# MAMMALIAN SPECIES No. 439, pp. 1-10, 3 figs.

### Ursus arctos. By Maria Pasitschniak-Arts

Published 23 April 1993 by The American Society of Mammalogists

# Ursus arctos Linnaeus, 1758

#### Brown Bear

Ursus arctos Linnaeus, 1758:47. Type locality "Sweden."

Ursus ursus Boddaert, 1772:46. Renaming of Ursus arctos.

Ursus badius Schrank, 1798:55. Type locality "forests on the Bohemian boundary of Bavaria, Germany."

Ursus alpinus Fischer, 1814:16. Type locality "Alps."

Ursus horribilis Ord, 1815:291. Type locality "Missouri River, a

little above mouth of Poplar River, northeastern Montana.'

Ursus cinereus Desmarest, 1820:164. Type locality "headwaters of the Missouri River.

Ursus collaris Cuvier and Geoffroy, 1824: pt. 42, pl. 212. Type locality "Siberia."

Ursus isabellinus Horsfield, 1826:334. Type locality "mountains of Nepal.'

Ursus candescens Hamilton Smith, 1827:229. Renaming of Ursus

Ursus formicarius Billberg, 1828:16. Type locality "northern Scandinavia."

Ursus syriacus Hemprich and Ehrenberg, 1828: sig. a, pl. 1. Type

locality "near Bischerre village, Mt. Makmel, Lebanon."

Ursus pyrenaicus Fischer, 1829:142. Type locality "Asturias, Spain." Ursus norvegicus Fischer, 1829:142. Type locality "Norway.

Ursus falciger Reichenbach, 1836:32. Type locality "Pyrenees Mountains.'

Ursus richardsoni Swainson, 1838:54. Type locality "assumed to be shore of the Arctic Ocean, on west side of Bathurst Inlet about 8 mi from mouth of Hood River, Mackenzie, Canada."

Ursus cadavarinus Eversmann, 1840:11. Renaming of Ursus arctos.

Ursus longirostris Eversmann, 1840:11. Renaming of Ursus formicarius.

Ursus euryrhinus Nilsson, 1847:212. Type locality ?Sweden (based on individual raised in captivity).

Ursus pruinosus Blyth, 1854:589. Type locality "Lhasa, Tibet,

Ursus piscator Pucheran, 1855:392. Type locality "Petropavlovsk, southern Kamchatka, USSR.'

Myrmarctos eversmanni Gray, 1864:695. Type locality "Norway." Ursus lasiotus Gray, 1867:301. Type locality "interior of northern China.'

Ursus leuconyx Severtzov, 1873:79. Type locality "upper Narym River, Tianshan Mountains, Kirgiziya, USSR."

Ursus lagomyiarius Przewalski, 1883:216. Type locality "Kokoshili Range (35°N, 92°E), Tsinghai, China.

Ursus middendorfii Merriam, 1896:69. Type locality "Kodiak Island, Alaska.

Ursus dalli Merriam, 1896:71. Type locality "Yakutat Bay (NW side), Alaska.'

Ursus sitkensis Merriam, 1896:73. Type locality "near Sitka, Alas-

Ursus melanarctos Heude, 1898:17. Type locality "Hakodae, Hokkaido, Japan.'

Ursus mandchuricus Heude, 1898:23-24. Type locality "near Vladivostok, Primorsk, Kray, USSR."

Melanarctos cavifrons Heude, 1901:1. Type locality "Tsitsihar, Heilungkiang, China.'

Ursus kidderi Merriam, 1902:78. Type locality "Chinitna Bay, Cook Inlet, Alaska.

Ursus merriami Allen, 1902:141. Type locality "Portage Bay, opposite Port Muller, Alaska Peninsula, Alaska.'

Ursus hylodromus Elliot, 1904:257. Type locality "Alberta, Can-

Ursus eulophus Merriam, 1904:153. Type locality "Admiralty Island, southeastern Alaska.'

Ursus kenaiensis Merriam, 1904:154. Type locality "Cape Elizabeth, extreme west end Kenai Peninsula, Alaska.

Ursus sheldoni Merriam, 1910:127. Type locality "Montague Island, Prince William Sound, Alaska.

Ursus kadiaki Kleinschmidt, 1911:27. Type locality "Kodiak Island, Alaska,'

Ursus alexandrae Merriam, 1914:174. Type locality "Kasilof Lake, Kenai Peninsula, Alaska.

Ursus eltonclarki Merriam, 1914:175. Type locality "Freshwater Bay, Chichagof Island, Alaska.'

Ursus orgilos Merriam, 1914:176. Type locality "Bartlett Bay, east side Glacier Bay, southeastern Alaska.

Ursus innuitus Merriam, 1914:177. Type locality "Golofnin Bay, south side Seward Peninsula, western Alaska.

Ursus internationalis Merriam, 1914:177. Type locality "Alaska-Yukon boundary, about 50 mi south of Arctic Coast.'

Ursus russelli Merriam, 1914:178. Type locality "Mackenzie Delta, Mackenzie, Canada."

Ursus stikeenensis Merriam, 1914:178. Type locality "Tatletuey Lake, near head of Skeena River, northern British Columbia, Canada.'

Ursus nortoni Merriam, 1914:179. Type locality "Yakutat, Alaska."

Ursus imperator Merriam, 1914:180. Type locality "Yellowstone National Park, Wyoming.

Ursus absarokus Merriam, 1914:181. Type locality "head of little Bighorn River, northern part Bighorn mountains, Carbon Co., Montana.

Ursus tahltanicus Merriam, 1914:181. Type locality "Klappan Creek (=third South Fork Stikine River), British Columbia, Canada.

Ursus toklat Merriam, 1914:182. Type locality "head of Toklat River, N base Alaska Range, near Mt. McKinley, Alaska.'

Ursus shoshone Merriam, 1914:184. Type locality "Estes Park, Larimer Co., Colorado."

Ursus klamathensis Merriam, 1914:185. Type locality "Beswick, near mouth of Shovel Creek, Klamath River, Siskiyou Co., California.'

Ursus pervagor Merriam, 1914:186. Type locality "Pemberton (=Lillooet) Lake, British Columbia, Canada.

Ursus caurinus Merriam, 1914:187. Type locality "Berners Bay, E side Lynn Canal, southeastern Alaska.

Ursus colusus Merriam, 1914:187. Type locality "Sacrimento River, probably between Colusa and Sacrimento, California."

Ursus magister Merriam, 1914:189. Type locality "Los Biacitos, head of San Onufre Canyon, Sanda Ana Mountains, San Diego Co., California."

Ursus henshawi Merriam, 1914:190. Type locality "southern Sierra Nevada, near Havilah, Kern Co., California."

Ursus nelsoni Merriam, 1914:190. Type locality "Colonia Garcia, Chihuahua, Mexico.

Ursus navaho Merriam, 1914:191. Type locality "near Fort De-

fiance (=Molhausen), Arizona, probably in Chuska Mountains."
Ursus bairdi Merriam, 1914:192. Type locality "Blue River, Summit Co., Colorado.

Ursus utahensis Merriam, 1914:193. Type locality "N fork Salina Creek, about 10 mi SE Mayfield, Sanpete Co., Utah.'

Ursus kennerleyi Merriam, 1914:194. Type locality "mountains near Los Nogales, Sonora, Mexico."

Ursus shirasi Merriam, 1914:195. Type locality "Bybus Bay, Admiralty Island, Alaska."

Ursus apache Merriam, 1916:134. Type locality "Whorton Creek, S slope White Mountains, a few miles W Blue, Greenlee Co.,

Ursus arizonae Merriam, 1916:135. Type locality "E side Escudilla Mountains, Apache Co., Arizona.

Ursus chelan Merriam, 1916:136. Type locality "T. 30N, r. 16 E, Wilamette Meridian, Wentachee National Forest, E slope Cascade Mountains, northern Chelan Co., Washington."

Ursus cressonus Merriam, 1916:137. Type locality "Lakina River, S slope Wrangell Range, Alaska."

Ursus eximus Merriam, 1916:139. Type locality "head of Knik Arm, Cook Inlet, Alaska.'

Ursus hoots Merriam, 1916:140. Type locality "Clearwater Creek, a N branch Stikeen River, British Columbia, Canada.

Ursus kluane Merriam, 1916:141. Type locality "McConnell River, Yukon, Canada.'

Ursus kwakiutl Merriam, 1916:143. Type locality "Jervis Inlet, coast of southern British Columbia, Canada.

Ursus mendocinensi Merriam, 1916:145. Type locality "Long Valley, N of Sherwood, Mendocino Co., California.

Ursus mirabilis Merriam, 1916:146. Type locality "Admiralty Island, Alaska.'

Ursus nuchek Merriam, 1916:148. Type locality "head of Nuchek Bay, Hinchenbrook Island, Prince William Sound, Alaska.

Ursus ophrus Merriam, 1916:148. Type locality "eastern British Columbia, Canada.

Ursus pallasi Merriam, 1916:149. Type locality "Donjek River, southwestern Yukon, Canada.'

Ursus selkirki Merriam, 1916:150. Type locality "Selkirk Mountains, Upper Columbia River, British Columbia, Canada.'

Ursus townsendi Merriam, 1916:151. Type locality "mainland of southeastern Alaska, probably between Cross Sound and Alsek River Delta.

Ursus washake Merriam, 1916:152. Type locality "N Fork Shoshone River, Abrasoka Mountains, between Bighorn Basin and Yellowstone National Park, Wyoming."

Ursus schmitzi Matschie, 1917:33. Type locality "Medschel Schems on W slope of Mt. Hermon, Lebanon.'

Ursus chelidonias Merriam, 1918:21. Type locality "head of Jervis

Inlet, British Columbia, Canada."

Ursus atnarko Merriam, 1918:22. Type locality "Lonesome Lake, Atmarko River, one of the upper forks of Bella Coola, British Columbia, Canada.

Ursus dusorgus Merriam, 1918:33. Type locality "head of Jackpine River, near Mt. Bess, close to British Columbian boundary, Alberta, Canada."

Ursus planiceps Merriam, 1918:37. Type locality "Colorado, probably in foothills or on western edge of plains."

Ursus macrodon Merriam, 1918:38. Type locality "Twin Lakes,

Lake Co., Colorado.'

Ursus mirus Merriam, 1918:40. Type locality "Slough Creek, Yellowstone National Park, Wyoming."

Ursus orgildoies Merriam, 1918:46. Type locality "Italio River,

Alaska.

Ursus rungiusi Merriam, 1918:49. Type locality "Rocky Mountains on headwaters of Athabasca River, Alberta, Canada.

Ursus macfarlani Merriam, 1918:51. Type locality "Anderson River, 50 mi below Fort Anderson, Mackenzie, Canada.

Ursus idahoensis Merriam, 1918:54. Type locality "N fork of Teton River, Fremont Co., Idaho."

Ursus pulchellus Merriam, 1918:55. Type locality "Ross River, Yukon, Canada."

Ursus oribasus Merriam, 1918:56. Type locality "upper Laird River, Yukon, near British Columbia boundary, Canada.'

Ursus perturans Merriam, 1918:64. Type locality "a canyon on Mt. Taylor," 12 mi E San Mateo, Valencia Co., New Mexico. Ursus rogersi Merriam, 1918:65. Type locality "high up on Graybull River," Absaroka Mountains, Yellowstone National Park, Wyoming.

Ursus pellyensis Merriam, 1918:82. Type locality "Ketza Divide, Pelly Mountains, Yukon, Canada.

Ursus andersoni Merriam, 1918:83. Type locality "E branch Dease River, near Great Bear Lake, Mackenzie, Canada."

Ursus crassodon Merriam, 1918:90. Type locality "Klappan Creek (Third South Fork Stikine River), British Columbia, Canada."

Ursus crassus Merriam, 1918:90. Type locality "upper Macmillan River, Yukon, Canada.'

Vetularctos inopinatu Merriam, 1918:132. Type locality "Ren-

dezvous Lake, N of Fort Anderson, Mackenzie, Canada."
Ursus pamiriensis Ognev, 1924:111. Type locality "Pamir Mountains, Tadjikstan, USSR."

Ursus holzworthi Merriam, 1929:173. Type locality "last slope of

Talkeetna Mountains, near headwater of Oshetna or Black River, Alaska.

CONTEXT AND CONTENT. Order Carnivora, Family Ursidae, Subfamily Ursinae. The genus Ursus includes four species: U. arctos, U. americanus, U. maritimus, and U. thibetanus (Honacki et al., 1982). Numerous species and subspecies names have been assigned to the brown bear, and as a result the synonymy is formidable and confusing (Erdbrink, 1953; Merriam, 1918). Most authorities now recognize U. arctos as one Holarctic species (Couturier, 1954; Honacki et al., 1982; Rausch, 1963; Stroganov, 1969). Nine subspecies from the New World and seven from the Old World are distinguished by Hall (1984) and Ellerman and Morrison-Scott (1966), respectively:

U. a. alascensis Merriam, 1896:74. Type locality "Unalaklik, Alaska."

U. a. arctos Linnaeus, 1758:47, see above.

U. a. beringianus Middendorff, 1853:252, pl. 1. Type locality "Great Shantar Island, Sea of Okhotsk."

U. a. californicus Merriam, 1896:76. Type locality "Monterey, California.'

U. a. collaris Cuvier and Geoffroy, 1824: pl. 212, see above.

U. a. dalli Merriam, 1896:71, see above.
U. a. gyas Merriam, 1902:78. Type locality "Pavlof Bay, Alaska Peninsula, Alaska."

U. a. horribilis Ord, 1815:291, see above.

U. a. isabellinus Horsfield, 1826:334, see above.

U. a. lasiotus Gray, 1867:301, see above.

U. a. middendorffi Merriam, 1896:69, see above.

U. a. pruinosus Blyth, 1854:589, see above.

U. a. sitkensis Merriam, 1896:73, see above.

U. a. stikeenensis Merriam, 1914:178, see above.

U. a. syriacus Hemprich and Ehrenberg, 1828: pl. 1, see above.

DIAGNOSIS. Urctos arctos (Fig. 1) has a distinctive dished facial profile, heavily built body with a prominent shoulder hump, and long, slightly curved claws on the forefeet, about twice as long as on the hind feet. Guard hairs are long and often variegated, giving the pelage a grizzled appearance (Brown, 1985; Hall, 1981; Murie, 1985). Crown length and width of the first mandibular molar are always >20.4 and 10.5 mm, respectively (Gordon, 1977). Greatest crown length of the second maxillary molar also is >31 mm (Storer and Tevis, 1955). These features differentiate U. arctos from U. americanus and other Ursus. Ursus maritimus is readily identified by its white fur, and U. thibetanus has a distinct white "V" on its chest (Hall, 1981).

GENERAL CHARACTERS. Brown bears have a massive head with a prominent nose, rounded inconspicuous ears, small eyes, short tail, and powerful body of great size and strength. Color varies from pale tan, blond, gold, gray, silver, cinnamon, and all shades of brown to almost black. Generally, head and shoulders are paler in color with darker sides, belly, and legs (Brown, 1985; Nowak and Paradiso, 1983). Animals from coastal Alaska tend to be darker and more uniformly colored than individuals from the interior; the latter often have pale-tipped guard hairs, hence the name grizzly. In the Yukon and Northwest Territories, the most common color is chocolate brown with silverish guard hairs over the neck and shoulders. Blond or yellow are the least common colors in the Yukon. About one-half the population in the Canadian Rockies is brown with a yellowish tinge on sides and back. In the Yellowstone ecosystem, the predominate color is medium to dark brown with brown legs, hump, and underparts (LeFranc et al., 1987). Fur tends to become darker from western to eastern Eurasia (Stroganov, 1969).

Length of head and body of adults varies from 1.0 to 2.8 m, shoulder height is up to 1.5 m, and length of tail is 65-210 mm. Body mass may vary from 80 to >600 kg (Nowak and Paradiso, 1983; Stroganov, 1969). Young-of-the-year and yearlings weigh 2-27 and 9-37 kg, respectively (LeFranc et al., 1987).

Adult males on average are larger and heavier than females. Mean body measurements (cm) of 55 adult males and 55 adult females, respectively, from Yellowstone National Park are: total length, 164.3, 151.1; height, 95.2, 87.4; girth, 130.5, 114.6; neck circumference, 78.6, 65.4; length of head, 41.7, 37.8; length of hind foot, 18.9, 16.3; and width of hind foot, 13.6, 11.8 (Blanchard, 1987). The heaviest individuals in North America are found along coastal Alaska; mean adult mass of males and females are 389 and



Fig. 1. Adult female *Ursus arctos*. (Photograph courtesy of F. Faigal, Metropolitan Toronto Zoo.)

207 kg, respectively, and, on nearby islands such as Kodiak, 312 and 202 kg, respectively (LeFranc et al., 1987). Mean adult mass (kg) of males and females, respectively, from inland areas are: interior Alaska, 243, 117; West Brooks Range, Alaska, 155, 112; Yellowstone National Park, Wyoming, 193, 135 (Blanchard, 1987); interior British Columbia, 117, 58; Jasper National Park, Alberta, 92, 55 (LeFranc et al., 1987); northern Yukon, 140, 83; northwestern Mackenzie, Northwest Territories, 159, 99 (Kingsley et al., 1988). In Eurasia, size increases from west to east, with the largest specimens found in Kamchatka and coastal Siberia. Mean body measurements (in cm) from 15 males and 8 females, respectively, from far eastern Siberia are: total length, 186, 160; height, 129, 96; length of tail, 17, 16; length of ear, 16, 14. Males weigh 140–320 and females weigh 100–200 kg (Stroganov, 1969).

Skulls of adult brown bears are stout and heavy (Fig. 2), and show sexual dimorphism and geographic variation (Couturier, 1954; Kurtén, 1973; Merriam, 1918; Rausch, 1963). Skull measurements (in mm) of 22 males and 9 females, respectively, from eastern Siberia are: condylobasal length, 380, 345; zygomatic width, 253, 223; interorbital width, 96, 83; postorbital width, 81, 76; width of rostrum above canines, 83, 75; width of nasals, 52, 50; length of nasals, 105, 93; length of upper toothrow, 143, 132 (Stroganov, 1969). Mean condylobasal length and mean zygomatic breadth (in mm; males, females) of skulls from North America are: Alaska Peninsula, (397, 346), (264, 217); east-central Alaska, (346, 298), (232, 192); Kodiak Island, Alaska, (393, 335), (284, 227); Yukon Territory, (332, 291), (216, 184); northwestern British Columbia, (340, 304), (222, 190); California, (365, 319), (227, 194; Hall, 1984). The dental formula is i 3/3, c 1/1, p 4/4, m 2/3, total 42 (Davis, 1964; LeFranc et al., 1987).

DISTRIBUTION. Ursus arctos inhabits North America and Eurasia (Fig. 3). Historically, this species encompassed most of western and central North America from the Arctic Ocean to central Mexico (Guilday, 1968). The distribution of U. arctos in Alaska shows little change from historic times. In Canada, the species is found in the Yukon, Northwest Territories, British Columbia, and Alberta, but no longer in the prairies. South of the Canadian border, populations are managed in six disparate ecosystems in Washington, Montana, Wyoming, and Idaho (Cowan, 1972; LeFranc et al., 1987; Servheen, 1990). Extirpation in Mexico occurred in the 1960s, but possibly a few animals might exist in northern areas of Mexico (Trevino and Jonkel, 1987).

Range and abundance of brown bears in western Europe and Scandinavia is limited: Spain—two populations in the Cantabrian Mountains; Italy—one in the Trentino Alps and another in Abruzzo National Park; France—two in the Pyrenees Mountains; Greece—one in Pindus and one in the Rhodope Mountains; Albania—status

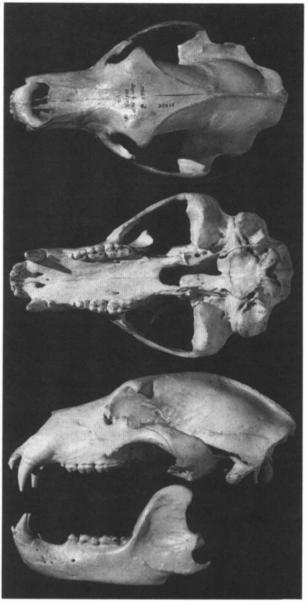


Fig. 2. Skull of *Ursus arctos* (Royal Ontario Museum 30426, male from Sugar Lake, British Columbia). Greatest length of the cranium is 345 mm.

unknown; Yugoslavia—the species inhabits the Dinara Mountains; Bulgaria—populations in the Nalken Range, Rilan and Pirin areas, and in the Rhodopa Range; Romania—populations found in the Carpathian and Transylvanina Mountains; Czechoslovakia—the species remains in High Tatra National Park; Poland—populations inhabit the border with Czechoslovakia and the bordering countries of the Commonwealth of Independant States & Russia (formerly USSR); Finland—numbers are apparently increasing; Norway—17 fragmented subpopulations remain; and, Sweden—species occur in central and northern areas of the country contiguous with Norway (Cowan, 1972; Servheen, 1990).

Historically, *U. arctos* ranged from the tundra and forests of the bordering countries of the Commonwealth of Independant States & Russia (formerly USSR) to the Himalayas. Populations and ranges are presently declining from Turkey eastward to China: Turkey—the species occurs in Artvin, Hakkari, Tunceli, and Erzincan areas; Lebanon—once found in the Al Sheikh Mountains, the species is now extinct; Syria, Iraq, and Iran—status unknown; India—animals are rarely seen in northern parts of the country; Pakistan—the species may be found in the mountains along the Chinese border, but is uncommon; Mongolia—four populations inhabit Hovsgol, western Altai, Hentei Mountains, and Onon and Uldz valleys; Democratic

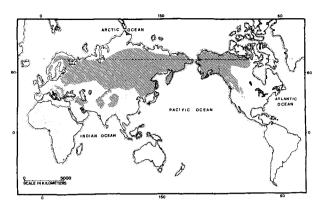


Fig. 3. Distribution of *Ursus arctos* in North America and Eurasia. (Map prepared by S. Poray-Swinarski, Royal Ontario Museum.)

People's Republic of Korea—status unknown; China—populations occur in Tianshan and Pamir Mountains of Xinjiang Uygur, on steppes and deserts of Qinghai-Xizang plateau, and in Tahinganling, Wanda, and Changbai Mountains; and, Japan—three populations live on Hokkaido Island (Servheen, 1990).

In eastern Europe, populations occur in the Caucasus and Carpathian Mountains, Volga-Vyatka region, and Ural Mountains. In eastern Russia, present-day range is similar to historical range. Large populations inhabit Kazakhstan, west and east Siberia, Sakhalin, Kuril Islands, Kamchatka, Khabarovsk, Primorye, Amurskaya, and Magadaskaya. A decline in numbers has been noted in the eastern Siberian central zone, and a small, isolated population in Estonia is protected (Cowan, 1972; Servheen, 1990).

FOSSIL RECORD. All living and fossil bears of the genus Ursus descended from U. minimus, a small forest-dwelling bear of the Pliocene. U. etruscus, a direct descendant of U. minimus, was a Eurasian species that gave rise to two distinct evolutionary lines: the cave bear of Europe, U. spelaeus, and the brown bear of Asia, U. arctos (Kurtén, 1968). The earliest records of U. arctos are from the Choukoutien, China, about 500,000 years ago. The species entered Europe some 250,000 years ago, and co-existed with cave bears in several areas in central Europe. In England, however, the brown bear replaced U. spelaeus about 10,000 years ago (Kurtén, 1968, 1976). U. arctos migrated to North America about 25,000 years ago and ranged from the Arctic tundra to Mexico. Remains from sites in Ontario, Ohio, Kentucky, West Virginia, and Illinois verify the former eastern distribution of brown bears (Churcher and Morgan, 1976; Guilday, 1968; Kurtén and Anderson, 1980).

Large bears of the genus Arctodus also inhabited North America from Alaska to Mexico but became extinct some 11,000 years ago. U. arctos may have competed with Arctodus and succeeded these bears over much of their range (Kurtén, 1976; Kurtén and Anderson, 1980).

FORM AND FUNCTION. Pelage of *U. arctos* consists of a layer of pale to dark brown, dense inner fur, and long outer guard hair. Winter fur is thick, course, moderately long, and appears shaggy. Both length of hair and color are extremely variable. As summer progresses, fur color fades, and guard hair and old inner fur are shed. By autumn, brown bears have a fully prime pelt, with guard hairs and underfur measuring ca. 10 and 8 cm, respectively (Murie, 1985; Obbard, 1987).

The skeletal structure of *U. arctos* is larger and more heavily built than most other ursids, but the axial and appendicular skeleton is similar to that of *U. americanus*. Neck vertebrae have much rotational movement, the limbs are almost equal in length, and bones of both the forearm (radius, ulna) and lower leg (tibia, fibula) are separate allowing for powerful twisting movements. Both fore and hind feet are large, plantigrade, and are cushioned by heavy pads of fibrous connective tissue. The walk is a shuffling gait. All limbs have five digits; the claws often exceed 8 cm in length, are not retractile, and are used to dig up tubers and burrowing rodents (Craighead and Mitchell, 1982; Storer and Tevis, 1955).

Seasonal changes in blood chemistry possibly may be related to renal function and seasonal variation in diet (Halloran and Pearson, 1972). In summer, calcium, urea, creatinine, and uric acid decrease and glucose and potassium increase. In spring, males have higher levels of uric acid than females. Live capture stimulates a rise in creatine kinase (indicating muscle damage), creatinine, blood urea nitrogen, and serum urea. Wild animals have a higher total lipid concentration than captive animals, probably because of differences in diet (Jamnicky et al., 1987). Lipids and fats are not deposited in blood vessel walls (i.e., *U. arctos* shows no arteriosclerosis), enabling brown bears to become obese every autumn (Craighead, 1979).

Average length of intestine of adults is 7-10 m. The caecum is small or absent. Stomach capacity is nearly 50% of the capacity of the total digestive tract (LeFranc et al., 1987).

Bears do not hibernate in the true sense; they are dormant rather than torpid, their dormancy is continuous for 3-7 months, and they can be aroused easily. Brown bears do not eat, drink, urinate, or defecate while in the den (Craighead and Craighead, 1972; Folk et al., 1972). Winter sleep begins between October and December and spring arousal occurs between March and May. In certain southerly and coastal areas, during years of large harvests of natural foods, or during winters of little snow, winter sleep may be brief or may not take place at all (Slobodyan, 1976; Storer and Tevis, 1955).

Brown bears appear to undergo four annual biochemical and physiological stages (Nelson et al., 1983). There is a noticeable decrease in heart rate from 40-50 beats/min in summer to 8-10 during dormancy (stage 1). This bradycardia and reduction in oxygen is associated with shunting of most blood to the heart, lungs, and brain. Body temperature of normally active brown bears ranges from 36.5 to 38.5°C. During winter sleep body temperature is only reduced by 4-5°C (Craighead and Craighead, 1972; Nelson et al., 1983). Metabolic water from fat is sufficient to satisfy water needs, and plasma and red blood cells retain a constant water content. Blood concentration of total protein, uric acid, and urea remains constant, but creatine concentration increases about twofold (Folk et al., 1976; LeFranc et al., 1987). Any urea formed is recycled, preventing uremia and preserving lean body mass. Mass loss is from adipose tissue only (Nelson et al., 1983). During winter sleep, mature females lose relatively and absolutely more of their autumn mass (40%) than males (22%). This larger mass fluctuation by females is due to the large energy expenditure during reproduction (Kingsley et al., 1983).

Upon emergence from their dens in spring, animals enter stage 2, walking hibernation. Both wild and captive brown bears appear to be anorexic until 10–14 days following waking. During periods of normal activity (stage 3) brown bears cannot duplicate dormancy responses. If at this time they are deprived of food and water they will utilize muscle tissue, suffer from dehydration, and become uremic. Prior to winter sleep, brown bears markedly increase their food consumption resulting in the deposition of adipose tissue and mass gain (stage 4, hyperphagia). Adipose tissue insulates brown bears from cold, provides a stored-energy source during dormancy, and may reduce risk of starvation during the first few critical weeks following spring arousal (Nelson et al., 1983).

Females have two pectoral and four abdominal teats (Couturier, 1954). Milk is high in protein (6-17%) and heavily concentrated in solids, of which one-half or more is fat. Milk of animals in zoos has higher levels of lactose than wild animals (Jenness et al., 1972).

Males have a large, straight, or slightly curved penis (Stroganov, 1969). The os penis of older animals can be up to 216 mm in length. Mean single testis weights of sexually mature, prepubertal, and infantile Alaskan bears are 80, 31, and 12 g, respectively (Erickson et al., 1968).

ONTOGENY AND REPRODUCTION. Ursus arctos exhibits a long life span, late sexual maturity, and protracted reproductive cycles (Craighead et al., 1976). Brown bears are polygamous and several males may follow a female, resulting in fights between males. Males may pair with females in estrus, but pairing depends on the male successfully defending the female from other competitors (Craighead et al., 1969).

Breeding occurs from mid-May to July (Curry-Lindahl, 1972; Murie, 1985; Slobodyan, 1976; Stroganov, 1969). Duration of estrus is 10-30 days, with variation among females and years. Successful copulation may take 10-60 min, averaging 23 min, and females may mate with two males in a day or a number of different males during the breeding season (Craighead and Mitchell, 1982; Craighead et al., 1969). In the eastern Carpathian Mountains

(Ukraine), females breed at 4 years of age (Slobodyan, 1976), on Kodiak Island between the age of 3 and 6 years, in the Yukon at about 7 years (Glenn et al., 1976), and in Hokkaido around 5 or 6 years (Aoi, 1987). In Yellowstone National Park, Wyoming, seven of 15 females gave birth at 5, two at 6, four at 7, one at 8, and one at 9 years of age. Females come into heat, copulate, and then may be non-receptive for 4–18 days. This interval likely coincides with follicular development following ovulation, after which females may mate again. Neither sex shows sexual interest during pre- and post-estrus periods (Craighead et al., 1969).

Female brown bears exhibit 2-, 3-, and 4-year reproductive cycles, and reproductive longevity appears to approximate physical longevity. At Yellowstone National Park, one female gave birth at 22.5 years and weaned her young 2 years later. The oldest live bear captured and aged was 25.5 years (Craighead et al., 1974, 1976).

After fertilization embryos develop to the blastocyst stage and remain free in the uterus rather than implanting. This embryonicarrest stage continues for ca. 5 months until the female enters winter sleep. In late November, the blastocyst implants and the active gestation period of 6–8 weeks begins. Young are born from January to March; they are small, helpless, sightless, and generally weigh ca. 0.5 kg. At a Moscow Zoo, newborn young ranged from 230 to 280 mm and weighed about 500 g. Litter size varies from one to four, but the typical size is two or three (Craighead et al., 1969; Curry-Lindahl, 1972; Erickson et al., 1968). By 3 months, young weigh about 15 kg and have fully developed milk teeth. They have circular-shaped skulls which lengthen during growth, and change over the entire life of the animal. During the first summer, young often have a whitish V-shaped neck patch, which usually fades by the 2nd year (LeFranc et al., 1987; Stroganov, 1969).

Lactation lasts 1.5-2.5 years and young usually remain with the female for 2-3 years (Craighead, 1979; Glenn et al., 1976). Occasionally, one youngster may remain with the mother into the 4th year. Males usually reach puberty at 4.5 years of age and their reproductive period begins before, and extends beyond, that of females (Erickson et al., 1968).

ECOLOGY. Diet of the brown bear includes numerous species of lush grasses, succulent herbs, tender shoots, flowers, leaves, roots, bulbs, a variety of tubers, mosses, horsetails, willows, and many species of berries, but they are not able to digest fibrous or course forage very well (Bunnel and Hamilton, 1983; Craighead et al., 1982). Various species of insects, larvae, grubs, fungi, birds, eggs, acorns, cones, and a variety of nuts are also consumed. Small mammals of the genera Spermophilus, Marmota, Lemmus, Synaptomys, Dicrostonyx, Thomomys, Clethrionomys, Phenacomys, Microtus, and Peromyscus supplement the diet (LeFranc et al., 1987; Nowak and Paradiso, 1983). U. arctos eats carrion of winterkilled big game such as moose (Alces alces), caribou (Rangifer tarandus), elk (Cervus elaphus), bison (Bison bison), deer (Odocoileus sp.), pronghorn (Antilocapra americana), sheep (Ovis sp.), and mountain goats (Oreamnos americanus). Healthy ungulates rarely are killed, but those weakened by severe winters, disease, malnutrition, old age, or injuries are preyed upon. Brown bears in Yellowstone National Park travel to winter grounds of elk and other ungulates between March and May. Predation is facilitated by extended winter conditions where deep snow prevents ungulates from escaping. In southwestern Yukon, southern and eastcentral Alaska, and Russia, U. arctos are the primary predators on moose and their calves (Ballard et al., 1981; Boertje et al., 1988; Larsen et al., 1989). Newborn <2 months old are the most vulnerable. The heaviest predation on female moose is during the calving and postcalving season when females are less mobile and trying to protect their young. Brown bears of different ages and both sexes prey on moose. Caribou and wild boar (Sus scrofa) are occasionally killed (Danilov, 1983). In Brooks Range, Alaska, both sexes prey on young and adult caribou. Capture techniques include locating calves by scent, charging herds, attacking prey at river crossings, and killing upon incidental encounters (Reynolds and Garner, 1987). Adult muskox (Ovibos moschatus) have been ambushed in the Northwest Territories (Gunn and Miller, 1982).

When in close proximity, brown bears learn to exploit domestic livestock (Clevenger et al., 1987; Jorgensen, 1983; Knight and Judd, 1983; Murie, 1948). Cattle are bitten on the neck, back, and head, the abdominal cavity often is opened, and the stomach and

intestines are removed. Predation is highest on calves and yearlings and is more common in forests than in open ranges. Evidence of *U. arctos* feeding on a carcass is not proof that the prey was killed by a brown bear (Murie, 1948). Sheep are taken when they graze on prime brown bear feeding habitats (Jorgensen, 1983; Knight and Indd. 1983).

Brown bears in coastal areas prey upon different salmonid species. Fishing techniques vary depending on topography of rivers and water falls, water level, and abundance of fish (Egbert and Stokes, 1976). The extinct *U. a. californicus* ate carcasses of whales and fish washed onto the shore (Storer and Tevis, 1955).

In North America and Europe, where ranges overlap, black bears, mountain lions (Felis concolor), bobcats (F. rufus), lynx (F. lynx), wolves (Canis lupus), wolverines (Gulo gulo), and foxes (Alopex and Vulpes) may compete with U. arctos (LeFranc et al., 1987; Murie, 1985). Occasionally, individuals have been attacked by tigers (Panthera tigris) in the USSR (Stroganov, 1969).

Ectoparasites of *U. arctos* are confined to two genera of fleas (Chaetopsylla and Arctopsylla) and one species of tick (Dermacenter). Internal parasites include 2 trematodes, 8 cestodes, and 17 nematodes. In addition, Eurasian brown bears had two protozoans and one rickettsia-like agent of Elokomin fluke fever (Rogers and Rogers, 1976). Intestinal parasites are well adapted to the dormancy stage and usually pass out of the alimentary canal before the animals den. Parasitism by Trichinella and the intestinal roundworm, Baylisacaris transfuga, are common. Trichinella spiralis is picked up from infected meat via cannibalism and scavenging, and the encysted parasite can be found in tongue, masseter, diaphragm, and femoral muscle. Examination of 254 bears from sites in Wyoming and Montana, and Yellowstone and Glacier National Parks, showed 61% were infected with Trichinella. The highest infections occur in animals >16 years old (Worley et al., 1983). Intestinal flukes rarely occur in brown bears (LeFranc et al., 1987).

Adult *U. arctos* are solitary, but home ranges overlap and there is no territorial defence. Dominant males have preferential access to females, but females may mate with more than one male. Rearing, foraging, and refuging systems of the sexes remain separate: adults forage and den alone, while females forage and den with their young, raising them alone (Craighead, 1976; Eisenberg, 1981; LeFranc et al., 1987; Murie, 1985).

Sizes of home ranges are largely determined by distribution of food. Rapid digestibility of high-quality food and rapid mass gain are essential if winter dormancy is to be a viable strategy (Bunnel and Hamilton, 1983; Hamer and Herrero, 1987). Where food is abundant, such as at salmon streams, berry patches, carrion, and garbage dumps, brown bears congregate in high densities and their home ranges become reduced (Craighead, 1979; Hamilton and Bunnel, 1987; Stonorov and Stokes, 1972). Size of home range is also influenced by age, sex, social status, condition of animal, foraging habits, distribution and availability of food and cover, topography, location of day beds and dens, and proximity of mates (Craighead, 1979; LeFranc et al., 1987; Murie, 1985; Roth, 1983). Females have smaller home ranges than males which may lessen the female's chance of encountering aggressive males and thus increase security for herself and her young. Upon mating, young females tend to stay near the maternal home range. Home ranges of mature males usually encompass home ranges of several estrous females, thus increasing the probability of breeding. Larger males may also have greater energy needs and wander farther in search of food (Craighead and Mitchell, 1982). Subadult males tend to disperse far from maternal ranges, possibly due to low social status and aggression from adults of both sexes. Sizes of home ranges (km2) of adult males and females, respectively, in North America are: Kodiak Island, 24, 12; Alaska Range, 710, 132; western Brooks Range, 776, 220; eastern Brooks Range, 702, 382; northern Yukon, 286, 121; interior British Columbia, 297, 79; Jasper National Park, 916, 244; Yellowstone ecosystem, 828, 384; Mission Mountains, 1,398, 133; and Cabinet/ Yaak ecosystem, 1,290, 430 (LeFranc et al., 1987).

Population density is affected by topography, cover, food abundance, and spacing behavior. Densities are: Kodiak Island, 1/1.5–4 km²; Alaska Peninsula, 1/16 km²; Denali National Park, 1/24–38 km²; eastern Brooks Range, 1/83–304 km²; northern Yukon, 1/48 km²; interior British Columbia, 1/18–32 km²; Jasper National Park, 1/86–102 km²; Cabinet Mountains, 1/44 km²; Yellowstone ecosystem, 1/50 km² (LeFranc et al., 1987); Norway, 0.6–7.9/1,000 km² (Mysterud and Falck, 1989); Gorski Kotar, Yugoslavia, 1/10 km² (Frkovic et al., 1987); mountainous regions of Ural, Altai,

and eastern Siberia, 4-6/100 km<sup>2</sup> (Vereschagin, 1976); Okhotsk Sea, 1/10 km<sup>2</sup>; and Kamchatka, 0.6/10 km<sup>2</sup> (Kistchinski, 1972).

Potential longevity of wild brown bears is 20–30 years (LeFranc et al., 1987). In Yellowstone National Park, the average lifespan is about 6 years. In captivity, animals live about 30 years, but possibly even 50 (Murie, 1985; Stroganov, 1969). Mortality may be attributed to severe winters, malnutrition, disease, senility, infanticide, and cannibalism. Bears gored by large ungulates may die from complications (Craighead, 1979; Gunn and Miller, 1982).

With the exception of man, mature brown bears have no natural enemies (Craighead, 1979; Herrero, 1985; Knight and Eberhardt, 1985; Wright, 1909). In the United States, extirpation of U. arctos occurred as follows: Texas, 1890; North Dakota, 1897; California, 1922; Utah, 1923; Oregon, 1931; New Mexico, 1933; Arizona, 1935; Colorado, 1979 (LeFranc et al., 1987). Brown bears were eradicated from Denmark ca. 5,000 years ago; Great Britain in the 10th century; eastern and western Germany in 1770 and 1836, respectively; Switzerland, 1904; French Alps, 1937; and North Africa about a century ago (Cowan, 1972; Curry-Lindahl, 1972). Habitat loss due to encroaching human settlement and illegal hunting are major factors responsible for the steady decline in brown bear numbers (Aoi, 1987; Clevenger et al., 1987; Jorgensen, 1983; Roth, 1976). Being opportunistic feeders and having nonstatic, large home ranges brings U. arctos into contact with human settlements, livestock ranches, orchards, and garbage dumps. When natural foods are low and extensive foraging is necessary, human settlements may become part of the home range of the brown bear. Areas with the highest human densities have the greatest ratio of non-sport to sport kills (Boscagli, 1987; Miller and Chihuly, 1987). Construction of roads provides extensive and easy access to settlers, hunters, and poachers, and, thus, greatly increases the vulnerability and rate of mortality of U. arctos (McLellan, 1989; McLellan and Shackleton,

In most of North America and Eurasia the trophy is the main hunting incentive (Frkovic et al., 1987; LeFranc et al., 1987). Pelt quality is highest just prior to brown bears entering winter dens and just after emergence. Most hides are mounted or prepared as rugs (Obbard, 1987). Indians and Eskimos used hides as bedding mats under camp beds, brown bear claws for necklaces, and other parts in totems and dances. The meat is nutritious and reputedly good tasting, and settlers used brown bear fat as oil for cooking (Storer and Tevis, 1955; Stroganov, 1969).

Brown bears are protected under the Convention on International Trade in Endangered Species of Wild Fauna and Flora. Appendix I includes *U. a. arctos* (Italian populations), *U. a. isabellinus*, *U. a. nelsoni*, and *U. a. pruinosus*. Appendix II includes North American subspecies. In 1975, *U. a. horribilis* was designated as threatened south of the Canadian border under the United States Endangered Species Act. Interagency grizzly bear guidelines have been developed for national forests, parks, and management lands in North America to promote conservation of the species. Management objectives aim to preserve and improve habitat, minimize brown bear-human conflicts, and protect the species where endangered, threatened, or declining (LeFranc et al., 1987).

Low reproductive rate and a slow response in compensating for population declines do not allow *U. arctos* to sustain high mortality (Craighead et al., 1974, 1982; Varney et al., 1976). As habitats are fragmented and populations decline, genetic isolation may become a major threat to remaining populations. Recovery and survival of isolated populations may be contingent upon augmentation of existing populations with bears from other areas or by cross fostering captive *U. arctos* young to black bears (Servheen et al., 1987). Protection of adult females is especially critical to survival of small populations. The margin between slow decline and extirpation is small for this species (Knight and Eberhardt, 1985, 1987). For brown bears of Yellowstone National Park, the minimum viable population was determined to be ca. 50–90 individuals in a 1,000–13,500 km² area (Shaffer, 1983).

**BEHAVIOR.** Adults are solitary except during the breeding season. Only females interact with their offspring, nursing and protecting them. Cub adoption or mixing of litters occasionally occurs (Craighead et al., 1969; Erickson, 1964; Erickson and Miller, 1963). Once the female comes into heat, she terminates association with her weaned young by threatening and chasing them away. Siblings may continue to associate, play, and feed together, sometimes for as long as 4.5 years (Murie, 1985). Establishment of social bonds,

mainly through social play, is largely dependent on age. Through play, young bears in zoos develop strong bonds with one another, whereas older animals appear unable to develop stable social relations with individuals of the same sex. Socially bonded males often share mates. The intolerance and aggression seen between wild males during mating season was observed in non-bonded captive brown bears (Colemenares and Rivero, 1983).

Relationships among *U. arctos* depend largely on spacing and mutual avoidance, thus limiting aggressive encounters. Highest ranking animals are dominant adult males, then females with young, followed by subadults (Craighead, 1979; Nowak and Paradiso, 1983). In areas of abundant food, large, aggressive individuals have priority and subordinate animals feed in the absence of dominant individuals. Occasionally, fights may result in the death of smaller bears (Craighead, 1976; Murie, 1985).

Newborn young and, occasionally, females are preyed upon by large males during the breeding season, so families tend to avoid crowded areas (Dean et al., 1986; Murie, 1985). Females with young will attack and sometimes kill a male that approaches too closely (Craighead, 1979; LeFranc et al., 1987).

Behavior of *U. arctos* is unpredictable, and because of their great strength, a bite or swipe with a paw can cause a major injury to humans. A female with young should always be avoided, as should brown bears that are eating or guarding carrion. Animals conditioned by handouts and accessible garbage learn to associate food with people, lose their avoidance behavior toward man, and may become directly aggressive (Craighead, 1979; Herrero, 1985; Murie, 1985). Brown bears quickly learn and revisit locations of abundant food (Knight et al., 1988; Servheen, 1983). In Yellowstone National Park, brown bears established a pattern of movement to and from garbage dumps during a period of 60-80 years. Due to their strong homing instinct, many relocated brown bears return to their original home sites and are killed (Knight et al., 1988; Miller and Ballard, 1982). Non-lethal techniques for controlling problem bears include ammonium hydroxide balloons, capsicum products, household chemicals, commercial repellents, acoustic, visual, explosive, and projectile repellents (LeFranc et al., 1987; Miller, 1983).

Brown bears may cache food to hide it from competitors or to slow decomposition. After covering food with sod and debris they often lie on top or next to the dirt pile (Dean et al., 1986; Murie, 1985). A brown bear guarding a cache often will chase or attack any intruder. Caching has not been observed in areas of abundant food (Elgmork, 1982). Brown bears often construct day beds in dry, sheltered spots with good visibility close to feeding areas (Craighead and Craighead, 1972; Murie, 1985).

Activity of *U. arctos* varies with environmental conditions, abundance of food, and human activity. In Yellowstone National Park, brown bears are active day and night in spring when food is relatively scarce, but mainly at night in summer (Craighead and Craighead, 1972). At McNeil Falls, Alaska, activity was observed at all hours (Egbert and Stokes, 1976). In more southerly regions, greater human activity may cause brown bears to be more secretive and thus more nocturnal (Elgmork, 1987). In Trentino, Italy, peak activity occurred at 0500-0800 h and 1800-2300 h (Roth, 1983).

Ursus arctos communicates by smell, sight, and sound, but like other fissipeds and solitary animals, it relies largely on olfaction (Peters and Wozencraft, 1989). At close range, body orientation conveys information. Dominance is demonstrated by frontal orientation and approach, with neck outstretched, ears back, and muzzle displaying canines. Subordinates assume lateral orientation with head kept low or turned away; they often sit, lie down, or back away before contact occurs (Schaller et al., 1985; Stonorov and Stokes, 1972). Threats and fighting occur between animals of similar social status, age, and sex. In fights, paws are used to strike the opponent, usually in the chest and shoulder regions and biting usually is directed towards the head and neck (Egbert and Stokes, 1976; Schaller et al., 1985). Brown bears do not vocalize much, except when wounded, threatened, or attacked (Craighead, 1979; Stonorov and Stokes, 1972). Distress calls are made by adults in pain, and by neonates and juveniles when hungry, cold, hurt, or separated from mother and siblings. No acoustic signal specific to the mother is known in fissipeds (Peters and Wozencraft, 1989). Apprehensive animals may huff and snort, while offensive threats are usually accompanied by growling and roaring (Schaller et al., 1985). Chuffing, a series of brief low-intensity sounds caused by a forceful exhalatory sound combined with a popping noise produced by movement of lips and cheeks, is a friendly, close-contact call made by adults and juveniles

of both sexes. Chuffing is used in greeting, coaxing, appeasement, during courtship and mating, and between a female and her young (Peters, 1984; Peters and Wozencraft, 1989).

Visual and olfactory cues are produced on trees by rubbing, biting, clawing, and striping tree bark. Marked trees demark territory, advertise sexual condition, or serve as grooming stakes. Trails are marked by rolling on the ground, urinating, and defecating (LeFranc et al., 1987).

Denning is an adaptation to seasonal changes in food availability and for birth of tiny young incapable of thermoregulation (Bunnel and Hamilton, 1983). In late autumn, winter dens are sought in mountainous and timbered areas, far from human disturbance. Brown bears may dig their own dens, sometimes in advance of winter sleep (Craighead and Craighead, 1972; Murie, 1985) or utilize natural caves and rocksplits (Lentfer et al., 1972; Reynolds et al., 1976; Schoen et al., 1987). Den construction improves with experience and dens may be reused. Dens are dug on well-drained sites, but size and shape of dens varies. In Yellowstone National Park, the den chamber averages 142 by 135 by 94 cm. Den entrances may lead directly into the chamber or have entrance tunnels. In more southerly regions, brown bears den on north-facing slopes to protect their dens against mid-winter thaws and flooding (Craighead and Craighead, 1972). In the Brooks Range, Alaska, mid-winter thaws pose no problem and 90% of dens are located on southerly slopes (Reynolds et al., 1976). Brown bears sleep on smooth dirt floors, beargrass, spruce, or fir boughs, and pregnant females cover the ground with mosses and grasses (Craighead, 1979). Dens are not defended against other brown bears. Brown bears with sufficient fat become lethargic and move to denning areas earlier, whereas individuals with insufficient fat reserves continue feeding until low temperatures and snowstorms force them to den. Interruption of winter sleep or den abandonment can be risky for adults, but often is fatal to young. In spring, males leave their dens first, while females with new young are last to emerge (Craighead and Craighead, 1972; Schoen et al., 1987).

GENETICS. Ursus arctos has a diploid number of 74 chromosomes consisting of 72 autosomes (60 acrocentric and 12 metacentric or submetacentric) and two sex chromosomes (a large metacentric X and small acrocentric Y). Most Ursidae have similar karyotypes with the exception of Tremarctos ornatus, from South America, which has a diploid number of 52 chromosomes (Wurster, 1969).

In captivity, crosses between *U. arctos* and *U. maritimus* have produced fertile offspring (Davis, 1950). Hybrids of brown and black bears have been recorded, but the young died when just a few weeks old (Gray, 1954).

REMARKS. Ursus arctos also is commonly called grizzly, griz, Old Ephraim, Moccasin Joe, range bear, great white bear, roach-back, and silvertip (Brown, 1985; Craighead and Mitchell, 1982; Jonkel, 1987). The term brown bear often refers to coastal bears of North America and European brown bears, while grizzly bear is used to describe brown bears living in the interior of North America (Jonkel, 1987).

I thank K. F. Koopman for assistance with the synonymy, the reviewers and editors for their helpful comments, and M. T. Arts for proofreading earlier drafts of the manuscript.

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