sustain this throughout her entire reproductive life (see table 25.6). Data suggest that a maximum for several females averaged 1.17, or about 1 cub per adult female per year. A reproductive rate of this magnitude for a population of females would indicate a potential for that population to grow if mortality was not excessive.

The minimum reproductive rate recorded for an individual female was 0.29; however, this was for only one reproductive cycle and was not considered representative. Minimum rates were calculated using methods employed for samples 1, 2, and 3 (table 25.6). The reproductive rate for female #120 averaged 0.36 over an 11-year period. The average of four females in samples 2 and 3 was 0.50. Therefore, an average minimum reproductive rate among marked females was approximately half the maximum. A rate of this magnitude among female grizzlies in Yellowstone would clearly indicate a declining population, even if human-caused mortalities were kept to a minimum (Craighead et al. 1974).

Reproductive Rate for Yellowstone Ecosystem Population. The reproductive cycle of 3.40 and rate of 0.66 are average parameters for 30 marked females observed over a 12-year period. To obtain a reproductive rate that would more accurately represent the entire population of grizzly bears inhabiting Yellowstone National Park and adjacent areas, the sample size was increased by including data from an additional 25 marked females. These had been omitted from reproductive cycle calculations because of observational discontinuities, but provided data valid for calculating litter size. Total data gave a long-term reproductive rate of 0.63 for the population. This long-term rate, derived from annual counts of 55 marked and recognizable females with litters over a 12-year period, is considered to be the most accurate long-term average rate for the population between 1959 and 1970. Reproductive rates summarized for several other grizzly bear populations are 0.66 for the Alaska Peninsula (Glenn et

TABLE 25.6. Maximum and minimum reproductive rates as illustrated by certain grizzly bears for which more than one reproductive cycle was observed

Bear Number	Sample 1 (19)	Sample 2 (19)	Sample 3 (24)
40	1.000	1.000	1.000
65	1.500	1.500	1.500
96	1.000	0.889	0.889
128	1.250	1.300	1.300
Average	1.188	1.172	1.172
101	0.333	0.500	0.500
120	0.500	0.364	0.364
10	0.500	0.571	0.571
15	0.500	0.556	0.556
Average	0.458	0.498	0.498

al. 1976) and 0.45 and 0.51 for the eastern and western portions of the Brooks Range, respectively (Reynolds 1976, 1978).

Before valid comparisons can be made and conclusions drawn between the reproductive status of these populations and those of the Yellowstone population and other populations currently under study, the reproductive rate data for each population must be quantitatively comparable. This degree of precision has not yet been obtained.

Reproductive Longevity. Pearson (1975) mentioned a female 24.5 years of age with a cub and Reynolds (1978) reported three females that produced cubs at 17.5, 21.5 (or 22.5), and 25.5 years of age. In Yellowstone, one female 14.5 years old when marked produced her last litter of two cubs at the age of 22.5, and weaned them when she was 24.5 (Craighead et al. 1974). Two other females produced litters when they were 19.5 years old and two when 17.5. The greatest age recorded for a female was 25 years. Therefore, reproductive longevity approximates physical longevity, most adult females producing offspring as long as they live. Although the minimum breeding age in Yellowstone is 4.5 years, a female cub born into the population required an average of 6.3 years to whelp her first litter. With an average reproductive cycle of 3.40 years and 2.24 the average litter size, a 25-year-old female could experience 6 reproductive cycles and produce 13 cubs.

Presumably, flexibility of these biological parameters should enable the species to adjust to environmental factors that affect the population favorably or unfavorably. However, for a long-lived species exhibiting delayed maturity, compensatory reproductive processes (increases in litter size, decreases in length of reproductive cycle, and/or higher survivorship rates for subadult bears) would act slowly. On the other hand, population-regulating mechanisms (infanticides from aggressive males and hormonal activity regulating the intervals between estrus in females) are factors that can offset compensatory processes. Infanticide was low in the Yellowstone population (eight instances) but may be higher in other populations (Pearson 1975; Reynolds 1978). The great variability in the length and sequences of reproductive cycles could be important in regulating reproduction, but it will be difficult to draw conclusions from this information until similar data are obtained from other populations and norms established.

ECOLOGY

Habitat. Various aspects of grizzly bear habitat south of Canada have been described by Shaffer (1971), Craighead and Craighead (1972), Sumner and Craighead (1973), Varney et al. (1974), Mealey (1975, 1976), Roop (1975), U.S.D.A. Forest Service (1975), Pearson (1975), and Craighead et al. (1976b). This literature deals with surveys, establishment of criteria for evaluating habitat, habitat typing and mapping techniques, distribution and occurrence of plant foods, and

relating food habits of grizzlies to habitat types and generalized vegetation complexes.

Some recent studies delineate critical habitat (Craighead 1980b) or describe and/or evaluate specific forest and range habitat types (Hamer et al. 1977, 1978, 1979; Hechtel 1979; Servheen and Lee 1979; Schallenberger and Jonkel 1980; Sterling Miller personal communication). Craighead and Scaggs (1979), Craighead and Sumner (1980), and Scaggs (1979) addressed the problem of developing a standarized system for describing, evaluating, and rating habitat types within climatic zones. Craighead (1980a) utilized multispectral imagery with computer assistance to map and evaluate grizzly bear habitat and to develop an ecospectral vegetation classification.

The grizzly has been able to survive in North America only where spacious habitat has insulated it from excessive human-caused mortality. Its habitat has traditionally been protected by rugged physiography or inaccessibility. These factors alone, however, are no longer effective. Populations in the contiguous 48 states have survived through the past decade primarily because suitable habitat was preserved by the Wilderness Act of 1964, which established a National Wilderness Preservation System. This system now includes much of the spacious, mountainous habitat where grizzly bears are found south of the Canadian border and where they presumably can survive in the future. The grizzly is not threatened in Canada or Alaska, primarily because large expanses of wilderness habitat still exist, unmodified by human development. Habitat in the contiguous 48 states is largely confined to three grizzly bear "ecosystems"—the Yellowstone, the Selway-Bitterroot, and the Bob Marshall–Lincoln-Scapegoat. In at least one, and probably two, of the three ecosystems, grizzly bears occur as geographically and genetically isolated populations. In the third, the Bob Marshall–Lincoln-Scapegoat, the population can be reinforced genetically and numerically by movement and interchange of individual bears from adjacent occupied habitat in Canada.

The purpose of the Endangered Species Act of 1973 is to perpetuate threatened and endangered species and, where possible, to extend their populations. On 1 September 1975, grizzly bears (*Ursus arctos horribilis*) were listed as "threatened" south of the Canadian border. With this designation, all U.S. federal agencies were required to conduct their land management programs to prevent destruction or adverse modification of critical grizzly bear habitat. Critical habitat determination involved delineating an area essential for the survival and recovery of the species. Federal rules published 22 April 1975 defined critical habitat as that necessary to provide for: nutritional and spatial needs of the species; specialized sites for breeding, reproduction, and shelter; and other specific physical, seasonal, and behavioral requirements.

Most of the range currently occupied by the grizzly bear has been proposed as critical habitat through professional and agency recommendations. A proposed rule by federal authorities delineating critical grizzly bear habitat in the contiguous 48 states was published in the *Federal Register*, 6 November 1976. This was followed by public hearings (U.S. Senate Hearings 1977). The extensive land areas proposed by the U.S. Fish and Wildlife Service as habitat for the grizzly bear's survival total about 5.3 million hectares and consist of four discreet parcels, as follows:

(1) the region where Wyoming, Montana, and Idaho come together in Yellowstone National Park and adjacent areas including parts of Custer, Shoshone, Teton, Targhee, Beaverhead, and Gallatin national forests and part of Grand Teton National Park;

(2) northwestern Montana in Glacier National Park, the Bob Marshall Wilderness Area, and most of the Flathead National Forest and adjacent areas, including parts of the Lewis and Clark, Helena, and Lolo national forests and small parts of the Blackfeet and Flathead Indian reservations;

(3) extreme northwestern Montana and northern Idaho in the Cabinet Mountains, mostly in the Kootenai, Kaniksu, and Lolo national forests; and

(4) extreme northern Idaho and northeastern Washington in the Selkirk Range, mostly in the Kaniksu National Forest.

The enactment of the Endangered Species Act of 1973 also spurred habitat studies in Canada and Alaska.

A vegetation/landtype classification of grizzly bear habitat in the Scapegoat Wilderness, Montana, was developed by Craighead and Scaggs (1979) for the grass-shrublands of the alpine, subalpine, and temperate climatic zones. It was based on the ecoclass methods of Daubenmire (1952), Peterken (1970) and Corliss et al. (1973). Twelve land units (habitat units) were delineated and described in the alpine zone, as were five landtypes in the subalpine zone. Forest habitat types of both the subalpine and temperate climatic zones were grouped as xeric, mesic, or hydric types. Eight major forest habitat types (Pfister et al. 1977) included within these groupings were sampled for ground cover and described in terms of grizzly bear food plants. The habitat type/land type classification allowed measurement and quantification of bear food plants on a comparative basis.

The most important habitat units of the alpine zone, based on the percentage abundance of food plants, were the Alpine Meadow, Alpine Meadow Krummholz, Glacial Cirque Basin, and Mountain Massif, all of which showed an abundance of bear food plants in excess of 50 percent of the total ground vegetation (figure 25.7). Landtypes in the subalpine zone with the greatest abundance of food plants were fire-caused Seral Stages, Dry Forb Grasslands, Snowslides, and Ridgetop Glades, all of which showed an abundance of bear food plants in excess of 50 percent of the total ground cover.

Forest habitat types of the subalpine zone had high potential as plant energy sources for grizzly bears. Those with the greatest abundance of food plants (in excess of 60 percent of total ground cover) were *Abies lasiocarpa/Luzula hitchcockii-Vaccinium scoparium* and *Abies lasiocarpa-Pinus albicaulis/Vaccinium scoparium*. The poorest was *Abies lasiocarpa/Luzula*

hitchcockii-Menziesia ferruginea. The presence of *Pinus albicaulis* made the subalpine zone unique as an energy source for grizzly bears.

Ecological landtypes of the temperate zone showed greater variation as energy sources than their equivalents in the subalpine zone. Seral stages (burns) and Dry Forb Grasslands showed the highest potential, based on food plant abundances exceeding 70 percent of the total ground cover.

The forest habitat types of the temperate zone exhibited the highest food plant potential of all vegetation units measured. Those with the greatest abundance of undergrowth food plants were *Abies lasiocarpa/ Xerophyllum tenax* (*Vaccinium globulare* phase), *Abies lasiocarpa/Xerophyllum tenax* (*Vaccinium scoparium* phase), and *Pseudotsuga menziesii/ Calamagrostis rubescens* habitat types (figure 25.8). Food plant abundance values for each of these habitat types exceeded 80 percent.

In potential energy sources for the grizzly bear, the subalpine zone rated highest, the temperate zone second, and the alpine zone third. The resources of all three zones are essential to the grizzly within the Bob Marshall–Lincoln-Scapegoat Wilderness areas. This is probably true for the other large wilderness ecosystems supporting populations of grizzly bears.

Those portions of the grizzly bears' total environment that contain preferred food plants in greatest abundance are critical to the bears' welfare. Some of these—for example, seepage areas where *Equisetum arvense* grows in heavy mats—are small in size. Others—for example, the *Abies lasiocarpa/Luzula hitchcockii* habitat type (*Vaccinium scoparium* phase) where grouse whortleberry may average 50 percent of the forest undergrowth—are quite large. Some critical food source areas are at high altitudes, including the semivegetated talus that supports *Claytonia megarhiza* and the glacial cirque basins with *Lomatium cous*. Others—for example, the sedge marshes and *Abies lasiocarpa/Xerophyllum tenax* habitat type (*Vaccinium scoparium* phase)—lie near the lower altitudinal limits

FIGURE 25.8. Grizzly bear (*Ursus arctos*) food plant abundance by forest habitat type of the temperate climatic zone. 691 = *Abies lasiocarpa/Xerophyllum tenax–Vaccinium globulare;* 692 = *Abies lasiocarpa/Xerophyllum tenax–Vaccinium scoparium;* 670 = *Abies lasiocarpa/Menziesia ferruginea;* 320 = *Pseudotsuga menziesii/Calamagrostis rubescens*.

of the bears' wilderness environment. High-altitude areas provide succulent vegetation in early spring; the lower areas, where 85 percent of the ground cover may be plants eaten by grizzlies, are a veritable storehouse of various plant foods.

Pearson (1975) provided a general description of bear habitat in the Yukon Territory; Mealey (1976) surveyed and evaluated the importance of specific forest habitat types west of Yellowstone National Park; Hamer et al. (1977, 1978) described a number of forest and vegetation types for Banff National Park. None of these researchers quantifies these in terms of percentage of food plants or evaluates or rates them as energy

FIGURE 25.7. Grizzly bear (*Ursus arctos*) food plant abundance by ecological land units of the alpine climatic zone. AM = alpine meadow, AMK = alpine meadow Krummholz, SRK = slab rock Krummholz, SRS = slab rock steps, VT = vegetated talus, GCB = glacial cirque basin, MM = mountain massif, SVT = semivegetated talus, FF = Fellfield.

sources for the grizzly. Scaggs (1979) described forest and vegetation types in the Selway-Bitterroot Wilderness area of Montana and Idaho using the same classification system employed by Craighead and Scaggs (1979) for the Scapegoat Wilderness, Montana. The use of specific forest habitat types and vegetation complexes by radio-instrumented bears was documented by Hechtel (1979), Servheen and Lee (1979), Schallenberger and Jonkel (1980), and Craighead (1980b).

Grizzly bears require spacious habitat, characterized by great diversity. The species thrives best when its habitat is isolated from humans and their activities. Although the grizzly bear is essentially a wilderness animal, it can, and does, adapt to the presence of humans; however, it cannot and has not adapted to mankind's intensive use and modification of its habitat. Mankind must adapt to the grizzly, a tolerance that may not yet have been attained.

Where grizzly and mankind are competing for the same habitat, human-caused bear deaths rise. The bear has a low reproductive rate that does not offset heavy and persistant human-caused mortality. Precautions must be taken to keep such mortalities to a minimum. These appear to be an even greater threat to the grizzly throughout its range than is direct modification of the habitat.

Ranges and Movement. The species' omnivorous feeding habits, complex population and social interactions, winter denning, and aggressive intraspecific and interspecific behavior require extensive movement throughout a spacious habitat. How a population unit moves and interacts within a large geographic area primarily depends on the spatial and temporal distribution of food. There appear to be at least two distinct types of bear populations as characterized by their movements: those populations that inhabit an ecosystem where concentrations of salmon or refuse attract them to feed communally, and those populations where no massive concentration of food exists. The hierarchical relationships that develop at communal sites have been described for the brown bear by Stonorov and Stokes (1972), Egbert and Stokes (1976), and Luque and Stokes (1976). Hierarchical behavior in grizzly bears has also been observed (Hornocker 1962; J. J. Craighead in preparation).

Both the grizzly and the brown bear establish traditional movements to exploit dependable sources of high-calorie foods. These food sources are generally seasonal and available for a period of only several months. They represent a long-established, seasonal pattern for some bear populations, attracting and holding large aggregations of bears for prolonged periods. In Yellowstone, as many as 137 individuals were observed in a single evening (Craighead et al. 1971) and at the McNeil River, Alaska, approximately 50 in a similar period of time (Larry Aumiller personal communication). Where such conditions occur, whether "natural" (figure 25.9) or human-induced (figure 25.10), they influence the daily and seasonal movements, as well as the spatial requirements, of

many members of the population. These population concentration sites can be characterized as population activity centers, or "ecocenters." They may best be visualized as ecological magnets that attract and hold high densities, not only of bears, but also of many other omnivorous species such as ravens, gulls, magpies, coyotes, and raccoons.

Specific information on movements of grizzly bears to and from ecocenters, and information on how such movements affected the development, size, and configuration of home ranges, were obtained in the Yellowstone ecosystem. This was accomplished by directly observing color-marked individuals, by recording the place of capture and locality of death of marked bears, and by monitoring radio-instrumented animals (Craighead et al. 1961; Craighead 1976, 1980b).

Movement data from color-marked grizzly bears within the park or immediately adjacent to it at Gardiner and West Yellowstone, Montana, showed that the bears moved extensively throughout a 2,023,500-ha ecosystem (figure 25.11) that could be considered as critical habitat for the population (Craighead 1980b). Bears marked at sites where they congregated to feed at open pit garbage dumps in Yellowstone Park were observed and recognized in four national forests. Twelve grizzly bears marked at Trout Creek (the geographic center of Yellowstone Park) were observed in the Shosone National Forest. The maximum recorded movement was 74 km. Similarly, other bears marked at Trout Creek were observed in the Gallatin (13), Targhee (2), and Teton (6) national forests. Maximum movements of 70, 72, 78, and 87 km were recorded. Among bears marked at Rabbit Creek approximately 27.5 km to the southwest of Trout Creek (figure 25.11), five were observed in Targhee National Forest and one in Teton National Forest. Of all bears marked in Yellowstone National Park but sighted outside, 67 percent were in the Shoshone and Gallatin national forests, an indication of the considerable spatial needs of the species.

Information obtained from kill records of marked animals provided further evidence for extensive movement of individual animals and for the vast spatial requirements of the entire population. Of 277 color-marked grizzly bears, there were 137 known mortalities: 79 were killed within Yellowstone Park, while 58 were killed outside the park. The deaths of 35 (15.6 percent) of 224 bears marked at or near the geographic center of Yellowstone National Park were recorded in the five adjoining national forests (figure 25.12).

The movement of grizzly bears from the original marking sites (ecocenters) was massive and extensive. The seven greatest airline distances from locality of marking to site of death ranged from 72 to 86 km and averaged 80 km.

Census data (Craighead et al. 1960, 1974, Craighead and Craighead 1967) showed that much of the movement between Yellowstone National Park and the national forests was seasonal. The summer aggregation of grizzly bears at Trout Creek (Craighead et al. 1971) also supported strongly the concept of major

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FIGURE 25.9. Grizzly bears (*Ursus arctos*) congregated on the salmon runs at McNeil River, Alaska.

FIGURE 25.10. Grizzly bears (*Ursus arctos*) congregated at the Trout Creek dump, Yellowstone Park.
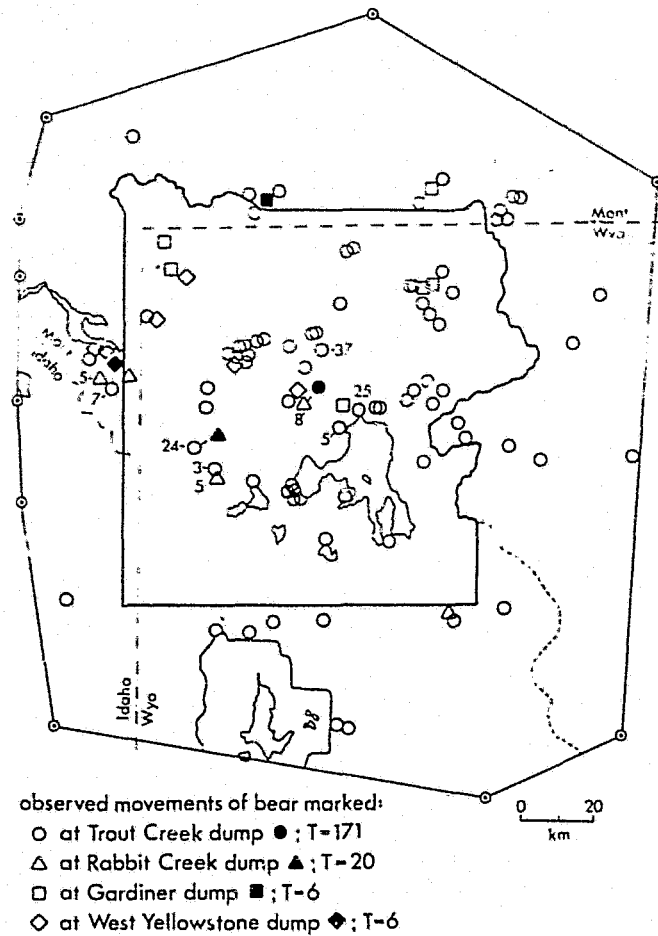
FIGURE 25.11. Individual natural movements of grizzly bears (*Ursus arctos*) in the Yellowstone ecosystem. 1959–74.

observed movements of bear marked:
○ at Trout Creek dump ● ; T–171
△ at Rabbit Creek dump ▲ ; T–20
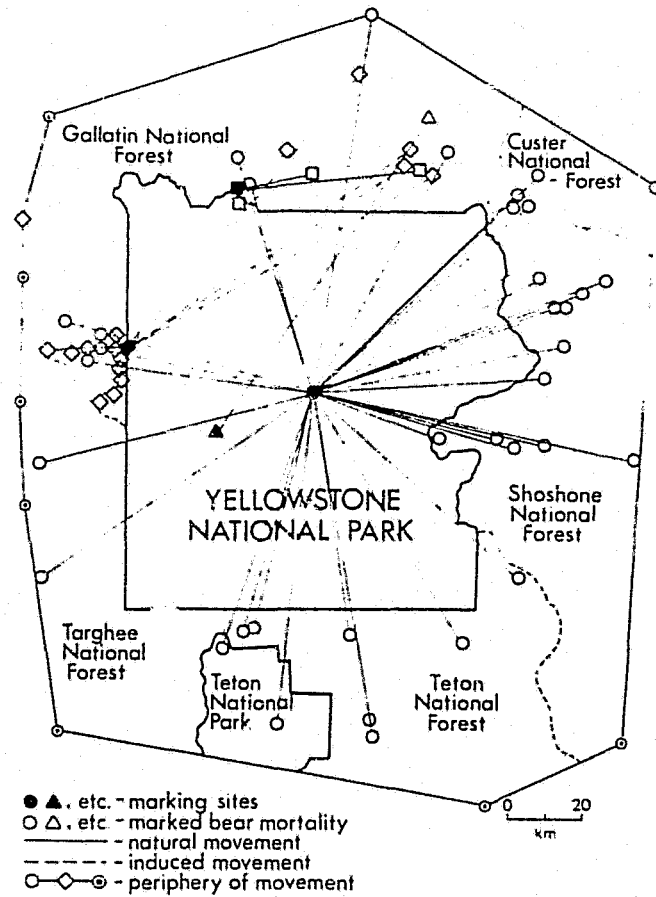□ at Gardiner dump ■ ; T–6
◇ at West Yellowstone dump ◆ ; T–6

FIGURE 25.12. Movements of marked grizzly bears (*Ursus arctos*) from site of marking to localities of death in the Yellowstone ecosystem. 1959–74.

● ▲ . etc. – marking sites
○ △ . etc. – marked bear mortality
———— – natural movement
– – – – – induced movement
○—◇—⊙ – periphery of movement

seasonal movement. Berns and Hensel (1972) reported established movement patterns among brown bears on Kodiak Island, Alaska. Similar movement to and from ecocenters occurs among brown bears of the Alaska Peninsula (see figure 25.9) at the McNeil River, at Katmai National Monument, and at other sites in coastal Alaska. Some individual bears within the Yellowstone ecosystem centralized their year-round activities near the food source, or ecocenter (see figure 25.10) and were not observed to move large distances (Craighead 1980b). Such individuals tended to have small, discreet home ranges, viz., females #40, #150, and #39 (see table 25.6). Other bears, such as #37 and #14, exhibited home ranges encompassing much larger geographic areas and including seasonal migratory "corridors" to and from ecocenters. Such ecocenters are characterized by a unique concentration of readily available high-protein food. The large aggregation of bears that is attracted has developed a high order of social interaction expressed as a linear hierarchy.

Home ranges are usually defined to be areas within which individuals meet all of their biological requirements. These requirements may be met for individual or family units within small core areas or centers of activity, or they may require extensive movement to range peripheries. Many home ranges delineated in Yellowstone contained well-defined seasonal ranges, some separated by long migratory cor-

ridors (Craighead et al. 1974). Reynolds et al. (1976) postulated migratory corridors between seasonal ranges of grizzlies in the Brooks Range, Alaska. Home ranges of the bears in Yellowstone varied greatly in area, depending on the sex and age of the animal, seasonal and annual food availability, foraging ability, reproductive condition of females, and other factors (table 25.7). Equally important was the influence that ecocenters exerted on the movement of most bears. Adult female #7 exhibited a home range of 275 km² during the spring, summer, and fall of 1963. She had three yearlings and traveled extensively, seeking food at the Trout Creek garbage dump (an ecocenter) and in the grass-shrub parklands and forest habitat types of the subalpine zone, with occasional foraging treks into the alpine zone. After weaning her offspring she remained anestrous until the following spring, during which time she exhibited a much smaller home range.

Female #150 with three cubs had a home range during 1963 of only 70 km². She regularly visited an open pit garbage dump and also occupied a core area nearby where meadow mice (*Microtus* spp.) and pocket gophers (*Thomomys talpoides*) were abundant. Sedges, grasses, and the starchy, onionlike bulbs of *Melica spectabilis* were also very abundant. This family met its nutritional requirements within a much more limited space than did female #7 and her three yearlings. Females #101, #39, and #187 had relatively small home ranges that overlapped one another. The

TABLE 25.7. Grizzly bear home ranges, Yellowstone ecosystem

Bear Designation	Sex	Age	Total Years Color Marked (1959–70)	Consecutive Years Radio-tracked (1963–68)	Mode of Detection[a]	Days Radiolocated[b] (1963–68)	Range (km²)
7	F	adult	10	1	R	44	275
150	F	adult	9	1	R	33	70
40	F	subadult–adult	9	6	R	400	78
101	F	adult	11	2	R	125	111
39	F	adult	12	1	R	51	57
187	F	adult	6	2	R	98	104
202	M	yearling–2 year old	2	2	R	174	324
158	M	yearling	1	1	R	51	57
37	M	subadult	3	1	C		1217
14	M	adult	10	1	R & C	41	2600

[a]R = radio-tracking; C = color ear tags.
[b]Radio-located refers to a radio fix, a series of bearings or a radio signal indicating the presence of the instrumented animal.

three females shared the ecocenter as well as much adjacent habitat. However, each utilized discreet centers of activity, seasonal foraging areas, and denning sites within her home range (Craighead 1980b).

Many bears in the Yellowstone population moved 65 to 90 km, or more, between denning areas or early spring foraging sites and ecocenters of localized food abundance. Such movement patterns become traditional and affect the size of home ranges, as well as the way in which bears utilize the space and the resources within those ranges. The home range concept implies that each animal is limited to a definable area from which it seldom ventures. When applied to a large, long-lived omnivore such as the grizzly bear, the concept has limited interpretive value. A range representing the spatial requirements of an individual for a period of years or for its lifetime is needed. For example, bear #16, a 340-kg male, had a radio-defined range of only 31 km² within Yellowstone National Park during the fall of 1964 and his home range that year did not greatly exceed this. Data from recaptures and sightings over a period of years, however, indicated that the life range of this male probably exceeded 2,600 km² (see table 25.7). Home and seasonal ranges of grizzlies in the Yukon are discussed by Pearson (1976); in the Brooks Range, Alaska, by Reynolds (1976, 1979); in Yellowstone National Park after 1970 by Knight et al. (1978) and Judd and Knight (1980); and in western Montana by Rockwell et al. (1978), Servheen and Lee (1979), and Schallenberger and Jonkel (1980). Summer ranging of brown bears in the alpine zone of Kodiak Island is described by Atwell et al. (1980). Information from these studies confirms the larger spatial requirements of males versus females, the utilization of seasonal ranges within the total home range, and the presence of discreet activity centers. Home range calculations for the brown bear on Kodiak Island are presented by Berns et al. (1980).

A life range can be defined as an area that provides the biological requirements of an individual bear for all or most of its lifetime. For females, this includes the requirements for bearing and raising offspring. Female #40 (see table 25.7) was radiotracked for eight consecutive years from 1961 through 1968 (Craighead 1976, 1980b). She was instrumented at the age of 2.5 years and shot when 10.5 years old. Her life range, smaller than home ranges of most females, encompassed an area of only 78 km². Her core areas remained basically the same year after year, none exceeding a square mile. Her seasonal and home ranges, however, varied considerably. During 1961 and 1962, her summer-fall range as a subadult did not exceed 21 km². In 1963, at the age of 4.5 years, she used an area of 21 km² during the summer, was observed breeding, and became pregnant. In 1964 she produced two cubs (one of which died) and had a fall range of 40 km². She entered her den on 10 November with her cub. In 1965 she weaned her yearling and mated; she was radio-tracked for 106 days beginning 28 June and is known to have entered a den on 11 November. Her home range was 52 km². Accompanied by two new cubs in 1966, her summer and fall range was 19 km². She dug a new den and wintered with her cubs. In the spring of 1967 she weaned the cubs and bred. During the fall of 1967 she ranged within an area of 29 km². Her den was not located, but she emerged in 1968 with three cubs and occupied a home range of 57 km². She was shot in 1969 at the age of 10.5 years. The life range of female #40 was small because it encompassed the Trout Creek dump, an ecocenter, where she satisfied many of her nutritional needs. This food source supplemented her "natural" food intake and that of her offspring, thereby reducing her foraging activities and her spatial requirements. Nevertheless, she made frequent and extensive seasonal movements to feed on winter-killed elk (*Cervus elaphus*) and bison (*Bison bison*) in the riparian communities and the sagebrush-bunchgrass habitat types. She also ate *Vaccinium* berries in the subalpine fir-huckleberry and dwarf whortleberry habitat types, both of which were well represented within her life range. In fall she traveled to the ridges for white bark pine nuts (*Pinus albicaulis*) in the subalpine fir-white bark pine forest types and hunted *Microtus* spp. in the sagebrush-bunchgrass parklands. Her
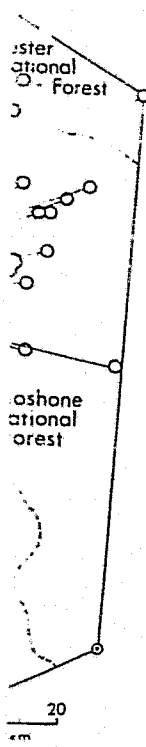
life range contained seasonal foraging areas, travel corridors, denning and escape sites, and activity centers. It lay entirely within the subalpine vegetative zone.

The life range of female #150 presented a similar developmental pattern throughout an 8-year period (see table 25.7). During this time, she raised three litters (Craighead et al. 1974) and showed area requirements linked closely to her reproductive condition and family responsibilities. Among the many biological needs that must be satisfied within a home range, food abundance and availability appear to be more important than all others in determining the size, character, and configuration of a life range.

The extent and duration of movements within a home or a life range are generally responses to specific needs of an animal. In general, distances moved by males radiotracked in the Yellowstone ecosystem were greater than those moved by females. Radiofixes made every 12 hours revealed that female #150 averaged an airline distance of 3.7 km over 13 separate movements. Female #7 averaged 5.1 km for 12 distinct movements and a young adult male averaged 11.5 km for 8 movements. The greatest distance covered by the young male in a 12-hour period, 16 km, was recorded on four separate occasions. He frequently moved 11 to 16 airline kilometers daily within a home range of 435 km². On one occasion, he traversed 3,122-m Mt. Washburn about the 2,750 m level, and crossed the Grand Canyon of the Yellowstone River five times, traveling 93 airline kilometers over extremely rough terrain during an 8-day foraging period. The ground distance was estimated to be three times the airline distance. Data on the movements of color-marked grizzlies in the park supported the observation of radioed animals. On an average, males moved greater distances than did female bears, and subadults averaged distances per move about equal to those of adult bears. However, averages for male subadults exceeded those for either male or female adult bears, while average distances moved by female subadults were much less than those observed for adults or for male subadults. This is explained, perhaps, by the fact that, within the population as a whole, less aggression was directed toward females than toward males; this was especially evident with regard to subadult females. Nevertheless, there were instances where both male and female subadults established home ranges within their mother's home range, indicating considerable spatial tolerance and compatibility in some individual adult females or unusual assertiveness by their offspring.

Grizzly bears in Yellowstone made daily (24-hour) movements from feeding sites to bedding sites. Some of these movements were only a few kilometers, while others were 10 to 11 kilometers. During the summer, a high percentage of the daytime bedding occurred from 1000 to 1600 hours. Movements to feed and to bed occurred at all times of the day and night. Maximum movements were recorded in late afternoon and evening, while minimal travel occurred during midday and the middle of the night. Comparative movements of male and female adult and subadult bears in the Yukon, Brooks range, Alaska, and Kodiak Island have been

recorded by Pearson (1975), Reynolds (1979), and Berns et al. (1980), respectively.

All grizzlies of both sexes were radiotracked in Yellowstone on prehibernation "treks" to locate suitable denning sites and to initiate digging of dens. For some individuals, treks began as early as 3 September (Craighead and Craighead 1972). Prior to entering dens for winter sleep, some individuals made as many as four trips from activity centers within their home ranges to their dens. The distances traveled from summer to fall foraging areas to dens or denning sites varied greatly among individual animals. The minimum distance recorded was 3 km and the maximum 25.6 km, although some treks were known to be greatly in excess of this maximum. Final movements to hibernate were generally shorter than the prehibernation movements and often were more direct and rapid. Movements associated with locating a site, digging the den, preparing it for winter, and finally entering it were numerous and closely related to fall foraging movements.

Dispersal from summering areas to fall foraging areas was common to all bears radiotracked. In some instances, the winter den was located within the fall range. In other cases, the den was located many kilometers away. Male #76 and female #96 moved 32 and 64 km, respectively, from summer to fall foraging areas. In general, movement from summer to fall foraging sites occurred in September and often was very abrupt and rapid. Movement to these areas within home ranges was partly a response to food availability, but also was due to a need to be near the winter denning sites while preparing the den. Some dens were not completed until mid-November. Final den entry did not occur for adult females #120 and #101 until as late as 21 November. Some grizzlies, such as #164, moved directly from a fall foraging area to enter a winter den; other bears, such as females #40, #101, and #34, spent many days at, or in the vicinity of, their dens prior to entering them for the winter.

Movement from the winter dens to spring foraging areas was less complex. Some animals simply moved to the nearest snow-free foraging site or to the carcass of a winter-killed elk or bison. Females #40, #101, and #34, for example, moved distances between 6.5 and 13 km within the subalpine zone. For a number of animals, the movements exceeded 50 or 60 airline kilometers and involved several days to several weeks of leisurely traveling, during which the individual or family unit descended from the subalpine zone, traversed river valleys in the temperate zone, and returned to their former spring and summer ranges in the subalpine zone many kilometers from the den sites. Some individuals were first attracted to emerging sedges and grasses, others to carrion, and still others to rodent populations exposed by the receding snow.

Den-related movements of grizzlies have been reported for the Yukon by Pearson (1975); for the Brooks Range by Reynolds et al. (1976); for Yellowstone after 1970 by Knight et al. (1978); and for western Montana by Schallenberger and Jonkel (1980).

Movements to seasonal food sources can be extensive. In Yellowstone it was not uncommon for indi-

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vidual animals of either sex to travel 16 to 30 airline kilometers to feed on the seeds of white bark pine. Similar movements were recorded in the Lincoln-Scapegoat and southern Bob Marshall wilderness areas of Montana (Sumner and Craighead 1973). In some instances, movements transected three climatic zones. Some individual animals moved many miles to feed on moths (Noctuidae), biscuitroot (*Lomatium cous*), and spring beauty (*Claytonia megarhiza*) in the alpine zone of the Scapegoat Wilderness.

Grizzlies congregate in relatively small numbers at unusually rich or extensive sources of pine nuts, berries, insects, forbs, and other green vegetation, and at carrion. Movements to such sites were repeated annually by some bears and appeared to involve a learning process (Craighead and Sumner 1980). Movements to food sources may be direct and rapid. One adult male traveled 14 km in a single afternoon. Movements to such food sources should not be confused with those to ecocenters. The food attraction is much more limited and dispersed and does not draw and hold animals in large seasonal aggregations.

Movement to carrion is normally rapid and directed by scent. Many bears were observed to move 5 to 12 km daily to and from carcasses. A subadult male in Yellowstone traveled an airline distance of 30 km to a carcass in 36 hours. On the other hand, an adult sow with three yearlings required approximately 60 hours to locate a carcass less than 3 airline km away. Similar daily movements to carcasses were observed in the Scapegoat Wilderness (Sumner and Craighead 1973).

Movements of bears to fall foraging areas were normally sudden and swift in Yellowstone. A female with siblings moved 24 km overnight. Another family unit traveled 19 km in 48 hours, while a lone adult female made a continuous move of 64 km in less than 36 hours. An adult male averaged 1 km per hour in a 24-km move to a fall foraging site, while another traveled 32 airline km in a similar type movement. A yearling male covered an airline distance of 88 km in 20 days. The most rapid movement to a winter den was 25.6 km in 12 hours from a fall foraging area. In nearly all instances where speed of travel was documented, the terrain traversed was rough; the airline distances recorded can be at least doubled to obtain approximate ground distances per unit of time.

Induced movements resulting from the release of a grizzly at some distance from the place of capture averaged greater for adult males than for adult females and greater for subadult males than for subadult females. Among 145 releases of grizzly bears within Yellowstone National Park at varying distances from the campgrounds and developed areas where they were captured, 68 percent returned to the same or another campground following release. As the following examples illustrate, the homing instinct of grizzlies is strong. Cub #78 was orphaned when his mother was captured and shipped to a zoo in 1961. The orphan began entering campgrounds and traveling the highways. Captured in the Lake Campground on 10 July, transported across Yellowstone Lake, and released on Promontory Point, a large peninsula extending into the

lake from the south, he returned to his old haunts at the north end of Yellowstone Lake 7 days later. To accomplish this, he traveled due south 9.7 airline km, east 6.4 km, north 24.1 km, and then west 4.8 km to Pelican Campground—a total airline distance of about 45 km. Actual ground travel was probably more than double this distance.

A two-year-old male bear, #38, captured at Lake Campground, was also boated to Promontory Point and released. Four days later he was back at the Lake Campground, after traveling essentially the same route used by bear #78.

Female #170 and her two cubs were captured just outside the northern border of Yellowstone at Gardiner, Montana. When they were released in Hayden Valley, the geographic center of Yellowstone National Park, the female was color marked and fitted with a radio transmitter. She traveled 50 airline km in 62 hours to return to her home range. The ground distance determined by radio fixes was approximately 80 km, not taking into consideration elevational movements. When again trapped, transported, and released, she returned a distance of 85 airline km.

Movements following transport and release have been recorded by Craighead and Craighead (1967, 1972), Pearson (1975), Reynolds (1979), and Servheen and Lee (1979).

The overlap of home and seasonal ranges of a large number of animals and the extensive travel to and from food sources, daytime retreats, and denning sites were not characterized by territorial defense. The social order inherent in grizzly and brown bear populations precludes the need for holding and defending a well-defined territory. In Yellowstone, grizzly bears did not defend activity centers, seasonal ranges, or their dens from other bears. Aggressive adults defended kills and choice feeding sites until their hunger was appeased, after which other bears shared the food and the site. For example, the carcass of an adult male bison was first defended by an alpha male, but, over a period of several days, more and more bears utilized the food source. Eventually, 23 animals attended the carcass at one time and shared it with only infrequent confrontations.

In summary, the extensive movements of grizzly bears is probably directly related to the absence of defended territories and the functioning of a social linear hierarchy that permits freedom of travel and maximum exploitation of rich food sources.

Dens. The denning tendency is well developed in the brown/grizzly bear group in northern latitudes. Earliest evidences of the Ursidae are cave associated (Kurtén 1968) and imply that natural shelters, at least, were utilized by European/Asian progenitors common to both the *Ursus americanus* and the *U. arctos* lines. As in other hibernating mammals, the adaptive value of winter denning by bears relates to survival during inclement weather conditions. Reduced food supply during winter, together with decreased mobility and the bear's increased energy needs for thermoregulation, have represented a real threat to its survival. The evolu-

tion of denning and associated behavior has been the biologic response. The strength of the behavioral mechanism is evident in orphaned cubs that were recorded to dig dens and hibernate successfully in Yellowstone Park.

As discussed earlier in the chapter, hibernation physiology of bears differs from that of most other hibernators in that bears do not assume a state of hypothermic torpor. A den aids in reducing the energy necessary to maintain body temperatures at levels only slightly lower than those maintained during warmer seasons of the year (Hock 1960; Folk et al. 1972, 1976; Craighead et al. 1976a). The period of denning coincides with the period of most inclement weather as well as with the length of gestation. Young, conceived between late spring and early summer, are born in midwinter in the comparative safety and isolation of the den.

Denning behavior, as observed in brown/grizzly bears, coincides with general time frames that relate to regional climates and latitudes. Dates of entry and emergence in a particular population vary in response to weather conditions from year to year. However, grizzly bears inhabiting the contiguous United States generally locate sites and excavate dens between early September and mid-November, enter dens between mid-October and mid-November, and emerge between late March and early May (Craighead and Craighead 1966, 1972; Knight 1975; Werner et al. 1978; Servheen and Lee 1979). Approximately the same chronology has been recorded for grizzlies farther north in the Banff National Park, Canada (Hamer et al. 1977; Vroom et al. 1980), and in the southern Yukon Territory (Pearson 1975), as well as for brown bear populations on Kodiak Island (Berns et al. 1980) and the Alaska Peninsula (Glenn and Miller 1980). Grizzly bears observed in the Brooks Range of northern Alaska entered dens throughout October, on an average somewhat earlier than more southerly populations (Reynolds et al. 1976; Reynolds 1979). Observations on emergence dates from the Brooks Range bears were not reported. Work by Harding (1976) on grizzly bears inhabiting Richards Island off the coast of the Northwest Territories revealed even earlier entry into and later emergence from the winter dens. Entry occurred from late September through mid-October, with emergence from late April through early May.

Factors that govern denning behavior are not as yet clearly understood. Several studies have noted that grizzly bears commonly become increasingly lethargic as winter weather becomes more inclement and finally move to and enter dens, some years, during heavy snowstorms (Craighead and Craighead 1966, 1972; Reynolds et al. 1976). Other workers have observed such responses only in some animals (Servheen and Lee 1979), or not at all (Pearson 1975). All workers have suggested that some factor(s) other than weather conditions provides the critical denning stimulus.

In general, adult male bears remain active longer and emerge from dens earlier than do other sex or age classes (Craighead and Craighead 1972; Pearson 1975; Reynolds 1979). Females with newborn cubs are usually the last to leave the denning areas in the spring.

The physiography of grizzly bear denning s including associated habitat types, and the phy nomy of the dens themselves have been studied sively in Yellowstone Park (Craighead and Crai: 1966, 1969, 1972, 1973a; Knight et al. 197 northern Montana (Werner et al. 1978; Servheen Lee 1979; Schallenberger and Jonkel 1980), in National Park (Hamer et al. 1977; Vroom et al. 19 in Yukon Territory (Pearson 1975, 1976), in nort Alaska (Reynolds et al. 1976; Reynolds 1979), a Richards Island off the coast of the Northwe ritories (Harding 1976). Similar data have been ported for dens and denning sites on Kodiak Isla (Lentfer et al. 1972; Glenn and Miller 1980). Beca the data reported by these workers are detailed and tensive, in the interest of brevity only an overview be presented. For more detailed treatments of denni topics, the reader is directed to the individual pape

The ranges of elevation within which discret grizzly bear populations den are variable relative latitude. Most sites in the continental interior are cated in the upper reaches of the subalpine biogeo limatic zone. Habitat types characteristic of the sub pine zone vary over the range of the grizzly and sei tion of the denning sites seemingly relates to the s sonal temperature extremes characteristic of the zo Just as the elevation of the subalpine zone is pr gressively lower with increasing latitude, so also a the ranges of elevation within which most dens a located. Ranges of elevation within which dens a most common decline from a high of 2,024–2926 m Yellowstone Park (Craighead and Craighead 197 Knight et al. 1978) to a low of 270–1,280 m in nort ern Alaska (Reynolds et al. 1976; Reynolds 1979 Where large bodies of water are in close proximity the topography is in low relief, denning elevation is n so clearly related to temperature zonation. Brown bea on Kodiak Island and along the Alaska Peninsula w reported to den at elevations ranging between 31 a 1,006 m (Lentfer et al. 1972). A subsequent study denning only on Kodiak Island reported elevation ranging between 487 and 670 m (Berns et al. 1980 On Richards Island, an area of low relief, grizzly bea were observed to den primarily in river or lake bank (Harding 1976).

Dens of both grizzly and brown bears have been observed in terrain sloped between 0° and 75°. However, the majority of dens have been reported from slopes of 30°–45°. Steep slopes, along with the porous soils into which the dens are generally excavated, provide relatively easy digging and good drainage of rainwater and snowmelt away from the denning chamber. In deep snow country they support snow cornices that may act as insulation for the den, as well as a physical barrier to any intruder.

The orientation of den openings varies within populations and from one population to another. A majority of den openings for a particular bear population commonly are found in slopes oriented toward some particular quadrant. Charting of seasonal wind directions indicates that the slopes most favored for dens are leeward of prevailing winter winds in the area. Such orientation would insure accumulation of heavy

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snow burdens to provide insulation to the dens. Those den openings not situated to the apparent leeward of the prevailing winds often are found oriented to local topography such that wind eddying provides heavy snow deposition (Reynolds 1979). Selection and construction of a suitable den appears to be a learning process, the sophistication of the den increasing with the age of the animal (Craighead and Craighead 1972).

Though grizzly bears are known to den in natural caves (Knight et al. 1978; Reynolds et al. 1976) and, in one instance, in a hollow tree (Knight et al. 1978), the majority of grizzly bear dens and all brown bear dens reported have been excavated. Den entrances are bare or may be enclosed by brush. Ideally, the dens are constructed such that they enclose a space of very minimal air movement. Tunnels and chambers are commonly excavated within the root systems of trees and shrubs or beneath large boulders or rock strata. This imparts structural strength to the top of the den and reduces the threat of cave-ins during midwinter thaws. Most bears apparently excavate new dens each year, but there is indirect evidence and suspicion on the part of many observers that dens are reused year after year.

The physical measurements of dens are probably determined most by the age and, thus, the physical excavating ability of individual bears. This translates into a volume of enclosed airspace that must be warmed by the hibernating bear. Accordingly, chambers are generally just large enough to permit minimal stretching and change of position by the bear. Tunnels often lead horizontally directly into the chamber, although chambers may open at right angles to the tunnel and the tunnel may angle up or down. The floor of the chamber is sometimes lower than the floor of the tunnel, but more often is shelved above the tunnel floor. The latter construction would provide a "well" system in which cold air would sump. The chambers are usually longer than wide, with ceilings higher than those of the tunnels. The chambers of Yellowstone dens

were usually lined with nests of grass and rootlets or tree boughs (Craighead and Craighead 1972, 1973a), but this was not always the case in other geographic areas. Such nests appear to relate to the age and sex of the bear, being more common among adults and/or females. Concise physical parameters of dens throughout the ranges of both grizzly and brown bears have been reported in the papers cited earlier.

Population Statistics. Estimates of grizzly bear numbers have been, until recent years, largely educated guesses. Storer and Tevis (1955) estimated that in California there were once 10,000 grizzlies; all had vanished by 1924. Grizzlies are notoriously difficult to census, and thus density figures for large geographic areas are often of limited value. Over the past two decades, greatly improved field techniques have enabled researchers to count members of population units and of small segments of those units more accurately.

During a 12-year period in the Yellowstone ecosystem, 264 grizzly bears were captured, individually color marked (Craighead et al. 1960), and returned to the population. Approximately 41 censuses of 3.5 hours each were made each year from 1959 through 1970 at five localities throughout Yellowstone Park. This enumeration of individually recognizable animals provided the population characteristics for deriving a mathematical model of this population (Craighead et al. 1974). The model was then used to estimate the size of the grizzly population and to predict future rates of growth or decline. The most probable estimate of numbers was 222 animals for the year 1959, with an upper bound for the population of 309 and a lower of 172. This provided a most probable density of one bear per 80.3 km² in an area of 20,200 km². Densities for small units of the ecosystem were much higher.

Reynolds (1978), working with a population of marked animals in the Brooks Range, Alaska, estimated 121 animals for a 5,180-km² area, a density of
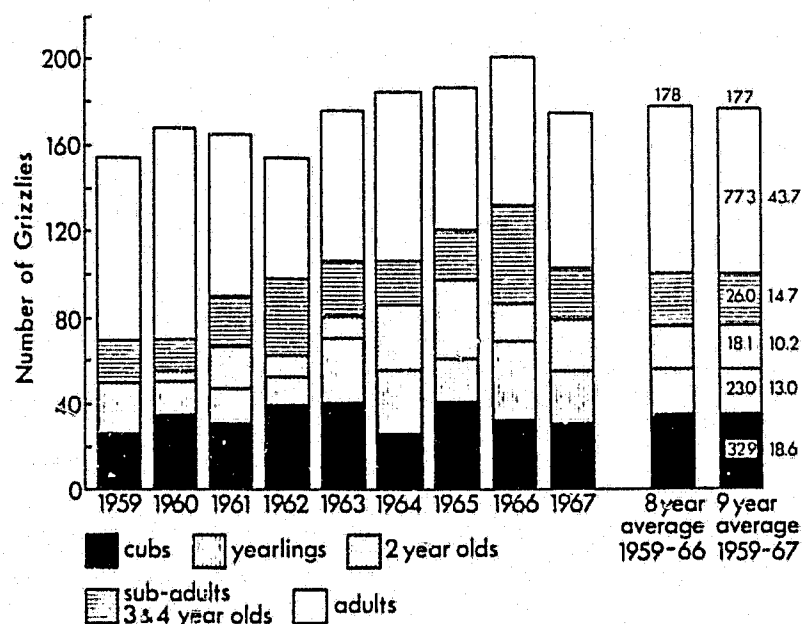

FIGURE 25.13. Age structure of the Yellowstone grizzly bear (*Ursus arctos*) population, 1959–67.

one bear per 42.8 km². By using densities derived on smaller areas of intensive study and extrapolating the data to broad areas, a population of 420 animals was estimated. Estimated densities within this large area were one bear 778 km² in the coastal plain, one bear/91 km² in the low foothills, one bear 52–130 km² in the range, one bear 130 km² in the high foothills, and one bear 259 km² in the mountains. Density figures for other areas have been reported by Mundy and Flook (1973), Martinka (1974), and Troyer and Hensel (1964).

Sex and Age Composition. The age structure of the Yellowstone grizzly bear population was determined for the years 1959–67 (figure 25.13). The average age composition was 18.6 percent cubs, 13.0 percent yearlings, 10.2 percent 2 year olds, 14.7 percent 3 and 4 year olds, and 43.7 percent adults. A further breakdown of the adult age structure was obtained by randomly capturing and determining the age of 52 adults (27 males and 25 females). Fourth premolars extracted from each captured adult before release were sectioned and cementum layers counted to determine age (Scheffer 1950; Craighead et al. 1970). The sample of 52 aged adults was increased to 60 by including 8 known-age adult members of the population. This adult age structure and the age structure of animals from 0.5 to 5.5 years old (see figure 25.13) were then combined and applied to an average population level of 177 animals in order to construct an age- and sex-specific life table (table 25.8).

The age- and sex-specific survivorship rates provided the basic data for determining the number of animals in each age and sex class that would die and/or survive from one year to the next. These are presented as mortality probabilities (Q_x) and as survivorship probabilities (P_x). The number of cubs born each year can be predicted by counting the number of adult females in the population each year and applying the proper reproductive rate and sex ratio (Craighead et al. 1974).

Age structure for the grizzly bear population in Yellowstone is compared with those for the Brooks Range, Alaska, and with a brown bear population at McNeil River, Alaska (table 25.9). Construction of reliable population age structures requires a number of years of consecutive data; therefore, the comparisons between populations and the conclusions drawn from table 25.9 must be considered tentative. The Yellowstone and McNeil River populations exhibit higher proportions of cubs than those in the Brooks Range. This is probably directly related to the much greater abundance of high-protein food annually available to them.

The Yellowstone population was increasing between 1959 and 1967 (see figure 25.13). The age structures for the eastern and western Brooks Range show low proportions of cubs and suggest that the populations either are declining slowly or are in equilibrium.

The McNeil River population shows a proportion of cubs lower than that for Yellowstone, but higher than that for the Brooks Range. The low percentages of yearlings and two year olds in the McNeil population would, in itself, indicate a declining population with heavy first- and second-year mortality. However, the very high percentage of three and four year olds suggests that the low percentages recorded for yearlings and for two year olds is not due to mortality. These age classes do not frequent the concentration area at the falls and therefore, are not recorded until they return as three and four year olds. At this age they can compete more favorably with the large number of adults present. The population appears to be increasing.

Age structures derived in terms of live animals in a population may appear quite different from those constructed from death statistics for the same population. Use of mortality statistics for the construction of a life table requires unrealistic assumptions that are difficult to reconcile.

Sex Ratios. Sex ratios are essential for understanding the dynamics of a population. Especially important is the ratio of males to females born each year. The cumulative cub sex ratio in Yellowstone from a sample of 78 cubs was 0.59 males to 0.41 females. This may have resulted from differential mortality of females in utero or immediately postpartum, or from sampling procedure. The ratio of males to females for yearlings and for two, three, and four year olds is shown in table 25.8. Among 577 observations of adult grizzlies, most recognized as individuals, 53.7 percent were females and 46.3 percent were males. A differential sex mortality was operative among adults, probably because of selective hunting of males and higher mortality caused by greater movement.

In the Brooks Range, Alaska, the sex ratio of a marked population was 39.8 percent males to 60.2 percent females. The sex ratio of cubs and yearlings was equal. Pearson (1975) reported a sex ratio of 68 males to 32 females among captured animals, but provided no data on the sex ratio of cubs.

Mortality and Survivorship Rates. Mortality in the Yellowstone population (Craighead et al. 1974) was measured in two ways: first by changes in sex-age structure from year to year, and second by verifying and recording actual deaths. Mortality and survivorship rates for the population were obtained by using age structures, sex ratios, and census data described earlier to construct an age- and sex-specific life table for the period 1959–67 (see table 25.8). Data for this 9-year period were used, rather than data for a longer period of time, because new management procedures greatly increased the annual death rate of the population after the summer of 1967. The survivorship rates for the 1959–67 period characterized a population in stable age distribution. The age structure data (see figure 25.13) were converted to an age- and sex-specific structure by applying the sex ratios and then smoothing this to the form shown in table 25.8. Mortality and survival expressed through the sex-age structure of the population were converted to the number annually dying and the number annually surviving in a population of 178 animals. The subadult age classes (0.5 to 4.5 years) represent 9-year averages for the population;

TABLE 25.8. Age- and sex-specific life table for the Yellowstone grizzly bear population, 1959–67

Males

Age	Number in Age Class	Number of Males	Number Dying in Age Class (Dx)	Number Surviving per Thousand (Lx)	Survivorship Rate (Px)	Mortality Rate (Qx)
0.5	33.0	19.5	5.0	1000.	0.7436	0.2564
1.5	23.0	14.5	4.6	744.	0.6828	0.3172
2.5	18.0	9.9	1.4	508.	0.8586	0.1414
3.5	14.0	8.5	1.5	436.	0.8235	0.1765
4.5	12.0	7.0	3.4	359.	0.5143	0.4857
5.5	7.7	3.6	0.2	185.	0.9444	0.0556
6.5	7.4	3.4	0.2	174.	0.9412	0.0588
7.5	7.0	3.2	0.1	164.	0.9688	0.0313
8.5	6.8	3.1	0.1	159.	0.9677	0.0323
9.5	6.6	3.0	0.1	154.	0.9667	0.0333
10.5	6.3	2.9	0.1	149.	0.9655	0.0345
11.5	6.1	2.8	0.1	144.	0.9643	0.0357
12.5	5.8	2.7	0.3	138.	0.8889	0.1111
13.5	5.2	2.4	0.3	123.	0.8750	0.1250
14.5	4.5	2.1	0.5	108.	0.7619	0.2381
15.5	3.5	1.6	0.4	82.	0.7500	0.2500
16.5	2.6	1.2	0.2	62.	0.8333	0.1667
17.5	2.2	1.0	0.2	51.	0.8000	0.2000
18.5	1.7	0.8	0.2	41.	0.7500	0.2500
19.5	1.4	0.6	0.1	31.	0.8333	0.1667
20.5	1.1	0.5	0.1	26.	0.8000	0.2000
21.5	0.8	0.4	0.1	21.	0.7500	0.2500
22.5	0.6	0.3	0.1	15.	0.6667	0.3333
23.5	0.4	0.2	0.1	10.	0.5000	0.5000
24.5	0.2	0.1	0.1	5.	0.5000	0.5000
25.5	0.1	0.1	0.1	3.	0.0000	1.0000
Total	178.0	95.4	19.6			

Females

Age	Number in Age Class	Number of Females	Number Dying in Age Class (Dx)	Number Surviving per Thousand (Lx)	Survivorship Rate (Px)	Mortality Rate (Qx)
0.5	33.0	13.5	5.0	1000.	0.6296	0.3704
1.5	23.0	8.5	0.4	630.	0.9529	0.0471
2.5	18.0	8.1	2.6	600.	0.6790	0.3210
3.5	14.0	5.5	0.5	407.	0.9091	0.0909
4.5	12.0	5.0	0.9	370.	0.8200	0.1800
5.5	7.7	4.1	0.1	304.	0.9756	0.0244
6.5	7.4	4.0	0.2	296.	0.9500	0.0500
7.5	7.0	3.8	0.1	281.	0.9737	0.0263
8.5	6.8	3.7	0.1	274.	0.9730	0.0270
9.5	6.6	3.6	0.2	267.	0.9444	0.0556
10.5	6.3	3.4	0.1	252.	0.9706	0.0294
11.5	6.1	3.3	0.2	244.	0.9394	0.0606
12.5	5.8	3.1	0.3	230.	0.9032	0.0968
13.5	5.2	2.8	0.4	207.	0.8571	0.1429
14.5	4.5	2.4	0.5	178.	0.7917	0.2083
15.5	3.5	1.9	0.5	141.	0.7368	0.2632
16.5	2.6	1.4	0.2	104.	0.8571	0.1429
17.5	2.2	1.2	0.3	89.	0.7500	0.2500
18.5	1.7	0.9	0.1	67.	0.8889	0.1111
19.5	1.4	0.8	0.2	59.	0.7500	0.2500
20.5	1.1	0.6	0.2	44.	0.6667	0.3333
21.5	0.8	0.4	0.1	30.	0.7500	0.2500
22.5	0.6	0.3	0.1	22.	0.6667	0.3333
23.5	0.4	0.2	0.1	15.	0.5000	0.5000
24.5	0.2	0.1	0.1	7.	0.5000	0.5000
25.5	0.1	0.1	0.1	4.	0.0000	1.0000
Total	178.0	82.7	13.6			

TABLE 25.9. Comparison of age cohorts of grizzly bears in four populations

Location	Number of Years Data Base	Percentage of Cubs	Percentage of Yearlings	Percentage of 2 Year Olds	Percentage of 3 and 4 Year Olds	Percentage of 5 Year Olds and Older	Status of Population
Yellowstone Park (Craighead et al. 1974)	9	18.6	13.0	10.2	14.7	43.7	increasing
Eastern Brooks Range (Reynolds 1976)	3	7.9	10.9	10.9	5.0	65.3	declining[a]
Western Brooks Range (Reynolds 1978)	2	10.8	9.5	10.8	9.5	50.0	unknown
McNeil River (Christopher Smith, Alaska Game and Fish 1980, personal communication)	5	13.2	8.2	6.9	19.1	52.5	increasing

[a]Based on reproduction and age distribution data.

the adult age classes (5.5 to 25.5 years) represent one-time samples of 60 adults as described earlier (see column 2 of table 25.8).

The age-specific mortality represents death from all causes (see table 25.8). Among these deaths, some were known and recorded; others were unknown and unrecorded, except as they were reflected in the age structure. Each year from 1959 through 1973, all known grizzly bear deaths were recorded. Because it was difficult to obtain the precise ages of these animals, they were grouped into three classes: subadults, adults, and a class of unknown sex and age. In general, the adult and subadult classes represent the reproductive and nonreproductive periods in the life of a female grizzly bear. From 1959 through 1967, a total of 170 known deaths occurred, an average of 18.9 bears per year, or a 10.6 percent known mortality in an average annual population of 178 animals. A total of 189 known deaths occurred from 1968 through 1973 (an average of 31.5 bears per year), with maximum deaths of 53 and 48 grizzlies in 1970 and 1971, respectively. Known deaths for the 15-year period (1959–73) thus totaled 359. Deaths of adult and subadult females alone increased from 39.8 percent (51/128) during 1959–67 to 44.7 percent (71/159) for the 1968–73 period (Craighead 1980*b*).

The mortality percentages by sex and age among the 359 known deaths show the adult and subadult deaths to be equal at 40.7 percent. Forty-six percent of all deaths were males, 34 percent were females, and 20 percent were of unknown sex. In all probability, the differential sex mortality has led to the unbalanced adult sex ratio of 46.3 percent males to 53.7 percent females noted previously. The preponderance of males to females in the subadult age structure does not reflect the differential male mortality among subadults. This may be due to sampling error.

Survivorship calculations and calculations of yearly increments based on reproductive rates provided the basis for describing the way grizzly bears enter and leave age classes from year to year. Simulation runs were made for three cases: the upper and lower bounds on the population, and the most probable case. The latter showed the ecosystem population increasing from 222 animals in 1959 to 245 in 1967, then declining to 136 animals in 1974 (Craighead et al. 1974).

Varied estimates of grizzly bear numbers utilizing the Craighead data have been made for the Yellowstone population by others (Cowan 1974; McCullough 1978; Shaffer 1978). Disparities have arisen primarily because of differences in simulation models and the problem of evaluating the relative strength of biological parameters used in the models by writers unfamiliar with the field conditions.

The Interagency Grizzly Bear Study Team has estimated 300–350 animals in the population from "inductive inference" each year since 1974, yet postulated that a population of this size should have recovered from the excessive 1970, 1971, and 1972 mortality (Roop 1980). However, field data does not indicate recovery. No scientific population estimates have been offered and the status of the population remains unanswered after summary displacement of one long-term research effort with another.

The threatened status of the grizzly focuses attention on the viability or survivability of grizzly bear populations. From biological parameters (Craighead et al. 1974) and from habitat variables, Shaffer (1978) gave a theoretical analysis of survivability. He concluded that populations of fewer than 30–70 bears occupying less than 2,500–7,400 km² have less than a 95 percent chance of surviving 100 years. The ease with which grizzlies can be baited and killed, the difficulties of detecting a wide range of illegal deaths, the threats to habitat security, the problems of making accurate censuses, and the longevity of the species are all crucial factors tending to mask detection of population declines. The lack of current scientific population information for the Yellowstone grizzlies leaves no alternative but use of stringent protective measures.

FOOD HABITS

John Muir said of the grizzly, "to him almost everything is food except granite." Recent quantitative studies of the food and feeding habits of grizzlies, as well as the casual observations of early explorers and naturalists, tend to confirm his statement. Grizzly bears are omnivorous, feeding on an extremely broad range of food items.

Early observers reported grizzly bears feeding on beached whales, acorns, and cultivated corn (Storer and Tevis 1955). The bears competed directly with Native Americans for such plants as blue camas (*Camassia quamash*), *Lomatium cous* and other species of biscuitroot, yampa (*Perideridia gairdneri*), the berries of *Vaccinium* spp., and the nuts of *Pinus albicaulis* and other nut-bearing pines.

Between 50 and 60 percent of the grizzly diet may be animal life varying in size from ants and moths to elk (*Cervus elaphus*) and bison (*Bison bison*). The grizzly is both directly and indirectly dependent on the plant base. Feeding behavior suggests that the grizzly prefers high-protein animal food but readily takes plant foods lower in protein when the former is unavailable.

Like other North American bears, grizzlies are attracted to garbage and refuse dumps, large and small, visiting them periodically during the foraging season. Foraging at open pit garbage dumps has been documented by Hornocker (1962), Craighead and Craighead (1967), and Cole (1972). The universal attraction of garbage dumps and carrion disposal sites is evidenced by the large number of animals captured and marked by all bear research biologists at such sites. Similarly, brown bears form aggregations to feed on salmon (Stonorov and Stokes 1972). Studies of feeding habits show clearly that grizzly bears are attracted to large and persistent energy sources, both natural and "artificial," and visit such ecosystems seasonally and annually. High-energy food sources attract both bears and humans and are generally closely associated with human activities; despite the solitary nature of the grizzly bear, this has tended to bring bears and mankind in close association.

The use and availability of food plants are readily quantified through direct observation, fecal analysis, and measurements of plant abundance. Food habit analyses have been made by Tisch (1961), Mundy (1963), Shaffer (1971), Russell (1971), Sumner and Craighead (1973), Mealey (1975), Hamer et al. (1977, 1978, 1979), Husby et al. (1977), Husby and McMurray (1978), Hechtel (1979), Servheen and Lee (1979), Craighead and Sumner (1980), and Schallenberger and Jonkel (1980).

Craighead and Sumner (1980) utilized a number of parameters to evaluate the plant food and feeding habits of grizzly bears in the Scapegoat Wilderness, Montana. An importance value percentage (IVP) of food plants identified in scats was calculated for a number of food items to permit direct comparison between food plant usage and food plant abundance (Sumner and Craighead 1973). The IVPs of food plants in the Scapegoat Wilderness were ranked for use in describing the dietary importance to the grizzly bear of individual food plants. Scat analysis indicated four major plant energy sources in the alpine and subalpine zones: graminales, forbs, berries, and pine nuts with IVPs of 29.7, 37.6, 12.5, and 20.4, respectively.

IVP values for specific plants varied from 20.4 for pine nuts (*Pinus albicaulis*) to 0.1 for several forb species. A positive correlation was found between grizzly bear use of grasses (Gramineae) and their relative abundance values in the grass-shrublands of the alpine and subalpine zones. The sedges (Cyperaceae) were not consumed in relation to their relative abundance values. The high IVPs of specific forbs such as *Lomatium cous* and *Claytonia megarhiza* indicated that preference and a high order of selectivity, rather than relative abundance, determined the extent to which they were utilized by grizzlies.

Energy values were determined for the more important food plants. Available energy of specific food plants varied from a low of 1.91 kcal/g in the roots of *Veratrum viride* to 3.99 kcal/g in white bark pine nuts (*Pinus albicaulis*). Specific energy values were then related to each plant's abundance, distribution, and seasonal and annual availability.

Among the four major energy sources utilized by grizzlies, the graminales and forbs were chiefly spring and summer foods, berries were almost exclusively summer food, and pine nuts were primarily fall food (except during years of exceptional seed production, when they were consumed in spring as well). The grasses, a highly stable energy source available during the entire foraging season, served as a "survival ration" to carry the bears through periods when other energy sources were low.

To quantify further the relative value to grizzly bears of food plants and food plant groupings, food plant value percentage (FPV) was calculated. This value incorporated five distinct values, strictly comparable for each plant (table 25.10). Based on the FPVs calculated for each food plant, it was concluded that most important, in order of ranking, for the grizzly were: Gramineae, *Pinus albicaulis*, *Vaccinium* spp., Cyperaceae, *Lomatium cous*, *Shepherdia canadensis*,

Claytonia megarhiza, *Fragaria* spp., and *Arctostaphylos uva-ursi*. Gramineae and Cyperaceae exhibited high food plant value percentages, but individual species of grasses and sedges could not be rated.

If this method of rating plant foods from a composite of values (see table 25.10) were adopted in other studies, more precise comparisons could be made between the food habits of bears inhabiting different biogeographical areas. At present, this is not possible.

Comparison of the importance value percentages (a single component of FPV) for major food plant groupings can be made between the Scapegoat and the Yellowstone ecosystems (table 25.11). The IVP for graminales in Yellowstone was twice that for the Scapegoat Wilderness, Montana. The values for forbs were sixfold greater in Scapegoat than in Yellowstone. However, graminales and forbs, both low-calorie food plant groups, when considered together showed almost identical values of 67.3 for Scapegoat and 67.1 for Yellowstone. The IVPs for the high-calorie groupings, berries and nuts, were also nearly identical. That the values presented for the two areas (widely separated in time and distance) would so closely match suggests that, in general, the abundant, highly dependable, low-calorie food plants represent about 2/3 of the grizzlies' vegetable diet. The less abundant, less dependable, high-calorie food plants comprise the remainder. Abundance and availability, rather than energy values, may well determine the grizzlies' long-term utilization of plant foods.

The wide assortment of plant species used as food by the grizzly is becoming increasingly evident. Mealey (1975) listed approximately 25 species for the Yellowstone area without specifically identifying grasses and sedges. J. J. Craighead (in preparation) recorded over 35 species utilized in the same area between 1959 and 1969 prior to the closure of the open pit garbage dumps.

Craighead and Sumner (1980) listed 68 species and plant categories (genera and families) as bear food plants in the Scapegoat Wilderness, Montana, between 1972 and 1978. Servheen and Lee (1979) recorded approximately 36 plant species for the Mission Mountains, Montana; Husby and McMurray (1978), 74 for northwestern Montana; and Hamer et al. (1978), about 41 for Banff National Park, Canada. There are undoubtedly well over 200 plant species whose seeds, fruits, foliage, flower heads, stems, roots, tubers, and root stocks are eaten by grizzlies within their North American range.

The utilization of any specific food plant by a population of grizzly bears is usually dependent upon the relative temporal and spatial abundance and availability of other food plants, as well as upon energy expended for acquisition relative to energy provided by the food. Thus, a plant or a plant group heavily utilized in one area may be recorded as lightly utilized in another. Nevertheless, sufficient information is available to indicate the most important and basic sources of food from the great variety of plants used by grizzlies in specific geographic areas.

Mealey (1975) listed the following as major plant

TABLE 25.10. Calculation of composite food plant values (FPV) for the Scapegoat study area from a series of five comparable food plant evaluations

	Importance Value % (IVP)	Preference Value % (PVP)	Random Abundance Value %	Climatic Zone Occurrence	Energy Value % (EVP)	Food Plant Value % (FPV)
Berries						
Vaccinium spp.	5.4	18.7	12.8	3.0	2.8	42.7
Shepherdia canadensis	3.5	10.4	0.8	2.0	2.7	19.4
Fragaria virginiana	2.0	2.6	0.8	3.0	2.5	10.9
Arctostaphylos uva-ursi	1.6	2.1	1.6	3.0	2.4	10.7
Plant group	12.5	33.8	16.0	11.0	10.4	83.7
Mean values	3.1	8.5	4.0	2.8	2.6	20.9
Nuts						
Pinus albicaulis	20.4	17.6	7.9	1.0	3.3	50.2
Berries and nuts combined						
Plant group	32.9	51.4	23.9	12.0	13.7	133.9
Mean values	6.9	10.3	4.8	2.4	2.7	26.8
Forbs						
Claytonia megarhiza	5.5	5.7	0.1	1.0	2.1	14.4
Lomatium cous	5.3	12.8	0.3	2.0	2.2	22.6
Equisetum arvense	2.3	0.9	0.3	3.0	2.2	8.7
Claytonia lanceolata	1.2	2.1	0.2	2.0	3.3	8.8
Polygonum spp.	0.9	2.0	0.4	2.0	2.0	7.3
Erythronium grandiflorum	0.5	2.1	0.5	3.0	3.0	9.1
Heracleum lanatum	0.1		0.3	3.0	2.1	5.5
Cirsium scariosum	0.1		T	3.0	2.5	5.6
Hedysarum spp.	0.1		0.5	2.0	1.7	4.3
Plant group	16.0	25.6	2.6	21.0	21.1	86.3
Mean values	1.8	2.9	0.3	2.3	2.3	9.5
Graminales						
Gramineae	25.9	7.0	16.6	3.0	1.8	54.3
Cyperaceae	3.8	4.6	12.3	3.0	1.9	25.6
Plant group	29.7	11.6	28.9	6.0	3.7	79.9
Mean values	14.9	5.8	14.5	3.0	1.9	40.0
Sum of food plant parameters	78.6	88.6	55.4	39.0	38.5	300.1

NOTE: The FPV percentages are the sums of the five plant values preceding them.

food sources for grizzlies in Yellowstone National Park, Wyoming: Gramineae/Cyperaceae, *Claytonia lanceolata, Cirsium scariosum, Perideridia gairdneri, Lomatium cous, Vaccinium scoparium, Equisetum arvense,* and *Pinus albicaulis.* Pearson (1975), working in southwestern Yukon Territory, Canada, recorded *Hedysarum alpinum, Shepherdia canadensis,*

TABLE 25.11. Comparison of importance value percentages for major food plant groups in the Scapegoat ecosystem to those for the Yellowstone ecosystem

Plant Food Group	Scapegoat Importance Value Percentages	Yellowstone Importance Value Percentages	Average (kcal/g)
Graminales	29.7 ⎫	60.8 ⎫	2.56
Forbs	37.6 ⎬ 67.3	6.3 ⎬ 67.1	2.81
Berries	12.5	12.0	3.21
Nuts	20.4	20.8	3.99

NOTE: Number of scats analyzed in: Yellowstone = 487 (J. J. Craighead 1968-70), Scapegoat = 282 (1972-76)

Gramineae, and *Salix* spp. as important sources of food. For grizzlies in the Mission Mountains, Montana, Servheen and Lee (1979) recorded Graminoids, *Amelanchier alnifolia, Equisetum arvense, Osmorhiza occidentalis, Prunus* spp. (domestic), *Taraxacum* spp., *Heracleum lanatum, Trifolium repens,* and *Malus* spp. (domestic) as major plant foods.

Husby and McMurray (1978), working in northwestern Montana, found the following to be important: *Vaccinium globulare,* species of Umbelliferae, Gramineae/Cyperaceae, *Equisetum* spp., *Arctostaphylos uva-ursi, Shepherdia canadensis, Amelanchier alnifolia,* and Formicidae. Hamer et al. (1978), working in Banff National Park, Canada, recorded as important: *Hedysarum* spp., *Equisetum* spp., Gramineae/Cyperaceae, *Heracleum lanatum, Rumex* spp., *Shepherdia canadensis, Vaccinium* spp., and *Arctostaphylos uva-ursi.*

The range of food plants available to grizzly bears and their omnivorous feeding habits does not necessarily ensure an adequate food supply from year to year. During years of widespread failure of such preferred food as *Vaccinium* berries and/or pine nuts, grizzlies generally must travel more, enlarge their home ranges,

visit man-made sources of food more frequently, and exhibit greater aggressiveness in defense of their food sources. When berries and nuts are scarce, grizzlies sustain themselves with green vegetation (grasses, sedges, and forbs), but generally will lose weight because these foods are not completely digested. Grizzlies feeding primarily on green vegetation in spring fail to gain weight, but those securing high-protein food such as carcasses, the young of big game species, or various man-derived food sources maintain or gain weight. When pine nuts are abundant, grizzlies gain weight rapidly from this high-energy plant food (3.99 kcals/g). A young adult male killed early in the spring following an exceptionally good pine nut season had 14 cm of fat over the rump. The excellent condition of individual Yellowstone bears captured and weighed in September and October correlated well with good crops of pine nuts. Similarly, grizzlies gained weight rapidly in those summers when berry crops were good.

Grizzlies exhibit different metabolic stages (exhibited in terms of nutritional status) that are associated with seasonal changes. Nelson et al. (1980) described four metabolic stages for the black bear: (1) hibernation, or winter sleep, (2) transition, or hypophagia, (3) normal activity, and (4) hyperphagia. Craighead and Sumner (1980) determined that these metabolic stages in the grizzly are closely attuned to plant and animal phenology and can be observed and documented in the behavior and activity of a bear population.

In spring when adult grizzlies leave their winter dens, they eat sparingly for several weeks (stage 2). Their movements are generally slow and deliberate. During this transition stage from hibernation to normal activity, they continue to metabolize body fat. As food becomes increasingly available, the bears' food consumption increases. Observations of feeding behavior and weight records taken in Yellowstone suggest that losses in body weight during April and May may exceed gains as grizzlies continue to utilize body fat (J. J. Craighead in preparation). By June, grizzlies are on a normal feeding regime (stage 3) involving a wide range of foods, but they still exhibit little or no gain in body weight. Not until late July and August are there noticeable increases in body weight associated with the seasonal increase in food quality and availability.

From mid-July through September a maximum amount of food (energy) is present from both plant and animal sources. Bears spend much of their time feeding (stage 4), and gains in body weight are substantial. Among 28 individual grizzlies captured and weighed periodically in Yellowstone, a two-year-old female showed an average weight gain of 1.65 kg/day over a 24-day period from mid-July to mid-August; a yearling male, 0.97 kg/day over a similar time span; and one adult female, 1.13 kg/day over a 26-day period. Bears for which weights were averaged over longer time spans of 111, 114, and 118 days showed gains of 0.41, 0.24, and 0.46 kg/day, respectively. In adults, the rapid weight gains are due largely to fat deposition, but in subadults, lean body mass also increases. The aver-

age annual increase in weight of yearlings was 145 percent for males and 130 percent for females.

As winter nears, metabolic changes occur that prepare the grizzly for winter sleep (stage 1). Among well-fed members of a population, feeding activity decreases in mid-October; some of these animals exhibit a state of lethargy before entering winter dens (Craighead and Craighead 1972). Those animals not so well fed may continue to feed up to the time they enter their dens for winter sleep. In Yellowstone, for example, color-marked animals were observed that moved almost daily from den areas to feed on elk carcasses. They terminated feeding only when heavy snow storms finally confined them to the dens.

In the northern rockies of the United States, grizzlies hibernate from October/November to March/April, a period when both plant and animal foods are unavailable. Normally they remain in the dens throughout the winter (Craighead and Craighead 1972). However, several instances were recorded in Yellowstone of adult grizzlies leaving dens in mid-winter when ambient temperatures rose and mild weather prevailed for five to six days. There was no evidence that grizzlies fed while on these excursions away from their dens. While in the den, grizzlies metabolize stored body fat (Folk et al. 1972). This requires no intake of free water and produces no wastes requiring defecation or urinary excretion. However, water is expelled through respiration. Body fat remains the sole ultimate energy and water source until late March or April (Nelson et al. 1980). At this time, all members of a population except females with cubs will normally leave the dens.

The transition from fat to carbohydrate/protein metabolism (stage 2) takes place slowly, in association with behavioral and activity patterns and changes in physical conditions. By mid-May to mid-July, the bears have again become active, exploiting all of the energy sources available to them. At this time, adult females come into estrus and the larger, more aggressive males breed them (Craighead et al. 1969). Agonistic behavior is common among adult males; many severe encounters occur during the mating period. It is a time of great energy expenditure by all members of a population. The relatively low energy intake and high energy utilization is reflected in the nutritional level of the population. Body weights of individual animals reach an annual low.

The six- to seven-month period from den emergence to return is, in general, one of preparing for hibernation. The entire year is defined in this cyclic phenomenon of metabolic stages that dictates the bears' behavioral patterns, especially those associated with foraging and feeding.

Most of the grizzlies' foraging movements are deliberate. Information obtained during 10 years of monitoring color-marked or radio-collared grizzlies of all ages and both sexes in the Yellowstone ecosystem (Craighead 1980b, in preparation) showed that individual grizzlies do not normally move randomly or aimlessly throughout their large home ranges, feeding

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From the Yellowstone study, and that in the Scapegoat, a general pattern of movement and activity for securing food emerged for populations south of the Canadian border. Some bears leave their hibernation dens as early as March, traveling when the snow is crusted or keeping to the bare south-facing ridges. They move from the subalpine zone where they have denned to the lower subalpine and the temperate zones where snow is light or absent. By late April to mid-May, many of the mature bears, and most of the subadults, have moved from winter dens to the lower altitudes. Females with cubs of the year may emerge from late April to late May. They also tend to move to lower altitudes. At this time, overwintering rodents such as voles (*Microtus* spp.), deer mice (*Peromyscus* spp.), and pocket gophers (*Thomomys talpoides*) are consumed. High overwintering populations of these rodents occur periodically. At such times, they are especially vulnerable as the snow cover melts. A female and three yearlings were observed to feed for several weeks on *Microtus* spp. During this time, these rodents constituted a significant portion of the total diet of this family group. When big game is abundant, grizzlies move to the winter ranges of these ungulates and feed on winter-killed animals or prey on those in a state of advanced malnutrition. Grizzly bear predation on big game species is generally greatest from mid-April to mid-May. At the periphery of the wilderness, the bears may kill livestock, feed on carrion, or routinely visit livestock disposal sites common on most large ranches. Often, more than one grizzly may feed on a carcass. Craighead and Sumner (1980) reported 172 grizzly bear sightings on 118 big game carcasses over a 13-year period in Yellowstone. Carcasses were usually visited before the snow had melted. Sometimes as many as 6–7 individual grizzlies utilized a carcass, and there were instances in which carcasses were periodically revisited for 10 to 15 days. One grizzly returned to a carcass at least nine times during a 15-day period. Grizzlies were readily attracted to carcasses distributed through three climatic zones and over a 259-km² area in the Scapegoat Wilderness of Montana (Sumner and Craighead 1973).

Where food is abundant and concentrated, aggregations of bears occur and a social order is operative (Hornocker 1962; Craighead and Craighead 1971; Craighead 1980b). The social hierarchy serves to increase foraging efficiency by allowing large numbers of a population to share a common food source. In Yellowstone, 23 grizzly bears were recorded feeding on a bison carcass and large aggregations in excess of 80 grizzlies per evening were documented at open pit garbage dumps (Craighead and Craighead 1971). Grizzlies supplement an early spring meat diet with the early emerging sedges and grasses. At this time of year they frequently forsake the relative safety of the large national forest and wilderness areas to forage on emerging grasses, sedges, and forbs in the temperate

zone. Individual bears may remain at low elevations, utilizing plant foods for several weeks or more. However, as big game species leave winter ranges and move to higher elevations, the bears tend to follow the same pattern, feeding primarily on grasses and forbs. If carrion or other high-protein food is not available, they sustain themselves almost exclusively on the plant resource. Adult males, the subadults of both sexes, and females without offspring are generally solitary foragers. Females with cubs, yearlings, or two year olds forage as family groups. A female with cubs may form a close bond with a similar age family, and they then travel and forage as a unit.

In early June elk begin dropping their calves in the temperate and subalpine parklands of northwestern Wyoming and western Montana. Calving sites tend to be traditional, the elk returning to them year after year (Craighead et al. 1972b). Grizzlies whose home ranges encompass these calving areas appear to locate elk by scent and follow them as they migrate to these areas. In some instances, individual bears apparently recall the locations from past experience. Calves are vulnerable to grizzlies for a relatively short period of time. Soon after calving, the cows and their offspring move to higher elevations, their movements determined by the recession of snow and the emergence of plants. Grizzlies follow the same general pattern, so by July they are feeding on the grasses, sedges, and forbs in both the subalpine and alpine zones.

From late June through July, the alpine zone is used extensively as a source of *Lomatium cous*, *Claytonia megarhiza*, and other succulent and nutritious tubers, bulbs, and greens. Insects become important items of diet during this period. Grizzlies seem to have a craving for such insects as moths, beetles, ants, and even earthworms that is partially, but not entirely, related to their high protein content.

As August approaches, the berries of *Vaccinium scoparium* and *V. globulare* begin to ripen in the temperate zone and those of *Shepherdia canadensis* in the subalpine. Grizzlies traveling within large, but undefended, home ranges move to lower elevations to utilize this energy resource, which, in years of peak abundance, is exploited until snow covers the subalpine country. When berries are abundant, bears tend to utilize this food source almost exclusively and gain weight rapidly. In years when berry crops are poor, the greens help alleviate the energy shortage; however, bears do not gain weight on this diet. At such times the nuts of the white bark and limber pines (*Pinus albicaulis* and *P. flexilis*) become a critical energy source. Grizzlies will move to the extremities of their home ranges to feed on pine nuts and will utilize them through September and October and, in some instances, until mid-November. Radiotracked grizzlies were observed to move over 80 km to feed on white bark pine nuts. In the Yellowstone ecosystem, and in the Scapegoat study area as well, the nuts of white bark pine provided the high-energy diet necessary for the grizzly to enter hibernation with a heavy layer of stored fat. Bumper pine nut crops occurred twice

throughout Yellowstone over a 12-year period and twice over a 7-year period in Scapegoat. This ideal situation never occurred uniformly throughout the Yellowstone ecosystem, but did occasionally occur within specific home ranges of individual bears.

Stored fat is vital to the bears' survival. During the long period of hibernation (a winter sleep of approximately five to six months), it is the bears' only energy source. Although most grizzlies leave their dens with sufficient body fat to carry them through the lean months of spring, females with cubs reach a lower nutritional level because energy reserves are expended to give birth to young and to produce milk. Lactating females m y not show renewed fat deposition until late August or September. The degree of fat deposition in fall may influence the estrous cycle, and thereby determine whether a female will wean her cubs as yearlings or carry them through another year (J. J. Craighead in preparation). When both berry and pine nut crops peak, grizzlies fare exceedingly well.

Grizzlies locate and learn to use specific locales where plant and animal foods are most abundant. The more productive sites become centers of activity within home ranges. In the course of a long life span, such areas become well known to individual bears. These may be large or small and at high or low elevations. Whether they support many or few bear food plants, they are all parts of larger vegetation units that the grizzly utilizes throughout the year with an uncanny sense of its biological needs and a knowledge of where it can meet its dietary requirements.

MORTALITY

An accurate measurement of mortality is essential for formulating long-range management goals and for annually evaluating hunting success. Holding the annual kill to a predetermined quota has been the basic management tool employed for both brown and grizzly bears. Human-caused mortalities can be categorized as hunting and nonhunting. The former data are quite accurate and relatively easy to obtain, but the latter are subject to inaccuracies because of the difficulty of detecting and verifying them. Deaths in both categories can be substantial and, therefore, data on both are necessary for making precise management recommendations. This is especially true where the species is threatened. In that respect, it is revealing that the basic brown bear management goal in southeastern Alaska where bears are abundant is to maintain a high-quality hunting experience. In the lower 48 states where the grizzly is threatened, the primary goal is recovery. Brown bear management in southeastern Alaska has been thoroughly reviewed by Johnson (1980). Hunting statistics and bear mortalities for northwestern and south-central Montana have been summarized by Greer (1980). The effect of heavy human-caused mortalities on the Yellowstone grizzly population was analyzed by Craighead et al. (1974); strong agency reaction and public concern resulted at that time (Craighead 1979).

An update of human-caused mortalities over the past two decades is revealing in its management impli-

cations for the Yellowstone population (table 25.12). Grizzly bear mortalities are summarized for the 11-year period 1959 to 1969 (Craighead et al. 1974, 1980b) and for the 10-year period from 1970 to 1979 (Knight unpublished data). Over the 11-year period prior to closure of the open pit dumps (ecocenters) in 1969-70, grizzly bear deaths averaged 19.4 bears per year. During the 10 years following elimination of the ecocenters, deaths averaged 19.0 bears per year. For the four critical years following closure of the ecocenters (1970-73), Knight's records show 14 fewer deaths than were recorded by Craighead et al. (1974). To avoid possible controversy, the lower death statistics have been employed in table 25.12; however, it should be noted that inclusion of those deaths indicates a total mortality of 204 and an annual mean of 20.4 bear deaths for the 10-year period following closure of the ecocenters. Also, use here of Knight's mortality data for the 1970-79 period does not apply to the mortality statistics reported for the same period as a basis for evaluation of the Yellowstone grizzly population discussed earlier (Craighead et al. 1974). Regardless of which set of data is used, it is evident that the mortality rate rose dramatically during the first 4 years following closure, and then gradually leveled off. If we assume that the level of sampling has been comparable (and we believe it has been), then one must conclude from table 25.12 that the percentage of nonhunting deaths, both inside and outside the park, increased nearly threefold in the decade following closure of the ecocenters. This can be attributed primarily to nutritional stress and dispersion (Craighead 1980b), which greatly increased the incidence of bear-human conflicts.

The percentage of hunter kills decreased in the latter decade from 36.4 percent to 22.6 percent, but this was due entirely to a partial hunting ban imposed by Montana and Wyoming in 1975. Although it is difficult to judge from the total of all bear deaths during the decade, the ban appears to have been effective in reducing the total of human-caused deaths. Relative mortality due to bear control within the park dropped from 45.8 percent to 25.7 percent, reflecting a concerted effort by park officials to reduce and/or to show a reduction in this cause of death concommitant with curtailment of hunter kills. Because of the consistently large number of nonhunting deaths occurring annually in the area around Yellowstone National Park (51.6 percent), the mean mortality for the 1970-79 decade equaled that of the previous 11-year period. This can only be viewed as a serious threat to the integrity of the population when analyzed in context with a decline in reproductive rate from 0.66 to 0.56 (Craighead et al. 1974; Knight personal communication 1980) and direct observations that show a 70 to 80 percent decrease in grizzly bear use of winter-killed elk and bison (Craighead and Sumner in preparation). Data presented in table 25.12 should eventually be incorporated into computer-modeled population analyses, but certain conclusions relevant to management do not require such sophisticated treatment. The hunting ban in Montana, Wyoming, and Idaho must continue; efforts to curtail nonhunting deaths, especially attributable to

TABLE 25.12. Kr

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TABLE 25.12. Known grizzly bear mortalities by year in Yellowstone National Park and adjoining areas, 1959–79

| Year | Area adjacent to YNP | | | | YNP | | Total | | Total without Hunting | |
| | Nonhunting | | Hunting | | | | | | | |
	No.	%	No.	%	No.	%	No.	%	No.	%
1959	0	0	4	5.1	8	8.2	12	5.6	8	5.9
1960	2	5.3	14	18.0	8	8.2	24	11.2	10	7.4
1961	7	18.4	5	6.4	9	9.2	21	9.8	16	11.8
1962	1	2.6	4	5.1	10	10.2	15	7.0	11	8.1
1963	1	2.6	5	6.4	9	9.2	15	7.0	10	7.4
1964	1	2.6	3	3.8	8	8.2	12	5.6	9	6.6
1965	1	2.6	7	9.0	7	7.1	15	7.0	8	5.9
1966	7	18.4	2	2.6	4	4.1	13	6.1	11	8.1
1967	8	21.0	24	30.8	11	11.2	43	20.1	19	14.0
1968	6	15.8	3	3.8	12	12.2	21	9.8	18	13.2
1969	4	10.5	7	9.0	12	12.2	23	10.8	16	11.8
Total	38	99.8	78	100.0	98	100.0	214	100.0	136	100.2
Percentage of 11-Year Total	17.8		36.4		45.8		11 yr. $\bar{x}$ = 19.4		11 yr. $\bar{x}$ = 12.4	
1970	10	10.2	13	30.2	20	40.8	43	22.6	30	20.4
1971	23	23.5	13	30.2	6	12.2	42	22.1	29	19.7
1972	11	11.2	4	9.3	9	18.4	24	12.6	20	13.6
1973	14	14.3	6	14.2	2	4.1	22	11.6	16	10.9
1974	5	5.1	7	16.3	2	4.1	14	7.4	7	4.8
1975	4	4.1			0	0	4	2.1	4	2.7
1976	3	3.1			3	6.1	6	3.2	6	4.1
1977	12	12.2			4	8.2	16	8.4	16	10.9
1978	7	7.1			2	4.1	9	4.7	9	6.1
1979	9	9.2			1	2.0	10	5.3	10	6.8
Total	98	100.0	43	100.2	49	100.2	190	100.0	147	100.1
Percentage of 10-Year Total	51.6		22.6		25.7		10 yr. $\bar{x}$ = 19.0		10 yr. $\bar{x}$ = 14.7	

SOURCE: 1959–69, Craighead 1980; 1970–79, Knight unpublished data.

poaching and illegal bear controls, must be greatly intensified; and the death rate within Yellowstone Park itself must continue depressed. Preliminary analyses indicate that, for recovery, the total annual human-caused deaths within the ecosystem must be held to a number considerably fewer than the mean death toll of 10 per year recorded between 1975 and 1979. To accomplish this will require changes in livestock, logging, and recreation competition within the ecosystem (Craighead 1980*b*) as well as enactment of the recommendations above. To effect these changes on the scale and intensity needed for recovery will require interagency recognition of the critical nature of the problem and cooperative interagency action. The lesson that the Yellowstone situation offers to management is that positive corrective action, based on solid research, cannot be delayed a full decade. Management must follow rapidly on the heels of research and, indeed, be concommitant with it.

Parasites and Disease. Most of the literature on North American ursine parasites concerns helminths. Rogers and Rogers (1976) provided a good review of parasites known from bears around the world.

Only two trematode species have been reported from *Ursus arctos horribilis*. Worley et al. (1976) found *Echinostoma revolutum* in the intestines of 2 of 31 Montana grizzlies. Schlegel et al. (1968) reported

Nanophyetus salmincola from Alaskan brown bears. Salmonid fishes serve as intermediate hosts for *N. salmincola*. Bears are infected when fishes, especially salmon, containing the metacercariae are ingested. *Nanophyetus salmincola* is well known to veterinarians as the vector of *Neorickettsia helminthoeca*, a bacterium that causes the highly lethal "salmon poisoning disease" in canids. Although ursids are apparently refractile to infection with *N. helminthoeca*, a different, uncharacterized rickettsia also carried by the fluke has been shown experimentally to cause Elokomin fever in black bears (Rogers and Rogers 1976). Presumably, this could also infect grizzly bears.

Tapeworms found in grizzly bears include species of *Diphyllobothrium*, a pseudophyllidean cestode. Infections are most likely incurred when bears eat fish containing the tapeworm pleurocercoids. Choquette et al. (1969) collected *Diphyllobothrium* from 3 of 21 grizzlies in northwestern Canada and tentatively identified the species as *D. ursi*. This species was provisionally described by Rausch (1954); however, it has not been consistently distinguished by many researchers from the much more common *D. latum*. Worley et al. (1976) reported *Diphyllobothrium* spp. from 16 of 66 grizzly bears, but did not determine the species. Interestingly, all 16 infected animals were from the Yellowstone ecosystem of Montana and Wyoming.

The only cyclophyllidean tapeworms reported in grizzlies are *Taenia* spp. Choquette et al. (1969) found *T. krabbei* in 2 of 21 bears in northwestern Canada. Worley et al. (1976) reported *Taenia* sp. from 14 of 66 grizzlies in Montana, but, again, did not determine the species. Although *Echinococcus* spp. have not been reported from grizzlies, the geographic distributions and natural intermediate hosts of the hydatid worms would imply that grizzlies are exposed via their natural prey. It seems likely that *Echinococcus* spp., and other cyclophyllideans common to feral mammals, will be reported from grizzly bears with continued work.

Of all helminths, nematode species are those most commonly found in bears. *Baylisascaris transfuga* was reported from the intestines of 16 of 21 grizzlies in northwestern Canada (Choquette et al. 1969) and 53 of 70 grizzlies in Montana (Worley et al. 1976). A hookworm, *Uncinaria* (=*Dochmoides*) *yukonensis*, was found in 10 of 21 grizzlies in northwestern Canada (Choquette et al. 1969); Worley et al. (1976) reported 12 of 69 Montana grizzlies infected with *Uncinaria* sp. Olsen (1968) described a new species of hookworm, *U. rauschi*, from both black and grizzly bears in Alaska. Rausch (1961; cited in Rogers and Rogers 1976) found *U. yukonensis* in Alaskan brown bears.

Choquette et al. (1969) observed the mosquito-borne, filarial nematode *Dirofilaria ursi* in 3 of 27 grizzlies in northwestern Canada; Worley et al. (1976) reported it from 2 of 13 Montana grizzlies. Rausch (1961, in Rogers and Rogers 1976) stated that *D. ursi* was observed quite commonly in Alaskan brown bears.

As a host-inspecific parasite of many mammals, including humans and bears, *Trichinella spiralis* is of major concern in contexts of public health and wildlife management. All species of *Ursus* have been found to host the nematode. Larvae encysted in the flesh of the bear, if not destroyed by cooking, are infective to humans. Infections appear to be maintained in wild bear populations more through cannibalism and feeding on the carcasses of other carnivores than through feeding on refuse at garbage disposal sites (Worley et al. 1974). *Trichinella spiralis* has been reported from 10 of 20 Alaskan grizzly bears (Rausch et al. 1956), from 21 of 24 grizzlies in northwestern Canada (Choquette et al. 1969), and from 103 of 141 grizzlies in Montana (Worley et al. 1976). The last group also noted that larval density, in terms of average larval cysts per gram of tissue, was highest in the tongue, followed by the femoral muscle, the masseter, and the diaphragm.

Few arthropod parasites have been reported from grizzlies. The fleas that appear to be native to grizzlies are all *Chaetopsylla* spp. Holland (1949) reported *C. setosa* from grizzlies in British Columbia and *C. tuberculaticeps ursi* from grizzlies in parts of western Canada and in Alaska. Worley et al. (1976) found *Chaetopsylla sp.* on one of three Montana grizzly bears. The single tick species reported from the grizzly bear is *Dermacentor andersoni* (Rogers and Rogers 1976).

Exactly what role is played by protozoan parasites in grizzly bear populations is undetermined. There is, likewise, virtually no knowledge of diseases of bacte-

rial, fungal, or viral etiology. It is likely that this paucity of information is related more to a lack of investigation than to unusual disease resistance in bears.

Although *Eimeria ursi* and *Isospora fonsecai* have been reported from *Ursus arctos* in the USSR and other coccidia have been found in North American *U. americanus*, no protozoan of any kind is reported from North American *U. arctos*. Worley et al. (1976) noted coccidian oocysts in the feces of grizzly bears, but they did not identify them or examine the intestinal tissues for sporozoites.

Although grizzly bears are known to show symptoms of gastrointestinal and respiratory illness, etiology has seldom been researched. As mentioned earlier, grizzly bears are undoubtedly exposed to the rickettsia that causes Elokomin fever experimentally in black bears and naturally in other mammals. Neiland (1975) found that a very high percentage of grizzlies in the Brooks Range of Alaska had antibodies to *Brucella suis* type 4, the agent of rangiferine brucellosis in caribou. Discernible antibody titres in such a large portion of the bear population indicate a high degree of exposure to *B. suis* through predation on infected caribou and suggest that brucellosis might be of importance in the dynamics of some grizzly bear populations. Heddleston (1976) reported a positive isolate of *Pasteurella multocida* from a bear (species unstated). This bacterium is widely distributed in North American birds and mammals, including, most likely, the grizzly bear.

Agents of disease, whether enzootic or explosively epizootic, can have a powerful effect on the status of an animal population. As regards the grizzly bear, it is clear that extensive work is necessary to develop even an elementary understanding of the health dynamics.

MANAGEMENT

Study Techniques. As has been shown, grizzly and brown bears generally have extensive spatial needs and tend to range almost continuously. This mobility, together with the animals' large size, secretiveness, and potential aggressiveness, has made scientific study difficult. As little as three decades ago, scientifically definitive data concerning the bears and their habits were lacking. Population enumeration based simply on counting tracks or recording sightings of bears not individually identifiable, practices all too common even today, were inaccurate and misleading. Current knowledge of grizzly and brown bears has been amassed through use of innovative study methods and application of inventive new technologies.

To study individual bears and to mark them distinctively requires that they be subdued with minimal injury. Animals are either baited into culvert traps constructed of steel bars and spiral pipe (often on trailer frames), trapped with baited snares, or approached and shot with propulsive syringe darts. A muscle-relaxing drug or anesthetic is administered intramuscularly by means of either a heavy syringe mounted on a long rod ("jab stick") or a gas-propelled dart fired from a rifle

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(developed by Crockford et al. 1958). Although pen-
tobarbital sodium, a potent general anesthetic, had
been used in earlier work on black bears (Erickson
1957; Black 1958), the first efforts to immobilize
brown bears (Troyer personal communication 1960)
and grizzly bears (Craighead et al. 1960) were based
on the fast-acting muscle relaxant succinylcholine
chloride (Sucostrin). This drug blocks nervous trans-
mission at the myoneural junction by competitively
inhibiting acetylcholine and is degraded by cholines-
terase only very gradually. For small to medium
grizzly bears, optimal dosage was about 1 mg per 1.41
kg body weight. This dosage was found to prolong
immobilization in larger bears, however, and had to be
modified to account for age and amount of body fat
(Craighead et al. 1960). Other drug preparations re-
ported in recent literature include phencyclidine hyd-
rochloride (Sernylan) alone (Craighead et al. 1964,
1969, 1972c; Pearson 1975, 1976; Reynolds 1979;
Glenn and Miller 1980) or in combination with prom-
azine hydrochloride (Sparine) (Joslin et al. 1977; Serv-
heen and Lee 1979; Schallenberger and Jonkel 1980)
and ketamine hydrochloride (Ketaset) in combination
with acepromazine or promazine hydrochloride (Joslin
et al. 1977). Phencyclidine hydrochloride appears to be
the preferred immobilizing agent for use on larger be-
ars, while ketamine hydrochloride is becoming more
common for use with smaller grizzlies and for black
bears.

Once the bear has been immobilized, primary
physical data can be collected. Morphometry, body
weight, breeding condition, general physiological
characteristics, and age can be determined. The age of
a bear, especially important in constructing life tables
and determining reproductive longevity for a popula-
tion, is accurately determined from preparations of an
extracted tooth. The technique, originated for study of
the Pinnipedia by Scheffer (1950), entails decalcifying
and cross-sectioning the tooth and staining the sections
to define annuli in the cementum. The annuli occur as a
result of seasonal variation in the rate of cementum
deposition; their number relates to the age of a speci-
men. Successful applications of the technique to third
molars, fourth premolars, and first premolars have
been reported by Craighead et al. (1970), Pearson
(1975), and Reynolds (1978). The extraction of fourth
premolars from live members of a population before
release permitted age determination necessary for con-
structing a life table (Craighead et al. 1974).

While immobilized, the bear may be marked in
some manner such that it is individually identifiable
while roaming free. Marking of grizzly bears is neces-
sary to obtain accurate biological data. Color-coded,
plastic ear tags, in conjunction with tatoos, were first
used to study the Yellowstone grizzly bears during the
late 1950s (Craighead et al. 1960). This marking tech-
nique has since become a common practice in popula-
tion work.

Of all technical innovations, the radio-transmitter
collar and tuned directional receiving antenna have
probably proven most valuable in documenting the
biology and life history of grizzly/brown bears. The

method was first applied when Yellowstone bears were
radioinstrumented in 1961 (Craighead et al. 1963) and
the population monitored for the next decade
(Craighead and Craighead 1965, 1969, 1971, 1973a,
1974). Many of the current data on movements, space
requirements, activity centers, nocturnal activity, re-
productive biology, denning ecology, and food habits
throughout the range of grizzly/brown bears have been
obtained by adoption of this technique. Application
was widened and further improved through use of or-
biting satellites to collect data transmitted by radio col-
lars and implanted sensors (Buechner et al. 1971;
Craighead et al. 1971, 1972a). Radiotracking, man-
datory reporting by hunters, scat analysis, and aerial
surveys have provided the methodology upon which
current management depends.

Modality-specific then.vi...ors coupled with mic-
rotransmitters have revolutionized in situ physiological
studies in bears. Radio receivers, coupled with appro-
priate signal transducers, are usually used in recording
data (Folk 1967; Folk et al. 1972, 1976; Craighead et
al. 1972c). The technology for recording data by satel-
lite has been demonstrated (Craighead et al. 1971).
Termed *biotelemetry*, the process involves implanting
a thermistor sensitive to the desired modality within the
body of the bear. The microtransmitter provides for
remote recording of data via land-based or satellite
radio receivers.

Understanding the ways in which bears depend on
and utilize their habitat requires a thorough understand-
ing of the physical, botanical, and faunal characteris-
tics of that habitat. Through indirect evidence and di-
rect observation, the feeding behavior of grizzly/brown
bears has been documented in many parts of their
natural range. The seasonal importance of food plants,
carrion, and prey species has been assessed and in
depth chemical analysis of many food items to deter-
mine nutritional values has been performed. Although
useful, such information alone is inadequate for
evaluating comprehensively the potential of a spacious
wilderness habitat. The distribution and availability of
the plant food base and the bear's ecological efficiency
in utilizing food items must be understood. A vital,
new technology developed during the 1970s provides
the means quantitatively to evaluate and to rate relative
habitat structure for very large biogeographic areas.
Such an evaluation was recently completed for grizzly
bear habitat in the Lincoln-Scapegoat Wilderness in
Montana and extrapolated to an adjoining 5,200-km^2
area in the Bob Marshall Wilderness (Craighead et al.
1976b; Craighead and Scaggs 1979; Craighead 1980a;
Craighead and Sumner 1980). First, a holistic descrip-
tion of the vegetation composing the grizzly bear
habitat must be organized quantitatively into a type
map demarcated according to zones of elevation. There
are many methods in the literature for typing
vegetation/land systems that could be adapted to de-
velop habitat classification systems. In those studies
cited above, forests were classified and mapped ac-
cording to the forest habitat types of Daubenmire and
Daubenmire (1968) and Pfister et al. (1977), while the
vegetation/landtype classification was developed for

the grass-shrublands of the alpine, subalpine, and temperate zones in terms of the "ecoclass method" of Daubenmire (1952), Peterken (1970), and Corliss et al. (1973).

The data derived from type mapping and from vegetation sampling allow vegetation complexes to be quantified with regard to bear food plants on a comparative basis. This information is then converted to a computer-enhanced simulation using satellite imagery. In the Scapegoat Wilderness study, the polar-orbiting LANDSAT-1 was the source of the high-altitude photographic frames (images) depicting 177-x-177-km areas. A frame is a record of spectral energy reflected from the earth's surfaces. It is composed of over 6×10^6 "pixels," each of which is a record of the brightness level of a 0.453-ha unit on the surface. The frame can be computer oriented and analyzed, pixel by pixel, for spectral value. When the vegetation characteristics of grouped pixels of similar spectral values are supplied, a user-interactive computer can be employed to identify and map all other portions of the frame having those same spectral values. Spectral values ("signatures") unique to specific vegetation groupings or complexes can then be color coded on a computer thematic map. Thus, an ecospectral classification of vegetation is constructed from a purely ecological classification, using satellite multispectral imagery and computer assistance. The resulting thematic map and summary statistical read-outs are checked in the field to develop the level of veracity (ground-truth data) and to perfect further the signature separations for the major vegetation habitat components (complexes). Also, the spectral signatures recorded for known vegetation/landform associations can be computer extrapolated directly to large unmapped geographic areas having comparable habitat structure. The final computer statistics and thematic map, corrected and verified, can then be used as an extremely valuable tool in designing bear management programs, estimating population levels, and monitoring habitat changes. Multispectral imagery mapping has unlimited potential for all aspects of wilderness, game, and forest management in any part of the world.

General Status. The grizzly bear presents a unique management problem among North American mammals because of its aggressive behavior and space requirements. The earliest management methods consisted of eliminating offending animals. Only within the last decade have serious efforts been made to manage grizzlies utilizing scientific information and interagency cooperation. The Wilderness Act of 1964 effectively prevented adverse modification of millions of acres of grizzly bear habitat in the lower 48 states. Thus, the most serious threat to the grizzly within the last 20 years has not been habitat destruction, but rather human-caused deaths. With a low reproductive rate, a history of competing with mankind for space and resources, and a propensity to attack humans occasionally, the grizzly has suffered heavy mortality. Current management must, of course, preserve existing

habitat, but equally critical is the need to reduce human-caused bear deaths throughout the range of this animal so that the birth rate equals or exceeds the mortality rate. The task is rendered yet more difficult by the need for verifiable birth and death statistics throughout millions of acres of rugged wilderness country.

Jurisdictional problems have proven especially troublesome. The bear's habitat transcends national park, national forest, and state boundaries. Management philosophies of the land agencies have varied widely, as have also their specific management objectives. Enactment of the Endangered Species Act of 1973, and resulting federal rules defining critical habitat, stimulated greater interagency cooperation, increased standardization of management objectives for development of detailed management guidelines, and synthesized a common philosophy of preservation rather than exploitation. That the grizzly bear is seriously threatened in the lower 48 states is now well established, if not well accepted.

Detailed guidelines for managing grizzly and brown bears under a wide range of habitat and jurisdictional conditions are currently being formulated by agencies responsible for their welfare (Habitat Management Guidelines for Grizzly Bears of the Greater Yellowstone Area 1976). In the lower 48 states, a recovery plan to restore the grizzly bear to nonthreatened status is being compiled through the U.S. Fish and Wildlife Service by a recovery plan leader and a group of knowledgeable biologists and administrators. Critical habitat has been delineated for the Yellowstone region (Craighead 1980b) and current investigations (discussed earlier in the text) are in progress for other regions. Recovery of the grizzly in the Yellowstone region and in two other regional areas where suitable habitat exists will require time. These distinct areas support either viable or remnant populations, and are composed of one or more "ecosystems" (ecosystem defined as a large biogeographic area supporting a common ecological vegetation classification).

The Yellowstone Ecosystem (Wyoming, Montana, and Idaho) of approximately 2.2 million hectares supports a population variously estimated at 130 to 350 grizzlies. Based on long-term population parameters (Craighead et al. 1974) and current death statistics and reproductive rates (Knight personal communication 1980), as well as on a sharp decline in utilization of winter-killed elk and bison (J. J. Craighead in preparation), the Yellowstone population could lie closer to the lower than to the higher estimate. The failure of the Interagency Grizzly Bear Study Team to make a scientific population estimate after 10 years of field effort has seriously delayed management and has created widespread public concern for the survival of the bears.

The Western Montana Region (including at least two distinct ecosystems) of over 2 million hectares is confluent with Canadian habitat with which it shares many bears. The population has not been enumerated, but preliminary data on female-cub ratios and long-

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trend.

The Selway-Bitterroot Region (Idaho and
Montana) of over 1.2 million hectares is not yet well
defined, but probably supported a viable grizzly popu-
lation historically. Recent observations suggest the
presence of a small resident population, but whether it
is viable is unknown.

Three other regions, each of sufficient size to
support viable populations in the future, are the
Cabinet-Yaak in northwestern Montana and northeast-
ern Idaho, the Selkirk Mountains in northeastern
Washington and northwestern Idaho, and the northern
Cascades from north-central Washington to the Cana-
dian border. Grizzly bears are rarely observed in these
areas and population structure, density, and relative
numbers are unknown. Whether viable populations
exist is also unknown, but if viable, then interchange
with larger population centers in Canada is probably
essential to their welfare and survival.

Thus, only two large population centers exist in
the United States, excluding Alaska. In both of these,
the Yellowstone and the western Montana region, the
populations are in trouble and need precise manage-
ment to lower the death rate and to maintain present
habitat conditions.

In Canada and Alaska, grizzly and brown bears
still have adequate habitat and present populations
have not been seriously threatened. However, in-
creased logging, mining, recreation, and energy de-
velopment are not compatible with continued survival
of the bears. Problems are rapidly emerging and will
continue to mount in the future. Fortunately, research
has accelerated to meet the challenge. As in the lower
48 states, management goals should include minimiz-
ing the death rate and preserving habitat.

Throughout North America, both research and
management efforts should be focused on the largest
wilderness areas of prime habitat. Space and solitude
are essential for maintaining grizzly bears in per-
petuity. Nonwilderness areas adjacent to wilderness
must be managed as critical habitat and, where feasi-
ble, reclassified as wilderness. In nonwilderness areas
grizzlies have but short-term security. Eventually, in-
tensified resource use will displace them. Maintaining
large wilderness areas of prime habitat inviolate to
energy exploitation is essential to the future of
grizzly/brown bears throughout their range in North
America. The threat of mining and energy exploration
in wilderness areas will abate considerably in 1983 by
virtue of provisions established by the Wilderness Act
of 1964. The next two years, however, will be a period
of great pressure for development of wilderness re-
sources.

Bear-Human Relations. The problem of managing
grizzlies and people has been most acute in American
and Canadian national parks where bear-human en-
counters and fatal maulings have increased over the
past decade. The causes for these are not well under-
stood and solutions have been hampered by agency

fears of litigation. Some of the problems have been
addressed by Craighead and Craighead (1967, 1972),
Cole (1972), Cowan (1972), Herrero (1972),
Craighead (1973), and Martinka (1976). With the list-
ing of the grizzly as "threatened" south of the Cana-
dian border on 1 September 1975, the problem of how
to manage bears and humans in national parks became
even more acute. Fatal maulings receive national pub-
licity. The culprit bears, and frequently other bears, are
killed. Though public sentiment is aroused both for and
against them, each new media-exploited incident dam-
ages further the general support for grizzlies. Investiga-
tions of incidents have too often been "in house,"
thereby creating a credibility gap. The cause or causes
proffered in explanation of specific attacks have varied
widely. Such improbable stimuli as severe thun-
derstorms, forest fires, perfume, cosmetics, and
menstruating women have been suggested.

Most attacks can be grouped into two categories:
incidents in which bears, especially females with off-
spring or bears defending food sources, have been star-
tled or approached too closely; and incidents involving
animals conditioned to humans from close association,
generally in national park or monument campgrounds.
Solutions in the first case include increased public edu-
cation concerning grizzlies and their behavior and
more intensive patrolling of potentially high-risk areas
and trails. In spite of the best management efforts,
there undoubtedly will always be some attacks by un-
conditioned grizzlies to the extent that they are codo-
minant with mankind in the wilds. The risk is very low
from this type of grizzly. By far the greatest danger is
from man-conditioned grizzlies—those that have lost
their fear and respect for humans. Such animals are
attracted to human-associated scents and have learned
by conditioning that these frequently lead to food-
rewarding experiences. Dominant and aggressive,
man-conditioned grizzlies behave as aggressively to-
ward humans as they do toward subordinate bears.
There are a wide range of situations in which man-
conditioned bears have attacked humans: sometimes in
the campgrounds and developed areas where most of
the conditioning has occurred; other times in back-
country, miles from the conditioning centers. There is
no simple or sure solution for preventing this type of
attack, but certain protective measures are logical.
Campgrounds and developed areas must be fully
sanitized. Once there is suspicion or evidence that a
grizzly has become man-conditioned, the animal
should be closely monitored. Radiocollaring of such
bears provides an excellent surveillance mechanism.
However, the technique must be used with moderation
and with judgment as to when monitoring is no longer
effective or justifiable. If confrontations continue, the
animal must be eliminated; transport and release have
not proven effective.

Man conditioning of bears is basically a result of
failing to manage bears and people properly in the
same environment. Human injuries or deaths can be
judged preventable, thereby making the responsible
agency subject to litigation. The risk of attack from

man-conditioned bears can be greatly reduced by providing funds for national park rangers well trained in bear management. Patrolling campgrounds and trails and monitoring suspected animals with the same expertise and fervor directed to patrolling park highways for errant drivers would surely reduce the risk of bear-man incidents. Problem animals could be controlled before a serious accident could occur. This preferred type of situation will be much more easily accomplished once the grizzly bear populations have recovered and stabilized and the species is removed from threatened status.

Other alternatives for reducing human-bear confrontations are reduction of visitor use, protection of large areas from human visitation, or great reduction in the number of bears. Although the last alternative is not biologically acceptable, it has been seriously considered. It would certainly severely threaten the survival of the species in its natural range. A biologically sound and feasible solution is to effect recovery of threatened populations. Then, if sanitation and other management procedures fail to prevent man conditioning, the subsequent elimination of rogue animals presents a minimal threat to restored bear populations.

To effect recovery of the grizzly bear populations in the lower 48 states, it will be necessary to conduct certain types of ongoing, management-oriented research and to apply the findings rapidly. There is justifiable concern that agencies may have overresponded to the plight of a threatened species with a surfeit of research. Certainly, habitat should be defined, described, rated, and mapped for all areas inhabited by grizzlies. However, it is highly questionable whether each population unit requires intensive study, and restudy, to document denning, home ranges, population structures, and reproductive biology. Radioinstrumenting of large numbers of bears to obtain biological parameters, already well documented elsewhere, should be reevaluated. Capturing and marking places stress on a population. It can be justified to obtain initially the basic biological information essential to a better understanding of the species. However, it becomes increasingly difficult to justify such measures for each of numerous population units inhabiting basically similar biogeographic environments. Handling of bears should be kept to a minimum with marking and monitoring techniques used only to meet specific and essential research and management objectives. The large-scale marking and radioinstrumenting that characterizes much of the current applied research can hardly be justified when used as a continuous monitoring and data-gathering technique in the ongoing management process.

Finally, if the prognosis for a population unit is for a slow decline based on long-term data, or nonviable based on very low bear densities, then the population should be declared endangered until recovery is documented.

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