

HUMAN IMPACTS ON BEAR HABITAT USE¹

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Abstract: Human effects on bear habitat use are mediated through food biomass changes, bear tolerance of humans and their impacts, and human tolerance of bears. Large-scale changes in bear food biomass have been caused by conversion of wildlands and waterways to intensive human use, and by the introduction of exotic pathogens. Bears consume virtually all human foods that have been established in former wildlands, but bear use has been limited by access. Air pollution has also affected bear food biomass on a small scale and is likely to have major future impacts on bear habitat through climatic warming. Major changes in disturbance cycles and landscape mosaics wrought by humans have further altered temporal and spatial pulses of bear food production. These changes have brought short-term benefits in places, but have also added long-term stresses to most bear populations. Although bears tend to avoid humans, they will also use exotic and native foods in close proximity to humans. Subadult males and adult females are more often impelled to forage closer to humans because of their energetic predicament and because more secure sites are often preempted by adult males. Although male bears are typically responsible for most livestock predation, adult females and subadult males are more likely to be habituated to humans because they tend to forage closer to humans. Elimination of human-habituated bears predictably reduces effective carrying capacity and is more likely to be a factor in preserving bear populations where humans are present in moderate-to-high densities. If humans desire to preserve viable bear populations, they will either have to accept increased risk of injury associated with preserving habituated animals, or continue to crop habituated bears while at the same time preserving large tracts of wildlands free from significant human intrusion.

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Humans (*Homo sapiens*) have preempted a large part of the Earth for their use. The attendant transformation and depletion of ecosystems has resulted in extinction rates comparable to any prehistoric mass extinctions. Increasingly, humans have turned their attention to preserving the remaining flora and fauna. At the same time, even in cultures where the impetus to preserve diversity has been greatest, humans have been reluctant to sacrifice their prerogative to use lands for their exclusive benefit (Ehrenfeld 1972). Consequently, much research has been undertaken to determine the level and nature of human use that is compatible with retention of extant flora and fauna. This research has characteristically fit into a minimalistic approach to managing wildlife habitat; that is, how much can we do and still retain a diversity of species sufficient to satisfy our needs?

For bears (Ursidae), this minimalistic approach is evident in harvest strategies, and park and wildlands management. Increasingly sophisticated management has entailed cumulative effects analysis (CEA) (Christensen 1986); that is, how do bear populations respond to the interacting total of human activities on a given meaningfully scaled piece of ground, and does that fit into our management objectives? How bears respond to humans and their foods is critical input to the CEA and bear management in general. The most sensitive management requires input concerning differences in bear response among different sex and age classes, given that survivorship and productivity of adult females are apparently critical to population viability (Knight and Eberhardt 1985, Yodzis and Kolenosky 1986, Ramsay and Stirling 1988).

In this paper, I summarize and interpret how bear habitat use is affected by humans and their foods. I use

information pertaining mainly to brown (*Ursus arctos*) and American black (*U. americanus*) bears; where applicable I also include information on polar bears (*U. maritimus*) and Asian black bears (*Selanarctos thibetanus*). Humans affect bears many ways. Generally, bear response to humans and their alterations is a function of food biomass changes, bear tolerance of humans and human-related habitat changes, and human tolerance of bears. Where and how bears use their habitat is an integration of these factors. I use this framework to structure my presentation of results and interpretation.

LITERATURE REVIEW

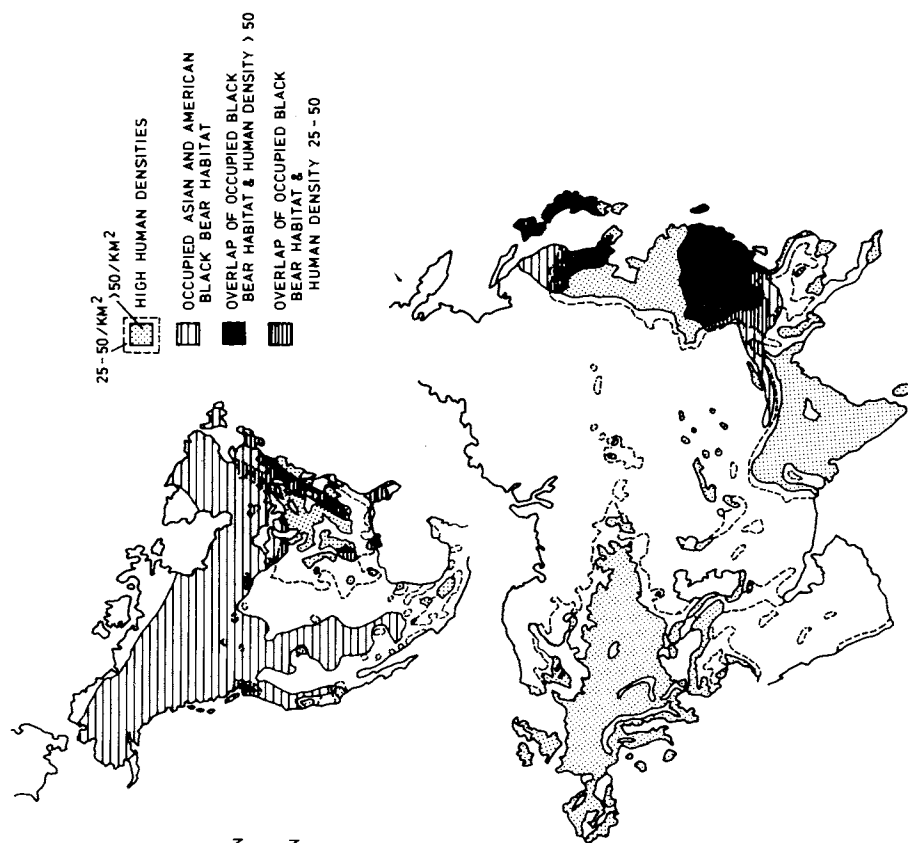
Distribution of Bears and Humans

There is relatively little overlap between occupied bear habitat and high human densities ($>25/\text{km}^2$) (Fig. 1). This is especially true for brown and polar bears and in North America, although even European brown bear populations are typically centered on wildlands and areas of low-to-moderate human densities. The Asian black bear exhibits the greatest proportionate overlap of occupied range with high densities of humans, although a more refined distribution map for the Asian black bear will likely show southern Chinese populations restricted to islands of forested higher relief terrain (cf. Servheen 1990). The Asian black bear is notably absent from east-central China, where islands of suitable habitat are absent.

This mutually exclusive distribution of bears and high densities of humans has probably resulted from niche differences and, more importantly, from human intolerance and predation. Humans inhabit extensive areas never occupied in recent millennia by bears. Humans have also eliminated bears from many areas, including much of temperate eastern North America (cf. Cowan

¹ Invited paper

Black bear



Brown bear

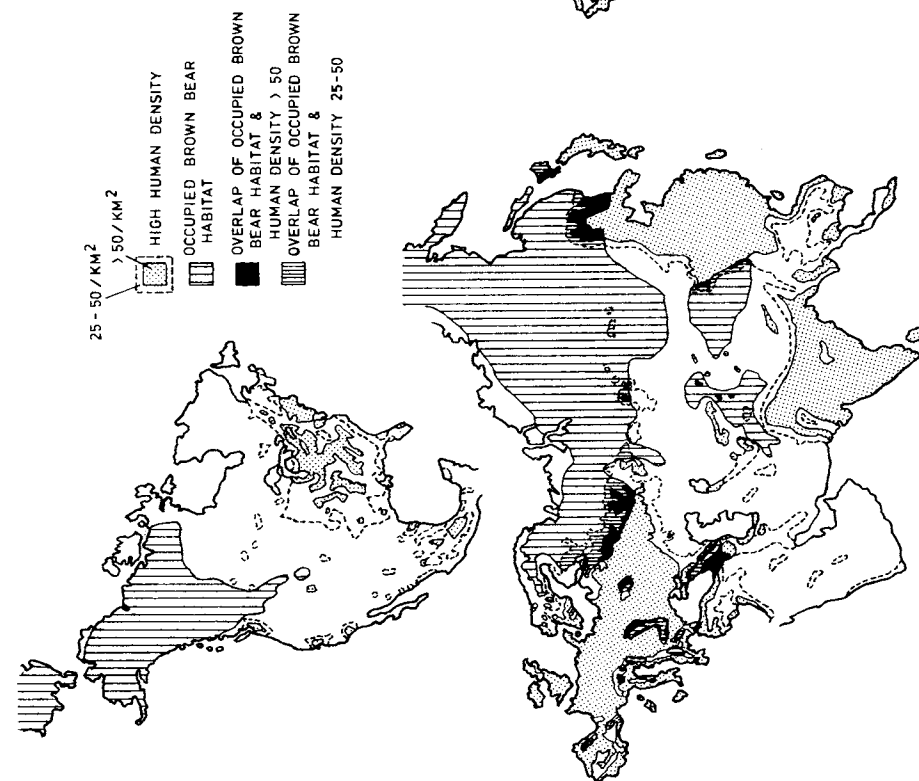


Fig. 1. Distribution and overlap of high human densities and occupied brown and black bear habitat (Banfield 1958, Bromlei 1965, Cowan 1972, Curry-Lindahl 1972, Herrero 1972, Zunino 1975, Vereschagin 1976, Yi-Ching 1981, Rand-McNally 1986, Clevenger et al. 1987, Elgmork 1987, Jakubiec and Buchalczyk 1987, Verstraal 1988).

1972, Burk 1979) and Asia (Servheen 1990), and most of Europe (Curry-Lindahl 1972). The elimination of grizzly bears from virtually all of the western United States in the absence of high human densities and extensive cropland, between 1850 and 1930, reflects an extreme case of human intolerance. Because of these exterminations, much bear habitat is currently unoccupied by bears because their progenitors were killed by humans.

Native Food Biomass and Habitat Structure

Pathogens and Habitat Conversion.—Availability of bear foods within occupied bear habitat has been most dramatically affected by intentional or accidental elimination by humans. This has been effected by large-scale conversion of land and waterways to intensive human use and by introduction of exotic pathogens.

In the course of hydroelectric development and manipulation of fisheries, humans have eliminated or reduced salmonid spawners in several major drainages occupied by bears, including the Columbia River headwaters (Butterfield and Almack 1985, Davis et al. 1986), and rivers in the northeastern United States (Cronon 1983), California (Piekielek and Burton 1975), Kamchatka (Lazarev 1978), and Hokkaido (Aoi 1985). This has affected a major bear food in these areas, and contributed to the decline or extinction of bear populations (Lazarev 1978, Davis et al. 1986).

In North America, humans introduced 2 tree pathogens that had substantial impacts on bears. Between 1904 and 1950 virtually all of the previously abundant American chestnuts (*Castanea dentata*) were eliminated by the chestnut blight (*Endothia parasitica*) (Harlow et al. 1979). Chestnuts were a prolific and regular fruit producer used by bears (Bennett et al. 1943, Harlow et al. 1979), and although oaks increased after the demise of chestnuts (Callaway and Clebsch 1987, Greller 1988), loss of the chestnuts probably resulted in less productive bear habitat. Similarly in western North America, white pine blister rust (*Cronartium ribicola*) has virtually eliminated whitebark pine (*Pinus albicaulis*) in wetter areas where seeds of the pine are an important bear food (Arno 1986).

Conversion of bear habitat to intensive agriculture, industry, and human habitation has been and continues to be widespread, with negative impacts on bear populations; as in California (Lawrence 1979) and Estonia (Kaal 1976). Loss of important foraging and refuge areas due to drainage and development of wetlands is an especially critical issue in both the United States (Hugie 1979, Hamilton and Marchinton 1980, Manville 1983, and others) and Europe (Stroganov 1962, Novikov et al.

1969a, Isakovic 1970, Pulliainen 1986, and others). In the Soviet Union, drainage has affected ca. 13 million ha (Ceriomuskin and Burminova 1969), and has negatively impacted brown bear populations (Sharafutdinov and Kortokov 1976, Vereschagin 1976).

Disturbance and Regeneration Cycles.—Humans have contributed to the frequency and intensity of fires under primeval conditions in most ecosystems (Wilhelm 1973, Russell 1983, Christensen 1988, Peet 1988); in this sense, humans have influenced bear habitat for millennia. Human-caused fires were more of a factor in inherently fire-prone areas such as coastal southeast North America and lower elevations of the Rocky Mountains, and were more common near traditional encampments (Russell 1983, Arno 1985, Gruell 1985). Primeval humans generally accentuated natural fire cycles in a way that reflected the dependence of humans on natural habitat cycles (Russell 1983, Arno 1985, Lewis 1985). With the exception of recent centuries, wildland fire cycles, including the human factor, have been more or less stable for at least 4,000 to 6,000 years in forested bear habitat (Wilhelm 1973, Wright 1974, Arno 1985, MacDonald 1987, Christensen 1988).

Primeval disturbance cycles have been sometimes dramatically changed by agricultural and technological human cultures. These changes have been effected by habitat alterations or deliberate fire control. Between 85 and 98% of virgin forests in the United States were harvested since European settlement, largely between 1800 and 1900 (Thomas et al. 1988). In many parts of the western and northern United States, this widespread timber harvest resulted in unnatural accumulation of fuels, that in turn precipitated unusually widespread and intensive fires (Whitney 1987, Peet 1988). In the north-central and northeastern United States, oak forests that replaced most presettlement pine forests after these fires (cf. Dahlberg and Guettinger 1956, Cronon 1983, Whitney 1987) were probably more productive bear habitat. In recent years, fire control has allowed maturation and, in places, senescence of forest stands initiated by 19th-century, human-caused disturbances. Simultaneously, initiation of seres has become dependent on more regulated smaller-scale timber harvest.

In southeast North America, European settlers tended to perpetuate Indian fire management practices. Frequent fires enhanced forage quality, fruit production of trees, and efficiencies of acorn and chestnut collection (Wilhelm 1973, Christensen 1988). These low-intensity fires also maintained pine forests at the expense of oaks (Waggoner 1975, Callaway and Clebsch 1987, Christensen 1988) and were probably detrimental to bears

especially on the coastal plains (cf. Maehr and Brady 1984). Since effective fire control began in the early 1900's, many pine forests have succeeded to oak (Waggoner 1975, Christensen 1988). At the same time, extensive pine plantations have been established and maintained by prescribed fire (Dixon 1965).

Vegetation succession on abandoned cropland is another factor introduced by humans in the landscape dynamics of eastern North America. Cropland abandonment increased since 1900, and typically resulted in highly productive bear habitat during early and mid-successional stages of recovery (cf. Alt 1980b, Keever 1983, Pelton 1987, Greller 1988).

Western and boreal Canada is in the early stages of widespread timber harvest (cf. Horejsi 1986) and effective fire control. In most of Canada as well as in wetter or higher elevation regions of the western United States, 40 to 60 years of effective fire control by humans have probably not had dramatic impacts on vegetation dynamics and mosaics, given 100- to 500-year natural fire cycles in most of these regions (Romme 1982, Foster 1985, Dyrness et al. 1986, Franklin 1988).

Assessing the impacts of human-caused changes in disturbance cycles depends on our understanding the comparability of timber harvest and wildfire effects. Several generalizations can be made about timber harvest effects on production of bear foods. Most post-harvest site scarification or harvest on dry or exposed sites is detrimental. Scarification eliminates most berry-producing shrubs for several decades (Minore et al. 1979, Zager 1980, Martin 1983), and overstory removal on dry sites removes the protective canopy that would otherwise persist with typically frequent and low intensity wildfires. Timber harvest followed by no post-harvest treatment or by broadcast burning produces the greatest amounts of bears foods, especially on moist-to-wet sites (Minore et al. 1979, Zager 1980, Bratkovich 1986, Hillis 1986, and others). Early successional communities following these silvicultural practices are most similar to those precipitated by wildfire (Martin 1983, Zager et al. 1983). Thinning also tends to enhance bear habitat productivity, and again more so on wetter sites (cf. Pelton 1979, Alaback 1984, Urness 1985, Young and Beecham 1986); fruit production by trees typically increases with thinning (Wilhelm 1973, Pelton 1979).

Most benefits associated with timber harvest are negated by intensive management designed to accelerate crown closure and eliminate competing vegetation. This usually involves scarification, planting, and control of shrubs and herbs, and is more common in the most productive timber producing areas where the economic

incentive for more intensive management exists. This is especially true of Pacific coastal North America, although more intensive silviculture is being increasingly practiced elsewhere. Very little bear food exists in young closed-canopy forests in wet Pacific coastal regions (A. Hamilton 1987, pers. commun.). Most shrubs in these regions are susceptible to herbicide control (Gratowski 1978, Lawrence 1979), and even shrubs that resprout after herbicide treatment tend to be less vigorous and produce substantially less fruit (Stewart 1974, Gratowski 1978). The same is true of shrubs important to bears in eastern deciduous and mixed-conifer regions of North America (cf. Gill and Healy 1974, Hall and Nickerson 1986, Rogers 1987), and in boreal regions (cf. Hall and Shay 1981).

Ultimately, the effects of timber harvest practices on bear food biomass in any given area depend on the autecology of individual bear foods. In areas where arboreal species contribute substantial amounts of food, management favoring forest development is beneficial. However, for stone pines (*Pinus*, subsection *Cembrae*), the potential benefits of timber harvest are very limited given the 100 years or more generally required for stands to start producing significant seed biomass, and the subsequent long-term productivity of a stone pine forest (Iroshnikov 1963, Kozhevnikov 1963, Arno and Hoff 1989). However, in most regions productivity of bear habitat is keyed to the first 100 years of succession (cf. Fowells 1965, Dyrness 1973, Gill and Healy 1974, Lindzey et al. 1986, Greller 1988, and others), and reflects responses by fire-adapted, fruit-producing species (Wright 1972). Again, wet Pacific coastal areas pose an exception to this general pattern (Alaback 1984, Lindzey et al. 1986, Hamilton 1987) (Fig. 2).

Timber harvest also affects availability of denning trees. Large-diameter hollow trees are preferentially used for den-sites by Asian and American black bears in temperate regions (Bromlei 1965, Jonkel and Cowan 1971, Lindzey and Meslow 1976, Hamilton and Marchinton 1980, Wathen et al. 1986, and others). Retention and production of these denning trees is not compatible with the 70- to 150-year timber rotation practiced in most temperate commercial forests (cf. Burns 1983). Loss of large-diameter, old-growth den-site trees is probably not critical to, but at the same time may stress, black bear populations (Lindzey and Meslow 1976).

In most areas, the vegetation mosaic differs between a natural fire and a fire control/timber harvest regime. Historically, European settlers and developers tended to reduce diversity of vegetation seres over a large area. As a result, the size of vegetation patches increased and

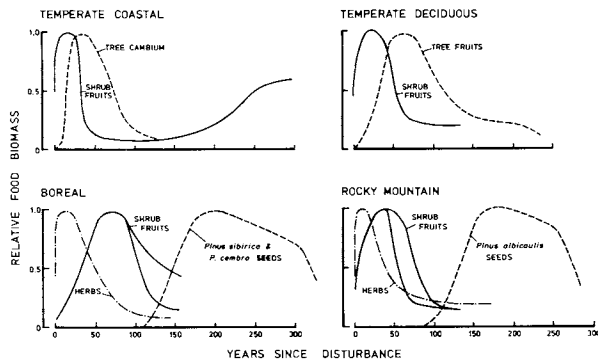


Fig. 2. Relative bear food production under primeval conditions in different vegetation strata for 4 major ecosystems. Production is scaled from 0-1, and is relative to each stratum and ecosystem. These graphs synthesize a review of literature that pertains to vegetation succession in each of these ecosystems. References can be obtained from the author.

probably rendered temperate bear populations more vulnerable to successional change. On the other hand, abandoned fields reintroduced a smaller scale mosaic. Recent silvicultural practices also emphasize smaller harvest units and "sustained yield" of wood products (cf. Burns 1983). This has resulted in an unstable vegetation mosaic of diverse-aged successional communities (Franklin and Forman 1987). The more recent tendency to generate smaller scale mosaics is also constrained by existing forest structure.

Forest management practices have almost certainly contributed to epidemic bear use of tree cambium in commercial forests. In coastal Washington state, widespread timber harvest at low elevations during the late 1800's and early 1900's produced a disproportionately large area of productive shrub fields, and local bear populations consequently increased (Poelker and Hartwell 1973, Lindzey et al. 1986). In most instances these shrub fields were succeeded without replacement by closed-canopy, pole-size forest. Local bear populations were likely under nutritional stress and probably reverted to use of secondary or successional abundant foods, including tree cambium. In wet coastal areas, tree diameter and age classes used most heavily by bears succeeded and replaced productive shrub fields (Fig. 2) (Fritz 1951, Glover 1955, Poelker and Hartwell 1973). This may explain the otherwise unexplained epidemic use of cambium in certain coastal locales. Poelker and Hartwell (1973) speculated that cambium use in western Washington was related to the lack of *Rubus spectabilis* in bear diets. *R. spectabilis* is abundant almost solely in open, typically newly clearcut areas (Franklin and Dyrness 1969, Smith 1978, Alaback 1984). In Honshu, Japan, Asian black bear use of tree cambium is also related to

widespread timber harvest (Azuma and Torii 1980, Furubayashi et al. 1980). Bears use commercial timber stands adjacent to areas being clearcut and generally in areas where timber harvest and manmade stands are extensive. Bear use of cambium on Honshu is probably related not only to landscape dynamics of food biomass, but also to avoidance of areas without cover (i.e., recent clearcuts).

Black bears will also very likely suffer from continued major habitat degradation in western Oregon and Washington. Within the next 50 years, unproductive mid-successional stages will increase from ca. 20 to 65% of the total forested landscape due to widespread historical and contemporary old-growth clearcutting (Harris et al. 1982). This shift will undoubtedly stress bear populations, even given continued propagation of early successional shrub fields. In addition, shrub control is widely practiced on commercial forest lands in western Oregon and Washington (cf. Dimock et al. 1976) and berry production on new seres will often not be realized.

Pollutants and Toxins.—Bear food biomass and habitat structure have been, and will continue to be, affected by atmospheric pollutants. Increased atmospheric carbon dioxide and trace gases, "smog", and acid deposition have already altered or promise to alter bear habitat. The effects of acid precipitation (pH < 5.6) on overall vegetation structure and productivity have not yet been conclusively documented (Smith 1981), although decline of spruce (*Picea* spp.) in western Europe and the northeastern United States has been almost certainly tied to acid deposition (Tomlinson 1983). On the other hand, significant air pollution impacts on vegetation have been conclusively documented (Smith 1981), but are restricted to limited areas downwind of smelters and major metropolitan areas. Generally, vegetation diversity decreases (Guderian and Kueppers 1980, Chubarov 1986) along with abundance of many fruit-producing species (cf. Vander Kloet and Hall 1981, Chubarov 1986). Although abundance of fruit-producing species may increase in some situations (cf. Kickert and Gemmill 1980, Shugart et al. 1980), fruit production of both shrubs and trees typically declines due to leaf damage and stresses associated with decreased photosynthetic efficiency (Cowling and Dachinger 1980, Scale 1980, and others). Typically, high levels of air pollution negatively affect bear food biomass, but over a small portion of occupied bear habitat.

Increased atmospheric CO₂ and trace gas concentrations will likely increase the Earth's temperature 1 to 5 C by the end of this century (Dickenson and Cicerone 1986). Temperature increases will be greatest at mid- to

high latitudes (Dickenson and Cicerone 1986), in the range of most occupied bear habitat. By the 22nd century, average temperatures may be higher than any in the last 10 million years (Dickenson and Cicerone 1986, Kerr 1986). In response to this change, vegetation zones would shift north, and shrink or expand. In Canada, greatest increases are projected for grassland, cool temperate forest, and maritime boreal forest, and greatest decreases for dry and moist continental boreal forest (Rizzo 1988, Zoltai 1988). Because grasslands and maritime boreal forest (Payne 1978) are typically not productive bear habitat, and cool temperate forest is likely to increase in the range of black bears, grizzly bears would likely suffer from these predicted changes in North American vegetation. The increasing number of confined and isolated bear populations would also be at greater risk with shifts in vegetation zones, given the static boundaries of their circumscribed range.

Other miscellaneous pollutants and toxins pose risks to bears. Polar bears could be greatly affected by ocean-borne oil spills as a result of thermoregulatory and metabolic stresses from toxicity of crude oil ingested during grooming (Anonymous 1981). Polar bears could also be indirectly affected by seal population declines. The risk of oil spills to any given polar bear population would be a function of the prevailing ocean current direction (Stirling et al. 1980, Stirling and Kiliaan 1980). Historically, strychnine poisoning killed a large number of grizzly bears in North America, whether by the intention of humans or not (Storer and Trevis 1955, Brown 1985). However, contemporary use of strychnine to control rodent populations in the Yellowstone area has not been considered a threat to bears (Barnes et al. 1980).

Ungulate Populations.—Bear populations have likely been influenced by human management of ungulate populations (Peek et al. 1987). Ungulates are a potentially important and high value diet item (Mealey 1980, Bunnell and Hamilton 1983), and bears preferentially use meat where it is available. This meat is often from scavenging on ungulate carcasses, but bears are also known to kill ungulates outright (Filinov 1980, Cole 1972, Semenov-Tian-Shanskii 1972, and others).

Ungulate populations have been dramatically affected by humans, beginning perhaps as long ago as the Pleistocene (Martin 1984). The extent, local densities, and sex and age classes of populations have all been manipulated. Generally, populations of large ungulates have not been compatible with intensive agriculture and high human densities (Reed 1981, Bryant and Maser 1982). But ungulates have fared better than bears and wolves, and rarely have large ungulates been eliminated and these

carnivores survived.

Typically, bear populations are benefited by high ungulate densities, whereas human hunting of ungulates can be both a benefit and detriment to bears. Density, productivity, and distribution of bears have been positively related to ungulate densities (Kaal 1976, Mattson et al. 1987, Reynolds and Garner 1987). However, even at moderate or high densities, a human-harvested ungulate population is likely to be less productive for bears. On the average, hunted ungulate populations are healthier and more vigorous, and significantly below ecological carrying capacity compared to an unhunted population (Connolly 1981, Mohler and Toweill 1982). Consequently, fewer winter-killed and weakened animals are available to bears during the spring. With harvest that usually emphasizes bulls, fewer adult male ungulates are also critically weakened by the rut and so vulnerable to bear predation. On the other hand, ungulate harvest by humans can benefit bears primarily by generating carcass remains and wounded animals (Haglund 1968, 1974; Servheen et al. 1986).

Human Foods

Agricultural Crops.—Bears make substantial use of agricultural crops wherever they are available. Bears principally use apiaries and cereal, fruit, and forage crops. Among cereal crops, bears make greatest use of oats (*Avena sativa*) and corn (*Zea mays*). Bear use of corn was mentioned in 11 and oats in 14 research articles (Fig. 3). Bears make less frequent or incidental use of barley (*Hordeum vulgare*) and wheat (*Triticum aestivum*). Peak use of oats and corn begins at the "milk" stage and continues until harvest, usually August through September for oats (Spencer 1955, Novikov et al. 1969b, Kaletskaya and Filinov 1986, Cicnjak et al. 1987), and fall (Davenport 1953, Alt et al. 1977, Aoi 1985, Garner and Vaughan 1987) into winter (Landers et al. 1979) for corn. Least corn use occurs in July in eastern North America, as a result of preference for native fruits at that time of year (Alt et al. 1977, Landers et al. 1979). Oats grow more commonly in areas with cool, and corn in areas with hot, growing seasons (Stoskopf 1985); bear use coincides with this distribution (Fig. 3). Use of corn appears to be more common than use of oats in areas where both crops occur and is probably a consequence of corn's greater usable energy concentration (cf. Subcommittee on Swine Nutrition 1979, Stoskopf 1985).

Usable energy does not explain infrequent bear use of wheat, the most widespread of northern hemisphere grain crops. Metabolizable energy for wheat is comparable to corn, and yet recorded instances of wheat use by bears are

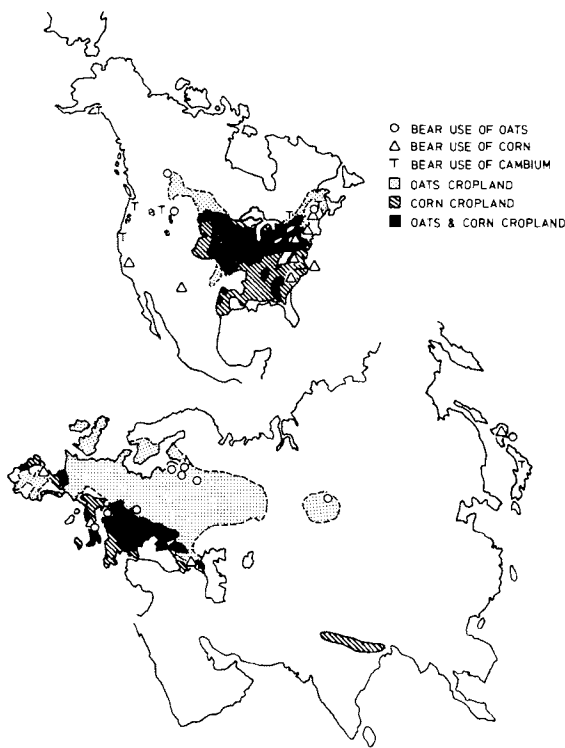


Fig. 3. Main distribution of oats and corn crops, and recorded instances of corn and oats use by bears (Ceriomuskin and Burminova 1969, C.I.A. 1974). Recorded instances of "epidemic" cambium use are also mapped.

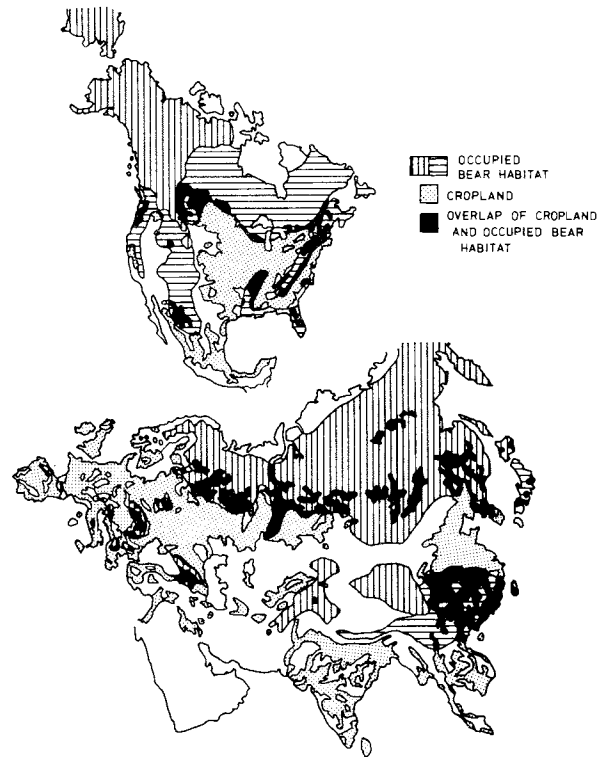


Fig. 4. Distribution and overlap of cropland and occupied bear habitat (Reader's Digest Assoc. 1985).

rare. The difference may be due to characteristics and distribution of wheat and oat fields. There is not a substantial difference in overlap between bear distribution and major oat and wheat cultivation. However, oats are more commonly cultivated in small forest fields and wheat in areas of extensive contiguous cropland (Symons 1972). Most bear use of oats and corn occurs in isolated forest fields or close to cover in more extensive cropland (Ognev 1931; Davenport 1953; Spencer 1955; Novikov et al. 1969a,b; Landers et al. 1979; Klenner 1987). Wheat may be less available to bears because there is typically unfavorable juxtaposition of wheat fields and cover.

Domesticated grains are potentially significant to bears. Oats are especially important to some European brown bear populations (cf. Kaal 1976, Cicnjak et al. 1987), and the availability of oats apparently influences bear density (Novikov et al. 1969a) and movements (Kaletskaia and Filinov 1986). Corn is of apparently equal importance to some eastern North American black bear populations (cf. Landers et al. 1979).

Bear use of grain crops is primarily restricted by the absence of bears from most intensively cultivated areas (Fig. 4). Most crop use occurs at the interface of wild- and

croplands. Grain crops are undoubtedly high quality bear food; crude protein content ranges from 9 to 13% and starch content from 54 to 73% for major northern hemisphere grain crops (Subcommittee on Swine Nutrition 1979). However, bear use of this high quality food in most bear habitat is prohibited by human intolerance.

Bear use of domesticated fruits, primarily apples (*Malus domestica*) and secondarily plums and pears (*Prunus* spp. and *Pyrus communis*), is also widespread. Domesticated fruits are known to be a major potential part of bear diets in western Montana (Servheen 1983), Shenandoah National Park (Garner and Vaughan 1987), and Pennsylvania (Bennett et al. 1943). Use generally peaks July through October, after the fruit crop ripens (Spencer 1955, Servheen 1983, Cicnjak et al. 1987, Garner and Vaughan 1987). Bears typically make greatest and most consistent use of "wild" trees and abandoned orchards (Bennett et al. 1943, Spencer 1955, Zunino and Herrero 1972, Manville 1983, Garner and Vaughan 1987). Use of maintained orchards more often occurs during years when native bear foods are in short supply (Slobodyan 1976, Novick and Stewart 1982).

Bears have used apiaries for centuries, wherever they

are accessible. Jorgensen et al. (1978) reviewed bear use of apiaries, in the context of human-bear conflicts. Generally, timing of bear use varies among regions, but is consistent with peak honey production.

Introduced forage, principally legume crops, receive substantial use by some bear populations, as in the Swan Hills of Alberta (Nagy and Russell 1978), northwestern Montana (Jonkel and Cowan 1971), and Yellowstone National Park (Graham 1978). Mixes of introduced legumes and grasses are especially significant during years when native fruits or seeds are in short supply.

Domestic Animals.—Bears use most domesticated animals common to the northern hemisphere (sheep [*Ovis aries*], cattle [*Bos taurus*], swine, horses [*Equus caballus*], and goats [*Capra bircus*]). Significant bear use of sheep has been recorded in western North America (Jorgensen et al. 1978, Johnson and Griffel 1982, Jorgensen 1983, Brown 1985), and for isolated European bear populations in Spain (Clevenger et al. 1987), the Pyrenees (Faliu et al. 1980, Roben 1980, Berducou et al. 1983, Camarra 1986), Italy (Krott 1962, Zunino and Herrero 1972, Zunino 1981), and Norway (Mysterud 1973, 1976, 1980a). More incidental use of sheep occurs elsewhere. Bear predation on sheep in all of these areas occurs primarily from July or August through September, coincident with the tenure of sheep on summer range. While on summer range, sheep are in closer contact with bears and are less closely attended than any other time of year (Mysterud 1973, Horstman and Gunson 1982, Johnson and Griffel 1982, Jorgensen 1983, Camarra 1986). In Alberta, Horstman and Gunson (1982) speculated that greater proportionate bear predation on sheep compared to cattle was largely a result of sheep being stocked in more remote areas. In the Pyrenees, sheep comprise a significant part of the overall summer bear diet (Faliu et al. 1980, Berducou et al. 1983), and in other areas, a significant part of individual bear diets (Mysterud 1980a,b; Jorgensen 1983). Bears tend to more often kill ewes than lambs (Brown 1960, Mysterud 1973, Horstman and Gunson 1982) and occasionally engage in mass killing of sheep (Mysterud 1976, Jorgensen et al. 1978).

Significant use of cattle has been noted throughout the Soviet Union and in western North America, more often by brown bears than black bears. For a brief period in the western United States, cattle constituted an important bear food and may have contributed to bear population increases (Bailey 1931, Storer and Trevis 1955, Brown 1985). Timing of bear predation on cattle varies more than for predation on sheep, but generally coincides with dispersal of cattle on summer ranges (Murie 1948, Knight and Judd 1983), or with spring and fall when high quality

native foods are scarce (Eide 1965, Brown 1985). As with sheep, predation on cattle appears to be greater in more remote areas with greater cover (Novikov 1956, Novikov et al. 1969a, Bjorge 1983). Bears often use carrion from cattle that have been poisoned by native toxins (Jorgensen et al. 1978, Brown 1985, Greer 1987). Much of this scavenging has been falsely interpreted as predation (Knight and Judd 1983, Brown 1985).

More than predation on sheep, bear predation on cattle appears to vary with availability of high quality native foods. In the Soviet Union, cattle and horse predation consistently increases during the summer and fall of years when high quality native foods are scarce (Ognev 1931, Bromlei 1965, Ustinov 1965, Shartafutdinov and Korotkov 1976, and others). Similarly, LeCount (1980) attributed lack of conflict between black bears and livestock in central Arizona to high quality bear habitat.

Bears exhibit distinct preferences for different species and age classes of domestic livestock. The order of preference from greatest to least is roughly: swine, ewes, lambs, calves and yearling cattle, cows, horses, and bulls. Several authors have observed that bears prefer swine over all other livestock (Storer and Trevis 1955, Brown 1985) or that swine are disproportionately preyed upon by bears (Brown 1960, Slobodyan 1976, Horstman and Gunson 1982). Aside from this apparent preference, vulnerability of domestic livestock is likely a function of size-mediated bear preference, local bear density, cover, and how closely the animals are attended. Bulls appear to be nearly invulnerable to predation; sheep are killed more consistently and at higher rates than cattle (Brown 1960, Horstman and Gunson 1982, Knight and Judd 1983, and others), and calves and yearlings more often than any other class of cattle (Murie 1948, Bjorge 1983, Knight and Judd 1983).

Domestic livestock has additional, typically detrimental, effects on bears. Livestock grazing has modified vegetation composition and structure in many areas. In California, the Rocky Mountains of Montana, and the Cantabrian Mountains of Spain, livestock browsing has reduced or eliminated recruitment of desirable tree species. Oaks have been most affected in California and Spain (Rossi 1980, Clevenger et al. 1987, Reed and Sugihara 1987) and aspen most affected in Montana (Aune 1985, Stivers 1988). Some studies indicate that in the absence of fire, livestock grazing reduces competition with mature mast-producing oaks in California (Duncan et al. 1987, McClaran 1987), but grazing probably does not mimic fire effects in long-term oak stand dynamics. Reduction of forest cover by livestock or by humans for livestock generally makes habitat less secure, especially

for European brown bear populations (Krott 1962, Camarra 1983, Clevenger et al. 1987).

Effects of livestock grazing on ground layer bear foods are more ambiguous and largely a function of timing, location, and intensity. In Montana and Wyoming, unregulated early season grazing in riparian zones or avalanche chutes is detrimental (Mealey et al. 1977, Irwin and Hammond 1985, Stivers 1988). Sheep browsing also reduces cover and productivity of most important fruit-bearing shrubs (cf. Sharrow et al. 1989). Although heavy grazing on mountain meadows tends to reduce overall vegetation biomass (Leege et al. 1981, Ratliff 1985, Ignat'eva 1987), plant species preferred by bears (such as, dandelion [*Taraxacum* spp.], clover [*Trifolium* spp.], timothy [*Phleum alpinum*], and bluegrass [*Poa* spp.]) tend to increase in abundance (Bonham 1972, Leege et al. 1981, Ignat'eva 1987). Brown (1985) suggested that widespread "overgrazing" resulting from introduction of cattle in Arizona and New Mexico caused the loss of many bear foods either from direct use or alteration of hydrologic regimes, and reduced productivity of riparian zones. With more conservative modern-day public land management, livestock grazing probably has little direct impact on bear food biomass (Stivers 1988).

Edible Human Refuse.—Not much needs to be said about human garbage as a bear food. Bears have used edible garbage virtually everywhere it is available. Edible garbage was an important food for bear populations in Newfoundland, Canada (Payne 1978) and Yellowstone National Park (Barnes and Bray 1967, Craighead and Craighead 1971), and served as an attractant in many other areas. Meagher and Hape (1987, Yellowstone National Park files) estimated that 4,800 tons of edible garbage were available each year from open-pit dumps in Yellowstone Park during the mid-1960's. Edible garbage is a high quality food that has been shown to explain differences in weights and productivity among individual bears and populations in Michigan (Rogers et al. 1976), Minnesota (Rogers 1987), and Yellowstone Park (Stringham 1986, Blanchard 1987). In national parks, where human activity is concentrated during the summer months, peak use of garbage and human foods occurs from June or July through August (Craighead and Craighead 1971, Harms 1980, Eagle and Pelton 1983). In other areas, garbage use occurs during spring and fall, when high quality native foods are less abundant (Hatler 1972, Alt et al. 1977, Young and Ruff 1982, Nagy et al. 1983a).

Bear Behavior

Use of Human Foods.—All bears do not benefit equally from human foods. There is considerable variation in use

of human foods among species, individuals, and sex and age classes, depending on the food, season, and proximity to humans.

Generally, larger bears prey on larger animals. Adult males prey most often on cattle (Eide 1965, Horstman and Gunson 1982, Knight and Judd 1983, data from Craighead et al. 1988) and are also the typical predators on sheep (Davenport 1953, Mysterud 1980a). Subadults more commonly prey on smaller animals such as sheep and yearling cattle (Mysterud 1980a, Knight and Judd 1983), and females are consistently underrepresented as predators on domestic livestock.

Few data are available that concern differences in bear-class use of agricultural crops. However, the few observations suggest 2 hypotheses: (1) adult females more commonly use crops within established ranges (cf. Alt et al. 1977, Garner and Vaughan 1987), and (2) subadult males more often use crops (and dumps) on the periphery of occupied bear habitat (cf. Gunson 1975, Gunson and Cole 1977, Young and Ruff 1982, Klenner 1987).

In many study areas, males are disproportionately represented among bears visiting human facilities or involved in depredations. In some areas representation of males has been in the range of ca. 60-65% (Alt et al. 1977, Claar et al. 1986, Mace et al. 1987, data from Craighead et al. 1988). This disproportionality can easily be attributed to the greater probability of males encountering point or linear features as a result of typically larger range sizes (Rogers et al. 1976; Bunnell and Tait 1981, 1985) and the seasonal exclusivity of adult females associated with core use areas in some regions: Alberta (Young and Ruff 1982, Pelchat and Ruff 1986), Minnesota (Rogers 1987), arctic regions (Nagy et al. 1983a,b), and central Colorado (Haroldson, in prep.). However, the >70% male composition of bears visiting dumps or other human facilities in Minnesota (Rogers 1987), northern Michigan (Rogers et al. 1976), northern California (Piekielek and Burton 1975), New York (Black 1958), and Great Smoky Mountains National Park (Beeman and Pelton 1976, Singer and Bratton 1980) defies such an explanation. In these areas some other factor, most likely active selection on the part of males, explains the disproportionality.

A positive relationship is apparent between dominance of a bear class and favorable attributes of sites used to forage on human foods. Adult males tend to use typically larger dumps farther removed from humans (Alt et al. 1977, Tietje and Ruff 1983, Rogers 1987). In Newfoundland and in Yellowstone Park before 1970, both sexes of adults either had prerogative on edible garbage (Hornocker 1962) or were nearly sole users of

larger dumps (Payne 1978). No black bears other than large males typically used dumps in Yellowstone in the face of competition from grizzlies (Barnes and Bray 1967, Craighead and Craighead 1971). In both Newfoundland and Yellowstone Park, edible garbage was an important food for the population whereas in other study areas, where dump use was mostly by adult males (Alt et al. 1977, Tietje and Ruff 1983, Rogers 1987), edible garbage was apparently a supplemental food important to only a few bears. The greater use of dumps by subadult males in east-central Alberta (Young and Ruff 1982) and northern Michigan (Rogers et al. 1976) may be explained by removal of adult males near dumps as a result of selective hunter harvest of trophies or less wary bears. Among polar bears near Churchill, Manitoba, family groups and subadults were the principal users of the dump, likely because adult males were disinterested in edible garbage during the period of onshore inactivity (Lunn and Stirling 1985).

Adult females and subadults tend to occupy areas near humans more than adult males; as along spawning streams on Admiralty Island (Warner 1987), near developments in Yellowstone National Park (Mattson et al. 1987), and along roads in the Flathead Valley of British Columbia (McLellan and Shackleton 1988a) and Denali National Park, Alaska (Tracy 1977). Nearly all panhandler black bears in Yellowstone Park and a disproportionately large number in the Great Smokies were adult females (Barnes and Bray 1967, Tate and Pelton 1983). Subadult males also comprised a large portion of bears foraging at campgrounds in Yellowstone Park, especially before 1970 (cf. Craighead et al. 1988), and at small dumps near human facilities in Alberta (Tietje and Ruff 1983). On the other hand, females with cubs-of-the-year tended to avoid developments in Yellowstone Park (Mattson et al. 1987), trails in Glacier National Park, U.S.A. (McArthur-Jope 1983, Jope 1985), and dumps in Alaska (Dau 1989). The closeness of humans may provide subadults and females with young refuge and an opportunity to use higher quality foods otherwise preempted by dominant adult males (Tietje and Ruff 1983, Mattson et al. 1987, McLellan and Shackleton 1988a). Whether a female with cubs-of-the-year uses the areas close to humans probably depends on the quality of food at stake and her level of habituation. The tendency for especially adult females and subadult males to range closer to humans may explain the greater number of habituated bears among these classes observed in Yellowstone Park and Alaska (Tracy 1977, Mattson et al. 1987, Warner 1987, Olsen et al. 1989).

Few studies have recorded differences in bear-class

use of human foods in the backcountry. In the Yellowstone area, adult females constitute a disproportionately large part of bears scavenging from outfitter camps (Hoak et al. 1983, data from Craighead et al. 1988). In the Great Smoky Mountains, "troublesome" backcountry bears are mostly adult males (Beeman and Pelton 1976, Singer and Bratton 1980). The situation in Yellowstone does not contradict the hypothesis that more subordinate or security-conscious bears are more likely to forage nearer to humans. Singer and Bratton (1980) hypothesized that high levels of adult male involvement at backcountry campsites in the Smokies were attributable to location of campsites in high quality bear habitat, along natural travel routes.

Two other behavioral phenomena characterize bear use of human foods. Use is typically nocturnal and usually increases when high quality native foods are in short supply. Bear use of oats in the Soviet Union (Ognev 1931, Novikov et al. 1969a) and corn in the United States (Davenport 1953, Brown 1985) typically occurs at night; as does use of campgrounds and areas near human facilities (Barnes and Bray 1967, Harms 1980, Schleyer 1983, Tietje and Ruff 1983, Harting 1985, Ayres et al. 1986, and others) and predation on confined domestic livestock (Davenport 1953, Zunino and Herrero 1972). During years of poor native food production, increased bear use of agricultural crops and human foods, and predation on livestock have been recorded for California (Piekielek and Burton 1975, Novick and Stewart 1982), the eastern United States (Spencer 1955, Elowe 1984), contemporary Yellowstone National Park (Knight et al. 1988), boreal Canada (Young and Ruff 1982), the Soviet Union (Bergman 1936, Bromlei 1965, Ustinov 1965, Slobodyan 1976, and others), and the Alps (Krott 1962). These 2 phenomena, as well as the propensity to use cropland isolated or close to cover, suggest that most bears tend to minimize contact with humans even while using human foods. Where reliance on human foods is greatest and competition from other bears significant, bears are more likely to expose themselves to humans in the process of getting human foods (e.g., Yellowstone National Park [Barnes and Bray 1967, Craighead and Craighead 1971] and Jasper [Herrero 1983]).

Response to Human Recreationists and Facilities.—Bears generally avoid humans traveling in the backcountry, although sometimes bears apparently preferred to use human-maintained trails (Garner and Vaughan 1987). In the Cabinet Mountains of Montana, bears used areas within 100 m of trails less than expected especially during hunting season (Kasworm and Manley 1990). With increased levels of trail use by humans in Glacier Na-

tional Park, Montana, habituated bears remaining near trails exhibited a weaker response to humans (McArthur-Jope 1983, Jope 1985). Bears tended to flee humans when encountered in open backcountry areas (Chester 1980, Haroldson and Mattson 1985, McLellan and Shackleton 1989, Gunther 1990), although when bedded in otherwise secure areas bears were inclined to either not move or to attack (Schleyer et al. 1984, Haroldson and Mattson 1985, McLellan and Shackleton 1989). There was also a negative relationship between number of people and number of bears observed in nonforested portions of Pelican Valley in Yellowstone Park (Gunther 1990). The response of grizzly bears to infrequent off-trail encounters with people in the backcountry was short-lived and not energetically costly in Yellowstone Park (Haroldson and Mattson 1985) but more extreme in the nonpark Flathead area of British Columbia (McLellan and Shackleton 1989). In Europe, off-trail or backcountry recreational activities such as mushroom and berry picking were apparently very intrusive to bears (Novikov et al. 1969a, Kaal 1976, Buchalczyk 1980, Zunino 1981, Roth 1983).

Bear response to people residing at backcountry campsites is usually stronger than their response to people on trails. Bears tend to underuse areas within 0.8 to 1.0 km of campsites (Gunther 1990; Mattson, in prep.) and to have their activities disrupted up to 2.5 km away (Zunino 1981; Mattson, in prep.). These effects were evident only for the most heavily used campsites (>40 people/month) (Mattson, in prep.) or campsites near open areas (Gunther 1990) in Yellowstone National Park.

Anglers also affect bear habitat use in the backcountry; a negative relationship existed between number of anglers and bear fishing activity on spawning streams in Katmai National Park, Alaska (Olsen et al. 1989) and Yellowstone Park (Gunther 1984). Olsen et al. (1989) also observed that during peak angler use, bears avoided anglers by shifting their fishing activity to evening hours when angler use was lowest.

McLellan (1990) has reviewed the effects of industrial roads and activities on bears; bears generally avoid open industrial roads. Bears also avoid daytime traffic on commercial and recreational roads, by as much as 500 m during spring and summer and 3 km during fall in Yellowstone Park (Mattson et al. 1987). There is also between 45 and 80% less use of ungulate carrion than expected during spring within 400 to 1,000 m of highways in Yellowstone Park, depending on presence of cover (Green and Mattson 1988, Henry and Mattson 1988). In Shenandoah National Park, males use areas near all roads, and females near light-duty and primary

roads less than expected year-round; greater than expected use of fire roads by females was attributed to use of native fruits growing in the road clearing (Garner and Vaughan 1987). In western North Carolina, frequency of road crossings by bears is negatively related to road traffic (Brody and Pelton 1989).

Bears generally exhibit the strongest avoidance of occupied front-country human facilities. In Yellowstone Park, spring bear use of ungulate carcasses is ca. 90% less and summer bear use of spawning cutthroat trout (*Oncorhynchus clarki*) 30-90% less than expected near recreational developments (Mattson and Henry 1987, Reinhart and Mattson 1990). The effect on carcass use extends out 5 km (Mattson and Henry 1987). Otherwise, bears tend to avoid Yellowstone Park developments during daylight hours out to 5 km during summer and 3 km during fall, and have their daylight foraging activities disrupted out to 3 km during spring and summer and 4 km during fall (Mattson et al. 1987). Habituated bears account for most use within 3 km of developments (Mattson et al. 1987). In Norway, Myrsterud (1983) observed that bears never bedded within 0.55 km of inhabited farms and Elgmork (1978, 1983) observed that bear use of areas within 2 km of cabins declined substantially as number of cabins increased. The decline in use of habitat near cabins was not explainable by hunting pressure (Elgmork 1978), and bear use of areas near abandoned farms was common (Myrsterud 1983).

European brown bears are vulnerable to human intrusion and require habitat secure from human use (Krott and Krott 1963, Elgmork 1978, Buchalczyk 1980, Zunino 1981, Camarra 1983, Roth 1983, Clevenger et al. 1987, and others). Apparently, traditional partitioning of habitat by European brown bears and rural human residents has facilitated mutual avoidance (Zunino 1981, Roth 1983, Clevenger et al. 1987). Certain, sometimes small, areas were rarely visited by humans and constituted extremely important refuges for bears. With the advent of modern recreationists, the traditional "balance" has apparently broken down and formerly secure sites are no longer so (Zunino and Herrero 1972, Zunino 1981, Roth 1983). The existence of specific sites secure from human intrusion is also known to be important to North American bears (Jonkel and Demarchi 1984, Almack 1985, Haroldson and Mattson 1985).

There is apparently still sufficient secure habitat in eastern Europe to accommodate major bear population increases; whereas in Norway and western Europe scarcity of secure habitat probably limits growth of relict populations (Zunino 1981, Elgmork 1988). European brown bear populations consistently and often dramati-

cally increased when protected from hunting in Finland (Pulliainen 1979, 1983), Estonia (Kaal 1976), the Volograd area (Kaletskaia and Filinov 1986), Poland (Buchalczyk 1980, Jakubiec and Buchalczyk 1987), Czechoslovakia (Sladek 1978), Bulgaria (Markov 1980), Rumania (Buchalczyk 1980), and Yugoslavia (Isakovic 1970). The same has not been true of more isolated populations in Italy (Fabbri et al. 1983), the Cantabrian Mountains (Clevenger et al. 1987), and the Pyrenees (Camarra 1983, 1986).

DISCUSSION

Behavioral Framework

To understand how bears respond to humans, some generalities of how bears respond to each other need to be established. There is considerable quantitative, inferential and anecdotal information available about bear behavior; there is also considerable variation among sex and age classes. Many behavioral differences appear to be size-mediated and reflected in dominance hierarchies; this is obviously modified by individual personality and experience, familial relationships, and the aggressive defense of young, (cf. Hornocker 1962, Egbert and Stokes 1976, Tate and Pelton 1983, Herrero 1985, Lunn and Stirling 1985).

In addition to size and experience *per se*, several other major factors almost certainly influence intra- and interspecific relationships of bears, including familiarity with a given area (Klopfer 1962:60, Davies 1987:552) and the demands of providing food and security for offspring. In terms of familiarity, subadult males are probably the most disadvantaged of all bear classes due to long-range dispersal from maternal ranges (cf. Alt 1978, Garshelis and Pelton 1981, LeCount 1982, Klenner 1987, Rogers 1987, and others) and young age; subadult females are more likely to reside closer to or within the maternal range. Adult females probably have the greatest familiarity with their ranges due to their age and the greater intensity of home range use implicit in smaller range-sizes compared to adult males (cf. Canfield and Harting 1987). On the other hand, adult females sustain the undoubtedly considerable energetic costs of providing food and security for dependent young, evident in the energetic costs of lactation (Sizemore 1980), the dependence of reproduction on food availability (Jonkel and Cowan 1971, Rogers 1976, Bunnell and Tait 1981, LeCount 1982), and disparity of age-weight relationships between males and females (Alt 1980b, Glenn 1980, Blanchard 1987, Kingsley et al. 1988, and others). Adult females apparently often deal with the demands of providing security especially for

cubs-of-the-year (COY) by using relatively unoccupied and typically less productive habitat (Pearson 1975, Russell et al. 1979, Miller and Ballard 1982, Mattson 1987, and others), and by being extremely aggressive to intruders. Then, when alone or when the cubs are more mobile, females use the most productive available habitat to recoup the incurred losses (Eagle and Pelton 1983, Mattson 1987). There are obvious exceptions to this strategy, such as females with COY among other adult bears at dumps and spawning streams; however, this class of females is consistently underrepresented in these situations (cf. Hornocker 1962, Stonorov and Stokes 1972, Egbert and Stokes 1976, Kendall 1986).

I used the foregoing information to rank bear classes in terms of characteristic unit-mass energy requirements and security-dominance-mediated access to productive habitat (Table 1). The difference between access rank (A) and energy requirement rank (B) indicates the relative predicament of different bear classes in meeting their energy requirements. A lower (negative) rank indicates greater stress and, perhaps, willingness to tolerate humans in the pursuit of food. As I mentioned before, lone adult females may be much more highly motivated to feed, to replenish depleted adipose reserves, than strict energy requirements would indicate (i.e., their body fat cycle is probably more meaningful viewed on a 2 to 3 year, rather than strict 1-year, basis). This rote calculation also needs to be tempered by the likelihood that security takes precedence over all else for females with COY. By this reckoning, females with young and subadult males are most likely to tolerate humans in the pursuit of both native and human-related foods.

An additional population-level perspective is required to interpret bear response to humans and their artifacts. The response of any given bear population is predictably a function of 4 main factors: (1) the nature and degree of historical interaction with humans and human-origin foods, (2) bear population density relative to ecological carrying capacity (K), (3) sex and age composition of the bear population; and (4) distribution of productive native habitat with respect to humans and their facilities. Hunting and frequency of contact are major variables in historical human-bear relationships, and influence how bears view humans (Herrero 1985). Frequency of contact between bears and humans in a given area is likely to increase as bear density increases, due to chance alone and the probable worsened energetic predicament of an increasing number of bears (Keating 1986). The proportions of adult and subadult males in a population probably has the greatest ramifications to bear-human interactions (cf. Young and Ruff 1982, Mattson et al. 1987) for

Table 1. Rank order of bear classes according to security-dominance mediated access to food and habitat (A), unit-mass energy requirements (B), and the relative predicament of bear classes in meeting their energy requirements (differences between B and A).

(A) Security-dominance mediated access	(B) Unit-mass energy requirements	(B-A) Relative predicament
1. Adult males	1. Females with COY (lactation)	Adult males (2)
2. Lone adult females		Lone adult females (2)
3. Females with yearlings	2. Females with yearlings (food-sharing)	Subadult females (1)
Subadult females		Subadult males (-1)
4. Females with COY ^a (security mediated)	3. Adult males	Females with yearlings (-1)
Subadult males	Subadult males	Females with COY (-3)
(dominance mediated)	4. Lone adult females	
	Subadult females	

^a COY = cubs-of-the-year.

reasons that I will address later. And distribution of the most productive spring and fall habitat with respect to humans has important consequences to the nature and level of contact between humans and bears (Mattson et al. 1987).

Bear Response to Human-Caused Habitat Changes

Bears and humans are flexible, adaptable omnivores and are natural competitors. Both are capable of and known to kill individuals of their own and other species for food and to resolve conflicts. It is not unexpected that competition between bears and humans should turn violent, and that each should pose some measure of risk to the other (MacPherson 1965, McCullough 1982). Humans of technological societies have had the decided advantage over bears and have not tolerated any appreciable bear use of common foods, including wild game and fruits, and domesticated livestock and vegetal crops.

Even though human-origin bear foods have supplanted native bear foods on wildland converted to agriculture, human intolerance has typically precluded bear use. On the large scale, most human foods are unavailable in bear habitat due to the elimination of bears, and virtually all remaining bear populations depend on wild native foods. Bear populations that rely heavily on human foods do so only in areas where sufficient secure habitat is available. All use of human foods, regardless of importance to a bear population, apparently depends on nearby refuge.

Human-induced changes in wildlands are probably of greater significance to surviving bear populations than introduction of exotic foods. Humans have disrupted otherwise stable, dynamically equilibrated processes in virtually all wildland ecosystems occupied by bears. This disruption has been effected primarily by fire control,

timber harvest, game management, and atmospheric pollution. Bears have been principally affected by greater spatial and temporal variation in pulses of bear food production and by the elimination of high quality foods (e.g., spawning salmonids, chestnuts, and whitebark pine nuts). The greatest divergence of contemporary from primeval conditions in wildlands has occurred and is likely to continue occurring in temperate Pacific coastal regions of North America. In this ecosystem, bears have a somewhat unique dependence on old-growth timber (Lloyd 1979, Schoen and Beier 1986, Hamilton 1987), although Siberian and Yellowstone brown bear populations are also dependent on old-growth stone pine forests for important food (Stroganov 1962; Bromlei 1965; Ustinov 1965; Mattson and Jonkel, in press). Compounding this disruptive scenario is the prospect of whole vegetation zones shifting, shrinking, and expanding with warming of the Earth's climate.

Another critical factor that has influenced and will continue to influence bear population responses to human-effected changes in their habitat is the increased isolation and fragmentation of bear populations. Although bears are flexible animals, evolutionarily adapted to variable environments (Herrero 1972, 1978; Kurten 1976:60), much of the species resilience must have depended on free interchange among populations for natural augmentation of locally stressed populations and emigration into new areas. In many areas, bears are endangered by population fragmentation and ongoing habitat fluxes greater than any in the last 10,000 to 12,000 years. Habitat available to a bear population must be sufficiently large that perturbations can be averaged across the landscape (Pickett and Thompson 1978). With historical human alterations, the area necessary to accommodate perturbations has probably increased. More

populations are probably at risk than managers would acknowledge, given that a mere 5 years of dramatic long-term change can look deceptively stable.

Human attitudes can also dramatically influence the ability of bear populations to respond to human-induced habitat changes. This is illustrated by differences in historical human-bear interactions between Eurasia and North America. In both regions, bears have been eliminated from most of their former range. The greater current proportionate overlap of bear populations with land intensively used and occupied by humans in Europe and China is very likely because European brown bears and Asiatic black bears are warier and less aggressive than their North American counterparts (Ognev 1931, Curry-Lindahl 1972, Zunino 1981). Culture plays a part in determining human tolerance of competition and risk from a large carnivore, as clearly demonstrated by human tolerance of the Bengal tiger (*Panthera tigris*) in India (Schaller 1967). In North America, it is likely that neither bears nor European settlers had sufficient time to adjust to each other, as they probably did to a greater extent in Europe. The rate of habitat transformation in North America was rapid and was apparently accompanied by intolerance to hindrance from bears or indigenous humans (Storer and Trevis 1955, Cronon 1983, Brown 1985). Dramatic alteration of habitat caused by introduction of livestock, eradication of native game, increased fire frequency and severity, and conversion of wildland to agriculture was accompanied by widespread and deliberate killing of bears. Ironically, in the past as well as present, human-caused habitat alterations probably contribute substantially to conflicts usually rationalized by humans as due to the "irascible" and "irredeemable" nature of bears (Bailey 1931, Storer and Trevis 1955, Brown 1985). Rate of habitat change and concurrent human attitudes almost certainly synergistically affect the ability of bear populations to persist in bear habitat.

Bear Response to Humans

Apparently, adult males more often have prerogative on the best human foods (i.e., dumps rich in edible garbage) in settings farther removed from humans. This is probably less of an individual and more of a class phenomenon where human foods are more important to a bear population. Under circumstances where human foods are critical or at least very important, as in Yellowstone Park before 1970 and in Newfoundland, both adult male and lone adult female classes make substantial use of dumps or hand-outs. In Yellowstone Park before 1970, there was a hierarchy of access to human foods based on quality and security of the foraging site. Adult grizzlies

and the occasional large black bear were primary beneficiaries of remote open-pit dumps, subadult male grizzlies and adult male black bears were the principal foragers at campgrounds, typically under cover of night, and adult female black bears were the principal roadside panhandlers. Heavy harvest by humans near dumps or habitations can remove most resident adult bears and instill fear in the rest (Rogers et al. 1976). Under this circumstance, subadult males may end up as primary consumers of edible garbage (cf. Rogers et al. 1976, Tietje and Ruff 1983) or agricultural crops (cf. Gunson 1975). Subadult male use of dumps may also characterize the periphery of occupied bear habitat, given that they are the primary dispersing class and conceivably unacquainted with native foraging options.

As a corollary, adult males apparently more often have the prerogative to use native foods farther from humans. In Yellowstone Park, the richest fall foraging sites are concentrated farther from humans and receive greatest use by adult males (Mattson et al. 1987). McLellan and Shackleton (1988a) suggest the same situation for their British Columbia study area. However, in Yellowstone, food production varies considerably among years, and during years of poor whitebark pine nut crops, rich foraging sites tend to be concentrated closer to humans (Mattson and Knight 1989).

Given the very likely pivotal role that adult males play in habitat selection, adult females and subadult males are probably more often left to use sites less secure from humans for feeding on human or rich native foods. Also, these bear classes probably have the motivation to feed in areas less secure from humans; not uncommonly, adult females, females with young, and subadult males have been observed to forage nearest to humans, especially when rich native foods were at stake. The nearness of humans may serve as a refuge from adult males, especially for subadult males and females with young; and where black and grizzly bears coexist, the nearness of humans may also serve as a refuge for black bears.

This disportment of bears has had and continues to have consequences. Because adult females and subadult males seem to more often end up feeding near humans out of necessity or by default, these classes more often comprise bears habituated to humans (Mattson et al. 1987, Olsen et al. 1987, Warner 1987). This is a generalization, given that adult males are known to habituate to humans (Herrero 1985). Still, in many regions, proportionately more adult females and subadult males come into conflict with, or are perceived as risks by, humans because of habituation. In areas where both grizzlies and black bears range, black bears may for the same reasons

fall into this "bad bear" category (cf. Barnes and Bray 1967, Mundy and Flook 1973). Consequently, subadult males and adult females are more often killed by humans, especially in areas where the bear population is protected from hunting (cf. Craighead et al. 1988). Where bear populations are hunted and where livestock predation is a major source of conflict between humans and bears, males are most prone to removal (Bunnell and Tait 1985, Aune and Brannon 1987, McLellan and Shackleton 1988b, and others). The consequence of these interactions among bears is that adult females and subadult males may be advantaged in the short term by a certain level of human presence, but the longer term probably results in lower survivorship for both classes.

For reasons outlined above, adult males may partly regulate the level of habituation and human food use in bear populations. Subadult males typically avoid adult males, presumably due to overt aggression on the part of the adults (Bunnell and Tait 1980, Young and Ruff 1982, Rogers 1987). Influx of subadult males may result from removal of adult males on a large or small scale (Young and Ruff 1982, Tietje and Ruff 1983). In the absence of adult males, subadult males probably exist at higher densities (Young and Ruff 1982) and may more often forage on human foods, whether garbage or crops. These 2 factors could result in a much higher incidence of crop damages and human food use on the fringe of occupied bear habitat, where adults have been eliminated, compared to areas where the adult segment is intact. This may explain the high level of apiary and grain crop use principally by subadult males in the Peace River region of Alberta during the 1970's (cf. Gunson 1975). Ironically, as long as a productive bear population persists in surrounding areas, a high level of bear harvest in agricultural districts will probably not alleviate and may even aggravate the depredation problems. On a smaller scale, removal of some adult males from a population at large might give other bears more short-term options, with resulting fewer front-country problems for an uncertain but probably short period of time. Thus, the observation that fewer bear-human conflicts characterize hunted bear populations (Herrero 1985, Dood et al. 1988) may reflect both greater wariness among bears and a greater number of options for subordinate or security-conscious bears; in addition, a hunted population is more likely to be below ecological carrying capacity, and bears at large are probably better able to avoid humans and meet their energetic needs because of greater intraspecific individual "space" (cf. Nagy and Haroldson 1990).

Habituation *per se* has major implications to bear populations confronted by even moderate densities of

humans. Habituation entails less fear of and greater proximity to humans (K. Jope, pers. commun.), and so may allow bears to use otherwise unavailable but important foraging sites near humans. Habituation is more likely to function in this manner in populations at or near ecological carrying capacity. But especially for more aggressive bear species or populations, habituation entails greater risk of injury to humans and food conditioning aggravates this risk (Herrero 1985). For this reason, habituated bears have been selectively eliminated by humans. However, the remaining warier bears are more likely to avoid humans and their facilities, and overall habitat effectiveness (i.e., behaviorally mediated access) and carrying capacity almost necessarily declines (Keating 1986). This may not be a significant factor where human densities are low and bears are not extremely wary, but in areas with high or increasing levels of human use and with continued cropping of habituated bears, loss of "effective" carrying capacity will compound the effects of mortality.

This predicament is more likely for brown and polar bears than for Asian and American black bears. There are differences in aggressiveness and consequent risk to humans between these 2 groups of bears that precipitate different levels of retaliation from humans (cf. Jonkel 1970; Herrero 1972, 1978). The European brown bear could be innately so wary that density of humans alone may influence population viability, even in the absence of hunting. It may be possible, although unlikely (Pelton 1987), for humans to intensively use land and have viable bear populations when dealing with the opportunistic but typically less aggressive black bear. The same is probably not true of polar and North American brown bears, given that aggressiveness and the ability to habituate are apparently innate (Rasa 1987) and complexly associated with the basic behavior of these species (Jonkel 1970; Herrero 1972, 1978). Innate aggressiveness and the ability to habituate can perhaps be selected against and reduced on the order of evolutionary time, but probably not on the order of decades, as has been implied by Dood et al. (1988) and Meagher and Fowler (1989). This seems especially likely given that bears apparently respond to humans much as they would to other bears (C. Jonkel, pers. commun.).

This review has demonstrated that (1) humans and bears are natural competitors, (2) bear habitat and populations will continue to be subject to disturbance and change, and (3) unless given no option or attracted by rich foods, bears generally try to avoid humans. If humans desire brown and polar bear populations that are capable of surviving ongoing and impending major habitat distur-

bances, then we retain only 2 options: either (1) increase human use of occupied bear habitat and accept the concomitant increased risk of injury associated with preserving habituated but hopefully not food-conditioned bears, or (2) continue to crop habituated bears, and maintain an expanse of wilderness habitat preserved from significant human intrusion. Humans have characteristically not accepted the risks entailed by the first option, and so long-term preservation of brown and polar bear populations is likely to be contingent on preservation of wildlands (Craighead 1980, Knight 1980, Peek et al. 1987), in conjunction with otherwise tenable levels of bear harvest. To a lesser extent, the same is true for black bears (Pelton 1987). Aversive conditioning is a promising methodology that may modify but will probably not fundamentally alter the premises of both options. Some degree of compatibility is apparent between bears and humans, however the more likely future scenarios where humans are impelled to exploit all but a small part of the northern hemisphere do not bode well for brown and polar bears.

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