Title:

Habitat criteria for recovery of grizzly bears in the Yellowstone ecosystem

Written contribution to:

Workshop to obtain input for the development of habitat-based recovery criteria for the grizzly bear (*Ursus arctos horribilis*) (*Federal Register* **62** (78): 19777)

Workshop location & date:

GranTree Inn
1325 North 7th Avenue
Bozeman, Montana

June 17, 1997

By:

David J. Mattson
Research Scientist
U.S.G.S. Biological Resources Division
Forest & Rangeland Ecosystem Science Center

Contact information for contributor:

Address: Department of Fish & Wildlife Resources
University of Idaho
Moscow, Idaho 83844-1136

Telephone: (208) 885-3589
Fax: (208) 885-3618
E-mail: matt7281@novell.uidaho.edu

Approach

This paper is organized around four main tasks that pertain to developing habitat-based criteria for grizzly bear recovery in the Yellowstone ecosystem: (1) articulate a rational framework for identifying habitat-related factors important to recovery; (2) identify these factors; (3) elucidate considerations when deriving related recovery criteria; and (4) articulate criteria with some basis in first principles or available scientific information.

The best scientific information known to this author is referenced in this paper (citations are referenced by key numbers in square brackets). This information includes papers published or in press as well as research results being prepared for publication. All of this information is available upon request from the author. Much of the cited work accompanies this contribution.

A Framework for Identifying Important Habitat Factors

By law and by accepted principles of conservation, recovery efforts should result in the finite rate of population growth (λ) equaling or exceeding 1 over some indefinite period of time, contingent on achieving goals for population size. This is logically the most fundamental measure of success [43]. Projections of current conditions to judge prospects of success defined in this way are contingent on point estimates of λ, estimates of annual and spatial variability in λ, point estimates of current population size (N), estimates of current carrying capacity (K), point estimates of finite rate of change in K, and estimates of annual and spatial variability in K [3, 4, 6, 49, 50]. Finite rate of population growth is, in turn, wholly defined by mortality and natality. Habitat factors important to conservation and useful as criteria for recovery are logically defined as those having demonstrable substantial impacts on mortality and natality and thus on λ and K (Figures 1 & 2).

Grizzly bears in the Yellowstone ecosystem die almost solely because humans kill them [20, 29, 44] although adult male grizzly bears may be a significant direct or indirect cause of death for some bears [18, 38, 52, 53]. Moreover, because mortality tends to be more variable than natality among grizzly bears, λ is more affected by death rate than by birth rate [5, 14, 18]. The focus of recovery efforts should thus be on habitat factors that determine the rate at which humans kill grizzly bears. Human-caused mortality is usefully construed as being defined by the frequency and lethality of contact between humans and grizzly bears [43, 44] (**Figure 1**). Each of these phenomena is affected by a suite of interrelated factors that logically constitute habitat features important to conservation. As such, analyses of current status and historical and future trends for each factor would provide critical information. More importantly, these habitat factors would be monitored and quantitatively tied to standards for recovery.

Although control of human-caused mortality is paramount to achieving $\lambda \geq 1$, natality is still consequential. This is high-lighted by the orders-of-magnitude difference in grizzly bear densities related to food resources and potential birth rates in Alaska [48]. In this case the focus is on foods that, because of nutrient content and abundance, have a demonstrated or likely effect on natality of female grizzly bears (**Figure 2**).

Important Habitat Factors Identified

In this section factors important to establishing habitat-based recovery criteria are identified and the nature of their relation(s) to frequency and/or lethality of encounter with humans or to natality is explained. The degree of my comfort or confidence in the qualitative or quantitative descriptions of relationships is also given, expressed as ranging from low to high.

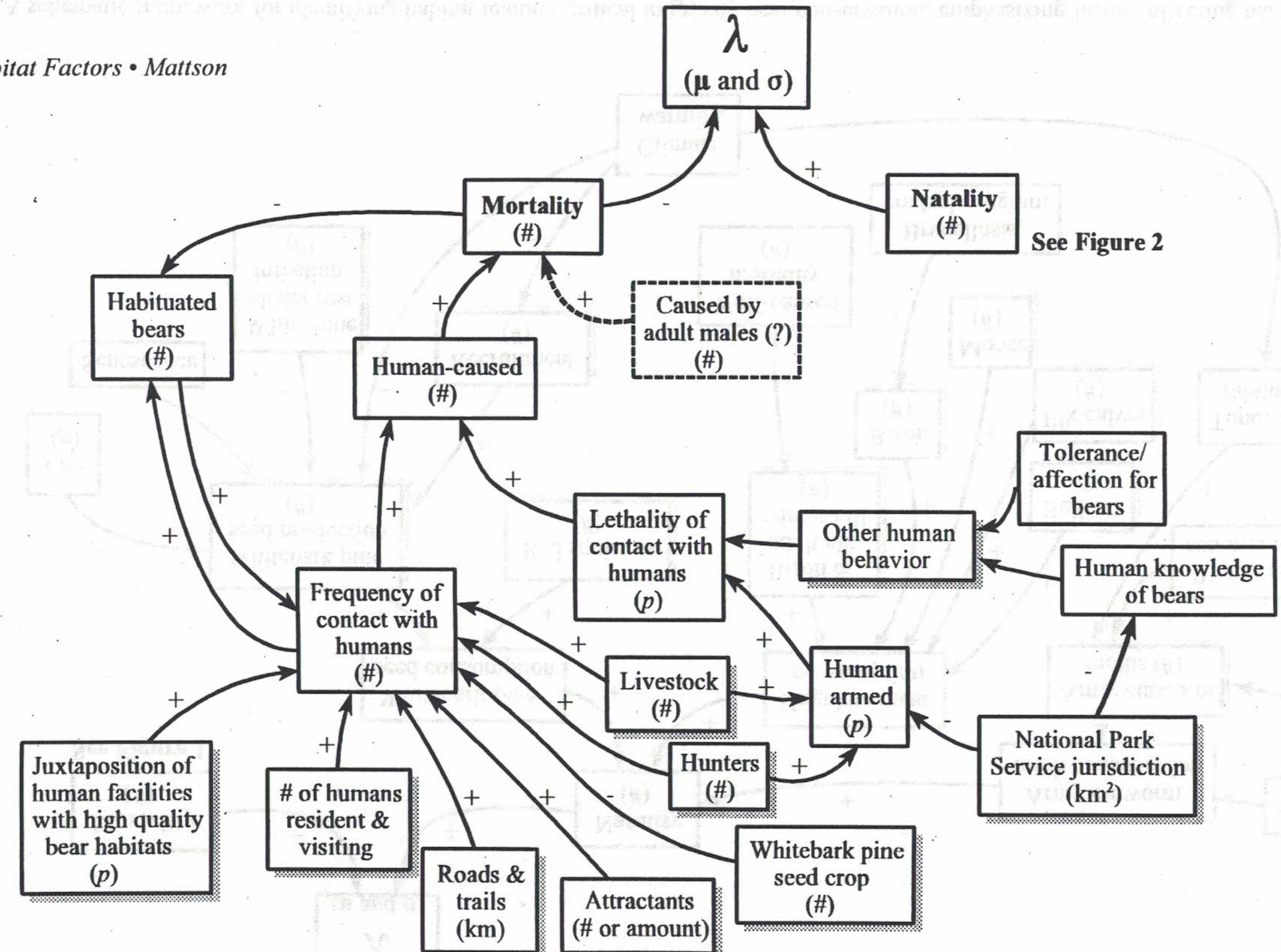

Figure 1. A schematic framework for identifying habitat features critical to grizzly bear conservation, emphasizing factors affecting mortality. Factors identified by shadowed boxes are important features of grizzlybear habitat in the Yellowstone ecosystem. These factors should ideally be monitored and logically comprise the basis for habitat-related criteria for recovery.

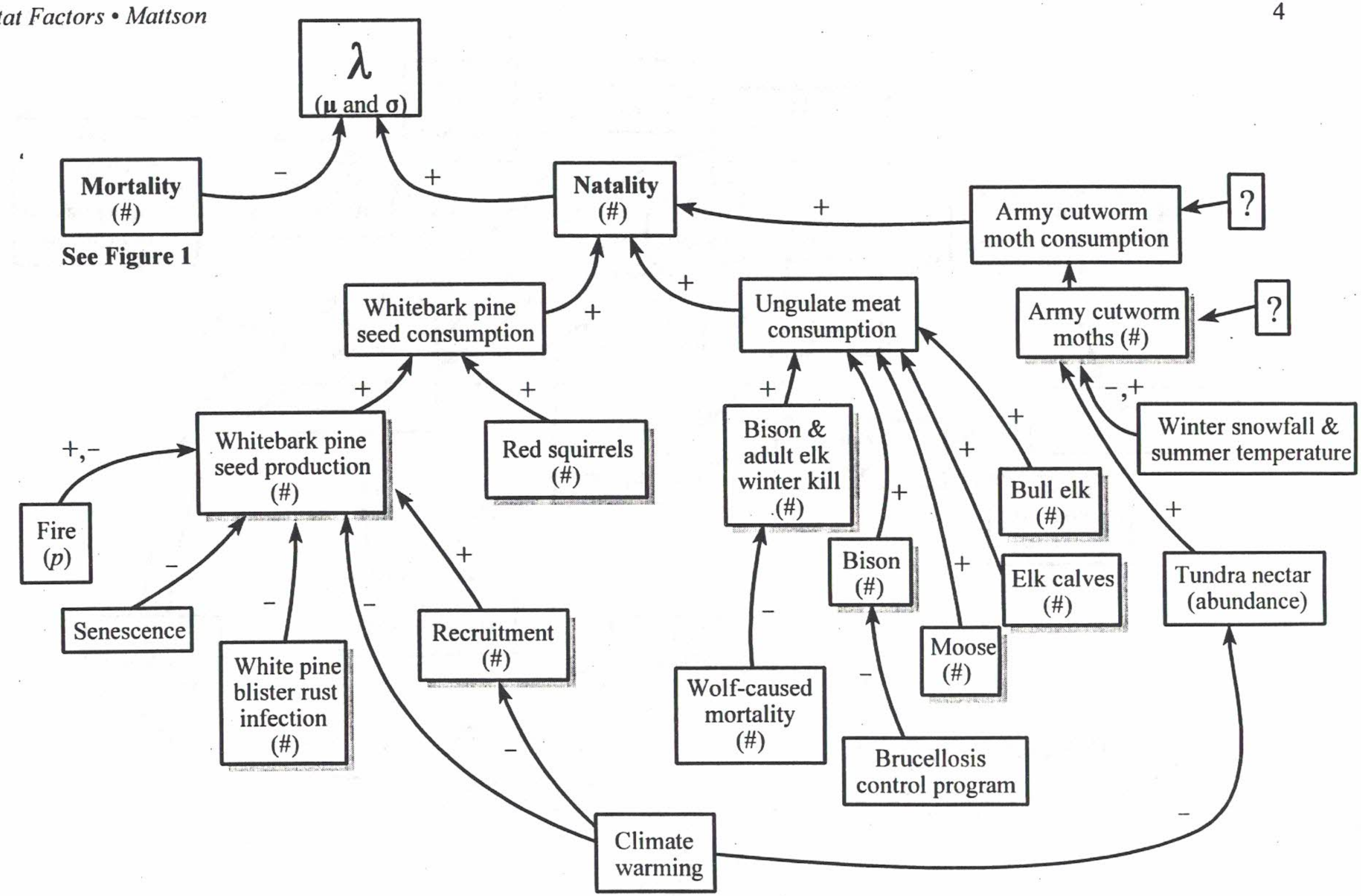

Figure 2. A schematic framework for identifying habitat features critical to grizzly bear conservation, emphasizing factors affecting natality. Factors identified by shadowed boxes are important features of grizzly bear habitat in the Yellowstone ecosystem. These factors should ideally be monitored and logically comprise the basis for habitat-related criteria for recovery.

Mortality-related

• *Juxtaposition of human facilities with highly productive bear habitats* — This is construed to primarily affect frequency of contact. Highly productive habitat serves as a 'natural' attractant for bears [9, 24, 39], which, if they survive initial contacts, predictably lose their fear of humans. This loss of fear increases subsequent frequency of encounters. It also increases lethality of contact either because the bear is more vulnerable to poachers or is viewed as an unacceptable risk to human safety by managers [10, 13, 43, 44, 46]. Known highly productive or otherwise attractive bear habitats in the Yellowstone ecosystem include:

- *Ungulate winter ranges, especially at higher elevations*, 15 March–15 May [9, 27]
- *Elk calving areas* during elk calving season [10, 28]
- *Alpine cirques where army cutworm moths aggregate*, 15 July–15 September [7, 42]
- *The whitebark pine zone*, especially 1 August–30 October and 1 June–15 July [1, 31, 32, 35, 37, 41]
- *The vicinity of cutthroat trout spawning streams* tributary to Yellowstone Lake, 15 May–15 July [33, 51]
- *Ridges where bears excavate biscuitroots*, 21 April–15 October [25, 36]
- *Meadows where bears excavate yampah roots*, 21 June–15 October [36]
- *Clover/bluegrass patches*, 1 June–15 August [8]
- *Meadows where bears excavate pocket gophers and their food caches*, 15 April–30 May [8, 59]
- *Open forests where globe huckleberry fruit production is high*, typically only found in wetter portions of the Yellowstone ecosystem to the south and west, 15 July–30 August [15].

Other habitats known to irregularly produce large quantities of high-quality food and to be heavily used by Yellowstone grizzly bears during certain years include:

- *Dry lodgepole pine forests with pole-size to mature canopies* where bears consume mushrooms, 1August–15 October [26]
- *Mesic lodgepole pine forests* where bears consume sweet-cicely roots, 1 August–15 October [26]
- *Mesic to wet forest habitats with mature to over-mature canopies at elevations <9000 ft* where bears consume ants and hornets, 1 July–15 October [23, 26]

This factor is identified with an important proviso. Productivity and use of specific habitats by Yellowstone grizzly bears is quite variable [36, 41, 42]. It is thus difficult to exclude any habitats as being 'unimportant' to grizzly bears, especially over a period of several hundred years. This issue of uncertainty is critical to managing grizzly bear habitat so as to reduce long-term risks; i.e., if this issue is not disclosed and somehow addressed, management of grizzly bear habitat will not reflect the best available scientific information. Additional aspects of this topic are addressed with respect to natality.

Degree of confidence — I have a high degree of confidence in the above qualitative descriptions of productive grizzly bear habitats. Reliable quantitative information is available, either published or in preliminary form, describing behavioral responses by bears to ungulate winter ranges, army cutworm moth aggregation sites, cutthroat trout spawning streams, ridges where biscuitroots are dug, and food in lodgepole pine forests.

• *Number of humans resident or visiting in areas containing or adjacent to grizzly bear range* — This factor is construed to primarily affect frequency of contact. The more humans there are in an area, the more chance that bears and humans will encounter each other [43, 44, 52]. The relationship between numbers of humans active in grizzly bear habitat and number of humans on roads or in developments is probably curvilinear (as evidenced by the relationship between Recreation Visitor Days and number of permanent residents of counties containing National Forests [47]). Regardless, there is mounting evidence that numbers of humans alone can have a substantial negative impact on grizzly bears, primarily because of increasing numbers of encounters and related risk of bear deaths [40, 43, 44, 47, 52].

Degree of confidence — I have moderately high confidence in this qualitative description. Reliable quantitative information on impacts attributable to human numbers alone is available in pre-published form for regional-scale analyses and for recreational developments in Yellowstone National Park.

• *Kilometers of roads and trails in the grizzly bear recovery zone* — This factor is construed to primarily affect frequency of contact. All else equal, the more access for humans, the more likely bears and humans will encounter each other [43, 44, 47]. This is obviously modified by the numbers of humans using roads (see above) and by the behavioral traits of bears (i.e., the numbers of bears that have habituated to humans and survived) [43, 44]. Roads can also directly affect lethality of encounter by increasing chances that automobiles will collide with bears.

Degree of confidence — I have a high degree of confidence in the qualitative description of this relationship. Ample quantitative descriptions of behavioral responses to roads by bears is available although little is available directly regarding frequency of contact.

• *Size of whitebark pine seed crops* — Whitebark pine seeds are an important food of grizzly bears, potentially available during the time of year (August–September) when human-bear conflicts are at their highest level. Whitebark pine occurs at high elevations typically remote from human facilities [37, 39]. Thus, during years when pine seeds are abundant and being used by bears, there are few human-bear conflicts [2, 37]. More importantly, because of this increased conflict, as a result of increased frequency of contact, many more bears are killed by humans during years when few pine seeds are available [37], and the growth rate of the population (λ) drops substantially below 1 [50]. The whitebark pine zone in this way serves as a critical refuge for bears, but only during years when pine seeds are available to attract bears and contingent on levels of human activity remaining low in this zone. Given these considerations, it is important to disclose and manage for identified threats to this resource, including global climate warming and white pine blister rust (a disease highly lethal to whitebark pine) [53; see papers in 54]. Without considering these threats, management will not be based on the best available scientific information.

Degree of confidence — I have a high degree of confidence in the above qualitative description of relationships between seed crops, distributions of bears and demographic outcomes. I have a moderately high degree of confidence in the quantitative description of the relationship between population growth rate and use of seeds by bears [50].

• *Number and nature of human-related attractants in the grizzly bear recovery zone* — This factor modifies both the frequency and lethality of contact between bears and humans. There is ample history of human garbage and other human-related foods (e.g., pet foods, livestock carcasses...) attracting grizzly bears to the vicinity of humans. If the bears survive initial encounters, they inevitably condition to these human-related foods often in addition to humans themselves, thus escalating vulnerability to poachers and the rationale for lethal control by managers [11, 13, 20, 44, 46].

Degree of confidence — I have a high degree of confidence in this qualitative description of the relationship between availability of attractants and demographic outcomes. Little reliable quantitative description is available.

• *Numbers of livestock in the grizzly bear recovery zone* — Because grizzly bears scavenge carcasses where available and are sometimes highly successful predators, the presence of livestock can attract bears to the presence of livestock handlers who are typically armed and often intolerant of depredation [15, 19, 29]. This factor thus modifies both the lethality and frequency of contact between grizzly bears and humans. Sheep are especially problematic because they easily fall prey to bears and can die in large numbers from other natural causes or from neglectful herding practices [15, 19]. Sheep herders or government agents have killed many grizzly bears because of conflicts over livestock [20, 29, 44].

Degree of confidence — I have a high degree of confidence regarding the qualitative description of this relationship, especially with respect to domestic sheep. There is very little quantitative basis for describing the relationship of livestock numbers or husbandry practices to grizzly bear demographic parameters.

• *Numbers of humans hunting ungulates or birds in the grizzly bear recovery zone* — This factor affects both the frequency and lethality of encounters between grizzly bears and humans. Hunters are the most likely of any identifiable users of grizzly bear habitat to encounter and kill bears. They are often stalking animals and are often associated with the remains of animals they killed. These conditions increase the probability of either surprising a bear or attracting a bear to the vicinity of humans. More importantly, hunters are almost always armed and thus in a position to resolve such conflicts by killing the bear. In fact, hunters have killed many grizzly bears and the portion of total bear mortality attributable to hunters has increased [20, 29, 44].

Degree of confidence — I have a high degree of confidence regarding the above qualitative understanding of this relationship. There is currently little quantitative basis for describing the relationship, although a quantitative description could be easily derived from existing data by existing demographic models.

• *Extent of management jurisdictions where assembled firearms are prohibited* (*i.e.*, National Park land) — This factor is not as variable as the rest, at least within ecosystems, but nonetheless has potentially substantial influence on the lethality of encounters between bears and humans. Without firearms, humans pose little immediate threat to bears. Backcountry (wilderness) areas of National Parks, in fact, exhibit the lowest levels of grizzly bear mortality of all jurisdictions [44].

Degree of confidence — I have moderately high confidence regarding the existence of this relationship. Some moderately reliable quantitative description is available [44].

• *Behavior of resident or visiting humans in grizzly bear range* — Human values vary with a number of factors such as gender, education, area of residence and occupation. Basic values affect acceptance of grizzly bears and, in turn, stand a good chance of affecting the likelihood that a human will harm a grizzly bear [16, 17]. Thus, human values and related behavior are likely to have a significant impact on the lethality of encounters between bears and humans. Whether subject to direct management control or not, the behavior of humans in grizzly bear range could be germane to establishing habitat-based criteria for recovery.

Degree of confidence — I have a high degree of confidence in the importance of this relationship. However, little information exists describing the nature of relationships between specific human values or attitudes and grizzly bear demography. Relatedly, little, if any, quantitative description exists of demographic consequences for bears attributable to differences in human behavior.

Natality-related

Preliminary analysis suggests that consumption of whitebark pine seeds affects the size of grizzly bear litters in the Yellowstone area [30]. Ungulates also have a potential influence on natality because ungulate meat is known to be a major source of energy for Yellowstone's grizzly bears [27]. Finally, there is circumstantial evidence suggesting that consumption of army cutworm moths may boost birth rates [7, 30].

Degree of confidence — I am moderately confident that consumption of these foods affects natality of female grizzly bears in the Yellowstone area. A moderately reliable quantitative description of the relationship between litter size and whitebark pine seed consumption is available.

● *Whitebark pine seed production* — Consumption of whitebark pine seeds by bears is partly determined by seed production tied, in turn, to abundance, vigor, and age of whitebark pine trees in grizzly bear range [31, 32, 35]. Several factors in addition to seed production *per se* are consequently important features of grizzly bear habitat:

- *Number of trees infected by white pine blister rust* — Blister rust is lethal to whitebark pine and is present in the Yellowstone region. If the blister rust infestation follows the course exhibited in regions further north and west, whitebark pine could be substantially diminished in grizzly bear range within the next 100 years [see papers in 54].

- *Recruitment of whitebark pine trees in burns and mature stands* — Global climate warming will probably substantially reduce the extent of the whitebark pine zone within the next 100 years [53]. This climatic influence will probably be effected primarily through increasingly frequent forest fires and failure of whitebark pine to subsequently reestablish in burned areas. Approximately one-quarter of seed-producing whitebark pine stands within Yellowstone National Park were burned by wildfires in 1988. Seedling and sapling whitebark pine are also vulnerable to blister rust [55]. Low recruitment is thus a potentially important early-warning of climatic influences and the effects of blister rust.

Degree of confidence — I am highly confident in the dependence of seed consumption by bears on seed production, and moderately confident in the prognosis for the effects of blister rust and climate warming. Reliable quantitative descriptions of the relationship between seed production and consumption of seeds by bears is available at 2 spatial scales. Other moderately reliable quantitative descriptions of relationships between recruitment and blister rust or climate warming exist.

● *Number of red squirrels in the whitebark pine zone* — Because almost all pine seeds consumed by grizzly bears are obtained by them from red squirrel seed and cone caches, total consumption is contingent on squirrel numbers [31, 32, 35]. Squirrel numbers have probably varied in the past due to variations in weather and climate [32, 34] and thus warrant monitoring. Timber harvest practices also affect squirrel numbers primarily though manipulation of forest overstory age, species composition and abundance [35].

Degree of confidence — I am highly confident that bear consumption of pine seeds is partly dependent on red squirrel densities. A reliable quantitative description of this relationship exists.

● *Numbers of bison and elk carcasses on ungulate winter ranges during the spring* — Most of the ungulate meat consumed by Yellowstone's grizzly bears is obtained by scavenging winter-killed elk and bison during the spring [27]. Demand for this meat is rarely satisfied; numbers of carcasses vary substantially among years depending on winter weather and pre-winter fat reserves of the ungulates [9, 27]. Wolves may have a longer-term effect on spring carcass availability by reducing numbers of elk otherwise vulnerable to winter conditions. Grizzly bears can scavenge wolf kills but it is uncertain how many grizzly bears avail themselves of this opportunity given the inherently limited number of wolf packs in the Yellowstone area.

Degree of confidence — I am highly confident that scavenging by grizzly bears is dependent on the availability of spring carrion. Several reliable quantitative descriptions of this relationship exist.

● *Numbers of bison in grizzly bear range* — Yellowstone's grizzly bears obtain a disproportional amount of meat by scavenging bison carcasses year-round [9, 27]. For this reason, bison are disproportionally important to bears and are available as carrion during seasons other than spring. Bison numbers have increased up until this year but are currently threatened by an aggressive program to kill bison leaving National Parks, as a means of controlling the spread of brucellosis (a disease that can cause abortion in domestic cattle).

Degree of confidence — I am moderately confident that meat from bison is disproportionately important to grizzly bears. A moderately reliable quantitative expression of this 'importance' is available.

● *Numbers of moose in grizzly bear range* — Moose also provide a disproportional amount of meat for Yellowstone's grizzly bears and are favored as prey [27]. More needs to be known about numbers of moose throughout grizzly bear range and factors threatening their abundance.

Degree of confidence — I am moderately confident that meat from moose is disproportionately important to grizzly bears. A moderately reliable quantitative expression of this 'importance' is available.

● *Numbers of bull and calf elk in grizzly bear range* — Yellowstone's grizzly bears obtain most of the meat they eat from elk and of the elk they obtain a disproportional amount from bulls and calves [27]. Calves are favored as prey [10, 27]. Many bulls and calves are killed and eaten in seasons other than spring (during early summer for calves and fall for bulls).

Degree of confidence — I am moderately confident that meat from bull and calf elk is disproportionately important to grizzly bears. A moderately reliable quantitative expression of this 'importance' is available.

- *Numbers of army cutworm moths in the grizzly bear recovery zone* — Moths aggregate in known sites where they could potentially be monitored. More still needs to be known about moth ecology, although nectar from tundra flowers is important [56], and circumstantial evidence suggests that winter snowpack, summer temperatures, and agricultural practices on croplands where the moths over-winter also influence moth abundance.

Degree of confidence — I am moderately confident that consumption of moths by grizzly bears depends on moth abundance. No quantitative description of this relationship exists.

- *Numbers of cutthroat trout spawning in streams tributary to Yellowstone Lake* — Trout are potentially a major source of energy for adult female grizzly bears [33, 51]. It is still uncertain, however, to what extent and how this food affects female fecundity [33]. Even so, because of the potential importance of trout to a substantial number of female bears, it is potentially consequential that the recent unauthorized introduction of lake trout into Yellowstone Lake could cause a substantial decline in the cutthroat trout population without replacement by availability of lake trout to bears.

Degree of confidence — I am confident that consumption of cutthroat trout by grizzly bears partly depends upon the numbers of trout in smaller streams. A moderately reliable quantitative description of this relationship exists [51].

Considerations For Deriving Recovery Criteria

➧ *Habitat criteria for recovery should be related to grizzly bear demography whether reckoned in terms of birth rates, death rates or population size and trajectory*. For example, Pease & Mattson [50] estimate death rate for grizzly bears as a function of whether whitebark pine seeds are or are not abundant and used and whether the bear is or is not conditioned to humans (a function of key habitat features). By contrast, *habitat influences are currently reckoned for management primarily in terms of behavioral responses by bears*. This is true of the grizzly bear cumulative effects model (CEM).

➧ *Models that attempt to relate demography to habitat strictly through behavior are problematic*. This holds for approaches that rely on estimating probabilities of resource use by radio-marked animals and, from that, estimating changes in bear numbers (or 'effective' ecosystem carrying capacity) as habitat features change. Such models reflect the odds that bears will use a site as a function of habitat features, but do not directly reflect the much more critical odds of births or deaths. Much of grizzly bear research has been expressed in terms of bear behavior [9, 33, 35, 39, 51]. However, the behavioral responses of bears do not necessarily reflect demographic consequences [24, 44]. Thus, habitat-related criteria based strictly on behavioral responses of grizzly bears to habitat features are inherently uncertain by requiring potentially subjective interpretations of demographic impacts.

➧ *Judging the current adequacy of habitat by the historical performance of demographic parameters incurs a non-trivial risk of assuming the* status quo *is adequate for recovery when, in fact, it is not.* Broad assumptions have been made about the adequacy of current habitat conditions from examining estimates of population growth rate (λ) for recent years. However, there are significant risks to this approach because demographic measures such as λ will exhibit substantial lags in response to changes in habitat conditions [4]; major deterioration in habitat conditions will predictably take several years to be manifest in population growth rate, at which time remedial actions may be much more difficult to implement. Without a causal understanding of relations between habitat and demography or habitat and demographic indices, it is also easy to mistake 'management effects' for the effects of natural variation in habitat conditions (*e.g.*, variation in whitebark pine seed crops) [28, 29, 50].

➧ *Our uncertainty in methods for monitoring grizzly bear populations and our uncertainty in empirically described relationships between habitat and demography are important to establishing criteria for recovery.* Logically, if the means by which grizzly bear demography is monitored are uncertain and prone to bias (as is the case with all currently adopted methods based on counts of dead bears and females with cubs-of-the-year [28, 29, 50]), this scientific information would be reflected in more conservative habitat-based criteria for recovery; i.e., because we have an unreliable basis for detecting or predicting demographic responses to habitat conditions. Management that does not disclose or consider such uncertainty would not be based on the best available scientific information.

➧ *Our uncertainty in future habitat conditions and the probable existence of constraints on future management options require a precautionary approach to establishing habitat-based criteria.* The future is inherently unpredictable, for good or bad for grizzly bears. It also seems to be the nature of management that options for conservation are consistently closed by incremental increases in capital investments and the development of physical infrastructure such as roads, campgrounds and other recreational facilities [21]. At present, the prognosis for grizzly bear habitat seems to be more negative than positive. Regardless, *current habitat criteria should reflect a rigorous examination of trends and projections for key habitat features and realistic consideration of the preclusive nature of historical natural resource management.*

➧ *Relationships and potential trade-offs among habitat factors and grizzly bear behavior should be recognized.* For example, increased numbers of resident or visiting humans may require reductions in access [47]. In such cases, knowledge of the magnitude of trade-off between access and human numbers would be necessary to achieve recovery objectives, or if the trade-off was uncertain, standards for recovery would be commensurately more conservative. As another example, criteria for road access may appropriately vary with the size of grizzly bear ranges in different ecosystems [25]. More needs to be known about the nature and magnitude of such trade-offs.

➧ *All important habitat factors should be monitored and, based on estimated trade-offs, factors amenable to manipulation should be adjusted to compensate for changes in factors that are not as amenable to control.* Managers should be informed about all important factors in the grizzly bears' environment. Some of these factors are more readily managed. However, these may not be the factors most critical to grizzly bear survival. Thus, factors beyond the control of land and wildlife managers, such as human visitation and local populations or changes in whitebark pine seed crops, should be monitored and considered so that compensatory measures can be taken within their purview.

➧ *Human psychology and social process is an important consideration in deriving criteria for recovery.* Although it is beyond my expertise to elaborate on this topic, several comments are warranted in light of recommendations that I make below. Humans seem to desire stability and control. Criteria that invoke continually changing management standards (*e.g.*, regarding allowable densities of open roads) may be less acceptable to people who are somehow impacted by them. Variable standards may also be problematic in light of well-documented tendencies in human management of natural resources; once a capital investment is made or expectations are altered because of liberalized management standards, reversion to more conservative standards becomes very difficult [*e.g.*, 21]. Thus, periodic liberalization of standards as part of a 'flexible' strategy may lead to long-term degradation of grizzly bear habitat. Regardless of the merits of these precise points, *individuals expert in these human dimensions would ideally be involved in the development of habitat-based recovery criteria.*

➧ *The current grizzly bear cumulative effects model (CEM) accounts for only some of the habitat factors identified above as important.* In particular, the CEM explicitly accounts for the extent of roads and trails and juxtaposition of human facilities with grizzly bear habitat scored for inherent productivity. The model indirectly accounts for numbers of attractants by registering the existence of townsites, residences and campsites. The model does not directly account for changes in numbers of visiting or resident humans, size of whitebark pine seed crops, numbers of livestock, numbers of hunters, management jurisdiction, human behavior, numbers of red squirrels in the whitebark pine zone, numbers of winter-killed ungulates, numbers of bison, numbers of moose, numbers of bull and calf elk, numbers of army cutworm moths, and numbers of spawning cutthroat trout.

Recommendations for Habitat-Based Recovery Criteria

Given the considerations in the previous section, *all recommendations expressed here are tentative.* These recommendations are premised on currently the most scientifically defensible demographic analysis of the Yellowstone grizzly bear population [50] and corroborating information [28, 29]. Aside from the overall rate at which humans kill bears, these analyses demonstrate that population growth rate (λ) is largely determined by season, the frequency of good whitebark pine seed crops, and the rate at which bears wary of humans become habituated (or conditioned) to the human presence.

In almost all of these recommendations I also emphasize the desirability of *measuring or applying these criteria over the approximate 10 year life-span of a Yellowstone grizzly bear.*

1. Given that $\lambda \approx 0.95$ during years when whitebark pine cone production at currently existing transects averages ≤ 20 cones/tree and that $\lambda \approx 1.07$ during years of greater cone production, a higher frequency of small ($\leq$20) than large (>20) cone crops will lead to a declining population. Thus, *'recovery' would be, at a minimum, contingent on there being more good cone crops than bad for 10 years (the approximate generation length of a grizzly bear in Yellowstone), considering each series of the previous inclusive 10 years.*

2. Given the importance of whitebark pine, *'recovery' would be contingent on demonstrating that numbers of prime cone-producing trees (~100–200-year-old) were being at least maintained in the ecosystem (i.e., recruitment into this age class exceeded losses either through aging or mortality) and that this pattern was evident averaged over an 10-year period.*

3. Given that the conditioning of bears to humans is a function of encounters without negative consequences, exacerbated by the presence of attractive resources near humans [13], that human-conditioned bears exhibit about 2× the death rate of unconditioned bears [46], that demographic lags can be expected [4], and that the Yellowstone population grew very little between 1975 and 1995 [50] — *'recovery' would be contingent on no net increase within the grizzly bear recovery zone of factors that escalate the frequency of contact between humans and grizzly bears during the next 10 year period, concurrent with growth rate of the grizzly bear population (λ) being ≥ 1 (at some agreed-upon level of confidence) for the same period of time, controlling for the effects of whitebark pine seed crop size.*

Population growth rate would be estimated using the scientifically most defensible demographic model available. *The factors of concern would be (i) numbers of visitors to grizzly bear range, (ii) numbers of permanent residents in or within 80 km of grizzly bear range, (iii) numbers of hunters in grizzly bear range, (iv) length of roads and trails in grizzly bear range, (v) number of facilities used by humans for residence, for commerce, or for recreation, and (vi) numbers of livestock allotments and livestock using them.*

4. Given that human numbers seem to have roughly the same effect as road milage on presence of bears at a regional scale [47], *'recovery' would be contingent on any increase in numbers of people visiting or living in/near grizzly bear range during the next 10 years being compensated by a proportional decrease in milage of open roads and trails, with human numbers judged at or averaged (as with Park visitation) over 5-year intervals or whenever information on human numbers was available (as after the next census)*. This criterion would be applied with the following proviso:

5. Given that hunters kill many more bears than other humans living near or active in grizzly bear range [29], *the relative weight given to changes in hunter numbers would be calculated as the ratio of the proportion of grizzly bear mortality attributable to hunters to the proportion of hunter numbers relative to all other human residents or visitors.*

6. Given the importance of the whitebark pine zone as a potential refuge for Yellowstone grizzly bears and as a source of food especially important to females [30, 37], *'recovery' would be contingent on no net increase in human activity within the whitebark pine zone over the next 10 years.* Road and trail closures would also be emphasized in the whitebark pine zone.

7. Given that encounters and conflicts between grizzly bears and humans are potentially highest in highly productive habitats, *'recovery' would be contingent on the establishment of a protocol for closing to human use, ecosystem-wide, habitats associated with known high-quality foods that averaged some agreed-upon probability of use by grizzly bears. As a starting point for discussion, at least 50% of the grizzly bear recovery area would be in such closures [24].* Food-specific and aggregate models of grizzly bear foraging behavior would be used to help identify these areas. This closure strategy would be implemented with the following provisos: *(i) where appropriate, closures would be seasonal based on known times when bears focused their feeding on identified high-quality foods; (ii) individual closed areas would be at least 28 km² in size [24]; and (iii) known areas of concentrated grizzly bear activity would be prioritized associated with ungulate winter ranges, productive whitebark pine stands, army cutworm moth aggregation sites, cutthroat trout spawning streams, meadows where yampah and/or pocket gophers are abundant, ridges where bears stand a high probability of excavating biscuitroots, clover/bluegrass patches, predictable elk calving areas, and areas known for high levels of globe huckleberry production.*

8. For the same reasons as 7, *'recovery' would be contingent on no change in habitat effectiveness values calculated using the Cumulative Effects Model, by Bear Management Unit, for the Recovery Zone.*

9. Given the extreme lethality of conflicts over sheep to grizzly bears, *'recovery' would be contingent on closing all remaining sheep allotments within the grizzly bear recovery zone, whether currently occupied or not by bears or sheep.*

10. Given the extreme lethality of conflicts and conditioning as a consequence of freely-available human-related foods and the increasing concentration of such conflicts on private lands [*e.g.*, 12], *'recovery' would be contingent on developing and implementing a sanitation program with demonstrated effectiveness for private lands in or adjoining the grizzly bear recovery zone.*

11. Given the potential importance of bison, moose, and bull and calf elk to grizzly bears, *'recovery' would be contingent on development and implementation of methods for monitoring abundance of these animals and on their numbers not declining over the next 10 years, with the proviso that declines in their numbers could be compensated in some as yet unknown way by increases in cone production by whitebark pine or other food resources.*

12. Given the potential importance of army cutworm moths to grizzly bears, *'recovery' would be contingent on the development of non-intrusive methods to reliably monitor the abundance of moths at moth-site aggregations, and on numbers of moths not declining over the next 10 years, with the proviso that declines in their numbers could be compensated in some as yet unknown way by increases in cone production by whitebark pine or other food resources.*

13. Given the large amount of energy currently obtained by grizzly bears from ungulate carrion, *'recovery' would be contingent on no decline in amount of carrion available during spring on winter ranges, especially in the northern and western parts of the ecosystem, averaged over the next 10 years, or if a decline occurred, a demonstration that compensatory amounts of carrion were available from wolf kills to an equal number of female bears during the bears' active season.*

14. Given the importance of red squirrels to grizzly bear consumption of whitebark pine seeds, *'recovery' would be contingent on implementing methods to monitor red squirrel populations in the whitebark pine zone and demonstrating that there was no decrease in squirrel populations over the next 10 years.*

15. *'Recovery' would be contingent on applying the above-listed criteria at the appropriate scales: 2–8, 11, 13, and 14 would be applied on a Bear Management Unit basis; 12 would be applied in Bear Management Units where the food resource was present and known to be important; and 1, 9, and 10 would be applied at the ecosystem level.* Application at the level of individual Bear Management Units would help to prevent fragmentation of the recovery zone.

16. *In the event that any of the above-listed criteria were not implemented for reasons of cost or complexity, 'recovery' would be contingent on some compensatory change in other criteria in acknowledgment of the uncertainty and risk added by failing to consider or monitor an important facet of grizzly bear habitat.*

Literature Cited

1. Blanchard, B.M. & Knight, R.R. (1991). Movements of Yellowstone grizzly bears. *Biological Conservation* **58**: 41–67.
2. Blanchard, B.M. & Knight, R.R. (1995). Biological consequences of relocating grizzly bears in the Yellowstone ecosystem. *Journal of Wildlife Management* **59**: 560–565.
3. Dennis, B., Munholland, P.L. & Scott, J.M. (1991). Estimation of growth and extinction parameters

for endangered species. *Ecological Monographs* 61: 115–143.
4. Doak, D.F. (1995). Source-sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. *Conservation Biology* 9: 1370–1379.
5. Eberhardt, L.L., Blanchard, B.M. & Knight, R.R. (1994). Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. *Canadian Journal of Zoology* **72**: 360–363.
6. Foley, P. (1994). Predicting extinction times from environmental stochasticity and carrying capacity. *Conservation Biology* **8**: 124–137.
7. French, S.P., French, M.G. & Knight, R.R. (1994). Grizzly bear use of army cutworm moths in the Yellowstone ecosystem. *International Conference on Bear Research & Management* **9**: 389–400.
8. Graham, D.C. (1978). *Grizzly bear distribution, use of habitats, food habits and habitat characterization of Pelican and Hayden Valleys, Yellowstone National Park.* M.S. Thesis, Montana State University, Bozeman.
9. Green, G.I., Mattson, D.J. & Peek, J.M. (In press). Spring feeding on ungulate carcasses by grizzly bears in Yellowstone National Park. *Journal of Wildlife Management.*
10. Gunther, K.A. & Renkin, R.A. (1990). Grizzly bear predation on elk calves and other fauna of Yellowstone National Park. *International Conference on Bear Research & Management* **8**: 329–334.
11. Gunther, K.A., Biel, M.J., Churchill, K.A. & Danforth, R.L. (In press). Changing problems in bear management, Yellowstone National Park, 20+ years after the dumps. *Greater Yellowstone predators: proceedings of the third biennial scientific conference on the greater Yellowstone ecosystem.*
12. Gunther, K.A., Bruscino, M.T., Cain, S., Chu, T., Frey, K. & Knight, R.R. (1997). *Grizzly bear-human conflicts, confrontations, and management actions in the Yellowstone ecosystem 1996.* Interagency Grizzly Bear Committee, Yellowstone Ecosystem Subcommittee Report.
13. Herrero, S. (1985). *Bear attacks: their causes and avoidance.* Nick Lyons Books, New York. 287pp.
14. Hovey, F.W. & McLellan, B.N. (1996). Estimating population growth of grizzly bears from the Flathead River drainage using computer simulations of reproduction and survival rates. *Canadian Journal of Zoology* **74**: 1409–1416.
15. Jorgensen, C.J. (1983). Bear-sheep interactions, Targhee National Forest. *International Conference on Bear Research & Management* **5**: 191–200.
16. Kellert, S.R. (1994). Public attitudes toward bears and their conservation. *International Conference on Bear Research & Management* **9**: 43–50.
17. Kellert, S.R., Black, M., Rush, C.R. & Bath, A.J. (1996). Human culture and large carnivore conservation in North America. *Conservation Biology* **10**: 977–990.
18. Knight, R.R. & Eberhardt, L.L. (1985). Population dynamics of Yellowstone grizzly bears. *Ecology* **66**: 323–334.
19. Knight, R.R. & Judd, S.L. (1983). Grizzly bears that kill livestock. *International Conference on Bear Research & Management* **5**: 186–190.
20. Knight, R.R., Blanchard, B.M. & Eberhardt, L.L. (1988). Mortality patterns and population sinks for Yellowstone grizzly bears, 1973–1985. *Wildlife Society Bulletin* **16**: 121–125.
21. Ludwig, D., Hilborn, R. & Walters, C. (1993). Uncertainty, resource exploitation, and conservation: lessons from history. *Science* **260**: 17–18.
22. Mattson, D.J. (1990). Human impacts on bear habitat use. *International Conference on Bear Research & Management* **8**: 33–56.

23. Mattson, D.J. (1992). *Use of log-dwelling ants by Yellowstone grizzly bears: preliminary results and guidelines*. Interagency Grizzly Bear Study Team, Bozeman, MT. 4pp.
24. Mattson, D.J. (1993). *Background and proposed standards for managing grizzly bear habitat security in the Yellowstone ecosystem*. Cooperative Park Studies Unit, College of Forestry, Wildlife & Range Sciences, University of Idaho, Moscow.
25. Mattson, D.J. (1997). Selection of microsites by grizzly bears to excavate biscuitroots. *Journal of Mammalogy* **78**: 228–238.
26. Mattson, D.J. (1997). Use of lodgepole pine cover types by Yellowstone grizzly bears. *Journal of Wildlife Management* **61**: 480–496.
27. Mattson, D.J. (1997). Use of ungulates by Yellowstone grizzly bears *Ursus arctos*. *Biological Conservation* **81**: 161–177.
28. Mattson, D.J. (1997). Sustainable grizzly bear mortality calculated from counts of females with cubs-of-the-year: an evaluation. *Biological Conservation* **81**: 103–111.
29. Mattson, D.J. (In press). Changing mortality of Yellowstone grizzly bears. *International Conference on Bear Research & Management* **10**.
30. Mattson, D.J. (In preparation). *Causes and consequences of dietary differences among Yellowstone grizzly bears (*Ursus arctos*)*. Ph.D. Dissertation, University of Idaho, Moscow.
31. Mattson, D.J. & Jonkel, C. (1990). Stone pines and bears. Pages 223–236 *in* W.C. Schmidt & K.J. McDonald, compilers. *Proceedings — symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*. U.S. Forest Service General Technical Report INT-270.
32. Mattson, D.J. & Reinhart, D.P. (1994). Bear use of whitebark pine seeds in North America. Pages 212–220 *in* W.C. Schmidt & F.-K. Holtmeier, eds. *Proceedings — international workshop on subalpine stone pines and their environment: the status of our knowledge*. U.S. Forest Service General Technical Report INT-GTR-309.
33. Mattson, D.J. & Reinhart, D.P. (1995). Influences of cutthroat trout (*Oncorhynchus clarki*) on behaviour and reproduction of Yellowstone grizzly bears (*Ursus arctos*), 1975–1989. *Canadian Journal of Zoology* **73**: 2072–2079.
34. Mattson, D.J. & Reinhart, D.P. (1996). Indicators of red squirrel (Tamiasciurus hudsonicus) abundance in the whitebark pine zone. *Great Basin Naturalist* **56**: 272–275.
35. Mattson, D.J. & Reinhart, D.P. (In press). Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. *Journal of Applied Ecology*.
36. Mattson, D.J., Blanchard, B.M. & Knight, R.R. (1991). Food habits of Yellowstone grizzly bears, 1977–1987. *Canadian Journal of Zoology* **69**: 1619–1629.
37. Mattson, D.J., Blanchard, B.M. & Knight, R.R. (1992). Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. *Journal of Wildlife Management* **56**: 432–442.
38. Mattson, D.J., Knight, R.R. & Blanchard, B.M. (1992). Cannibalism and predation on black bears by grizzly bears in the Yellowstone ecosystem, 1975–1990. *Journal of Mammalogy* **73**: 422–425.
39. Mattson, D.J., Knight, R.R. & Blanchard, B.M. (1987). The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. *International Conference on Bear Research & Management* **7**: 259–273.
40. Mattson, D.J., Merrill, T. & Scott, J.M. (In preparation). Extirpations of grizzly bears in the western United States of America, 1850–1970. For *Conservation Biology*.
41. Mattson, D.J., Reinhart, D.P. & Blanchard, B.M. (1994). Variation in production and bear use of whitebark pine seeds in the Yellowstone area. Pages 205–219 *in* D.G. Despain, ed. *Plants and their environments: proceedings of the first biennial scientific conference on the Greater*

Yellowstone Ecosystem. U.S. National Park Service Technical Report NPS/NRYELL/NRTR-93.

42. Mattson, D.J., Gillin, C.M., Benson, S.A. & Knight, R.R. (1991). Bear feeding activity at alpine insect aggregations in the Yellowstone ecosystem. *Canadian Journal of Zoology* **69**: 2430–2435.
43. Mattson, D.J., Herrero, S., Wright, R.G. & Pease, C.M. (1996). Science and management of Rocky Mountain grizzly bears. *Conservation Biology* **10**: 1013–1025.
44. Mattson, D.J., Herrero, S., Wright, R.G. & Pease, C.M. (1996). Designing and managing protected areas for grizzly bears: how much is enough? Pages 133–164 *in* R.G. Wright, ed. *National parks and protected area: their role in environmental protection*. Blackwell Science, Cambridge, Massachusetts.
45. McLellan, B. (1994). Density-dependent population regulation of brown bears. Pages 15–24 in M. Taylor, ed. Density-dependent population regulation in black, brown, and polar bears. *International Conference on Bear Research & Management Monograph Series* **3**. 43pp.
46. Meagher, M. & Fowler, S. (1989). The consequences of protecting problem grizzly bears. Pages 141–144 *in* M. Bromley, ed. *Bear-people conflicts: proceedings of a symposium on management strategies*. Northwest Territories Department of Renewable Resources, Yellowknife.
47. Merrill, T., Mattson, D.J., Wright, R.G. & Quigley, H.B. (In review). Defining suitable landscapes for re-introduction of grizzly bears *Ursus arctos* in Idaho. *Biological Conservation*.
48. Miller, S.D., White, G.C., Sellers, R.A., Reynolds, H.V., Schoen, J.W., Titus, K., Barnes, V.G., Jr., Smith, R.B., Nelson, R.R., Ballard, W.B. & Schwartz, C.C. (1997). Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. *Wildlife Monographs* **133**: 1–55.
49. Mills, L.S., Hayes, S.G., Baldwin, C., Wisdom, M.J., Citta, J., Mattson, D.J. & Murphy, K. (1996). Factors leading to different viability predictions for a grizzly bear data set. *Conservation Biology* **10**: 863–873.
50. Pease, C.M. & Mattson, D.J. (In review). Demography of the behaviorally-structured Yellowstone grizzly bear population. *Ecology*.
51. Reinhart, D.P. & Mattson, D.J. (1990). Bear use of cutthroat trout spawning streams in Yellowstone National Park. *International Conference on Bear Research & Management* **8**: 343–350.
52. Renkin, R.A. & Gunther, K.A. (In press). Predicting grizzly bear mortality in relation to frontcountry developed areas in Yellowstone National Park. *Greater Yellowstone predators: proceedings of the third biennial scientific conference on the greater Yellowstone ecosystem*.
53. Romme, W.H. & Turner, M.G. (1991). Implications of global climate change for biogeographic patterns in the greater Yellowstone ecosystem. *Conservation Biology* **5**: 373–386.
54. Schmidt, W.C. & Holtmeier, F.-K., compilers (1994). *Proceedings — international workshop on subalpine stone pines and their environment: the status of our knowledge*. U.S. Forest Service General Technical Report INT-GTR-309.
55. Tomback, D.F., Clary, J.K., Koehler, J., Hoff, R.J. & Arno, S.F. (1995). The effects of blister rust on post-fire regeneration of whitebark pine: the Sundance burn of northern Idaho (U.S.A.). *Conservation Biology* **9**: 654–664.
56. White, D.D., Jr. (1996). *Two grizzly bear studies: moth feeding ecology and male reproductive behavior*. Ph.D. Thesis, Montana State University, Bozeman.
57. Wielgus, R.B. & Bunnell, F.L. (1994). Dynamics of a small, hunted brown bear Ursus arctos population in southwestern Alberta, Canada. *Biological Conservation* **67**: 161–166.
58. Wielgus, R.B. & Bunnell, F.L. (1994). Sexual segregation and female avoidance of males. *Journal of Wildlife Management* **58**: 405–413.

59. Youmans, C.C. (1979). *Characteristics of pocket gopher populations in relation to selected environmental factors in Pelican Valley, Yellowstone National Park.* M.S. Thesis, Montana State University, Bozeman.