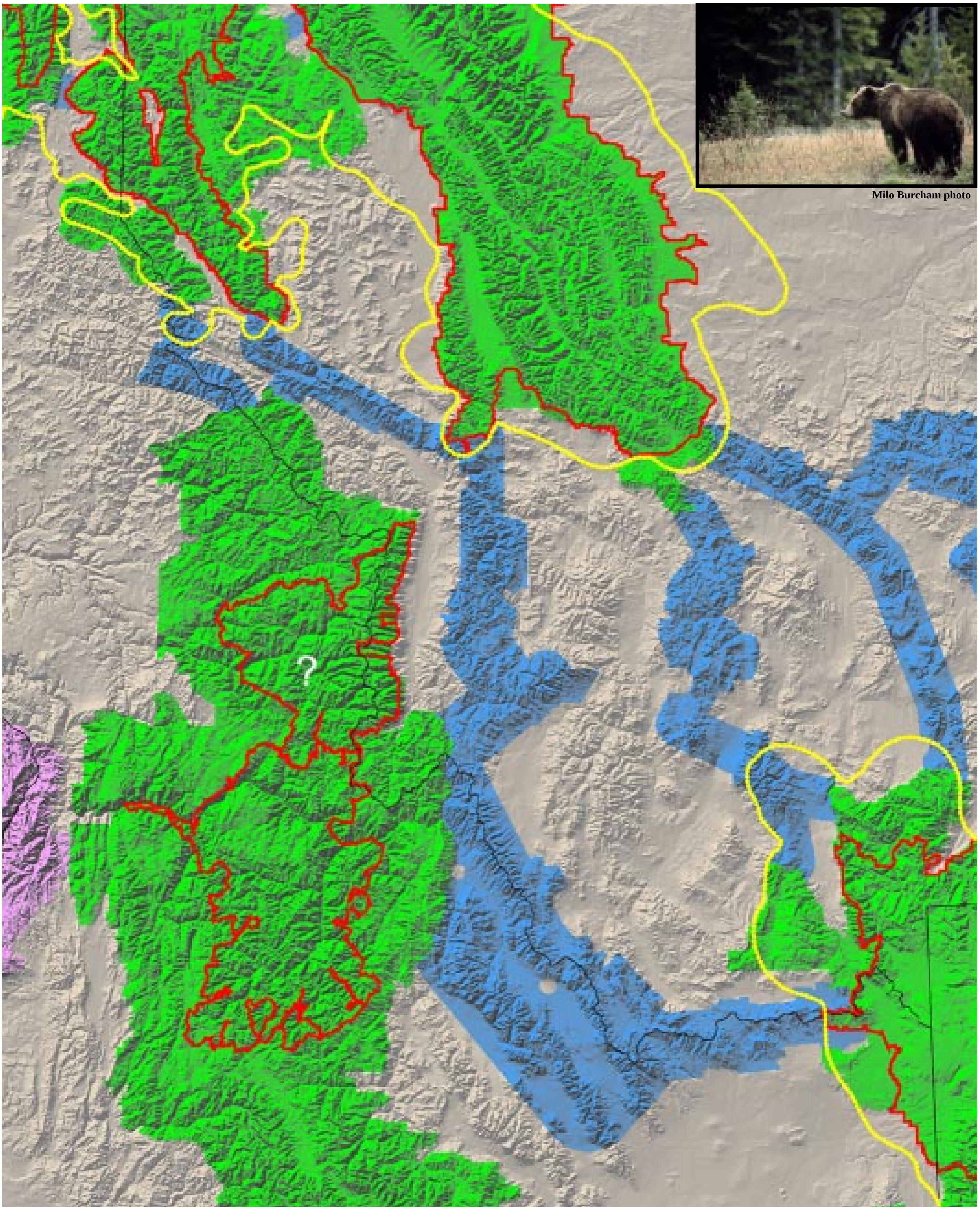
Spatial Needs of Grizzly Bears in the U.S. Northern Rockies



Milo Burcham photo

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Any mistakes in interpretation or assumptions are mine alone.

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Abstract

Calculation of spatial needs at the population level is necessary to provide habitat area adequate for recovery of threatened and endangered species. Building blocks for calculation of spatial needs include estimated population viability size, mean densities, home range sizes, current and historic distribution areas, and analysis of potential linkage habitats. Applying these indices, the spatial needs of a self-sustaining grizzly bear metapopulation in the U.S. northern Rockies are estimated to be ≈ 147,883 km^2 - 184,919 km^2. Both the indices and total spatial requirements are compared to recovery goals embodied in U.S. Fish & Wildlife Service recovery planning documents. I conclude that current U.S. Fish & Wildlife Service recovery objectives will not achieve a genetically diverse, demographically viable grizzly bear population. Federal managers may have reached a de facto conclusion that grizzly bears residing beyond delimited recovery areas are non-essential. A proposed habitat network ≈ 190,777 km^2, based on federal public lands, is outlined to accommodate the estimations for population and space.

Key words: grizzly bear, mean density, distribution area, habitat security, population viability, linkage corridors, metapopulation, habitat network.

Introduction

The grizzly bear (*Ursus arctos*) was listed as a threatened species pursuant to the federal Endangered Species Act (ESA) in 1975. The ESA mandate to prevent species extinctions and recover healthy populations, coupled with continued public support for this national policy direction, requires recovery and maintenance of self-sustaining grizzly bear populations in the conterminous 48 states. The central goal of recovery planning for species listed as threatened or endangered is to increase both the numbers and distribution of the species. Grizzly bears, with lifetime home ranges up to 5,374 km^2 (Blanchard & Knight 1991) present significant challenges to managing for persistence. By the same token, the large spatial requirements of grizzly bears may qualify them as an umbrella species (Noss, et al. 1996) under whose span numerous other species might be conserved.

Biodiversity conservation at the landscape level encompasses thousands of species, about many of which we know little or nothing. For practical reasons, we focus our conservation plans on a few species that serve as indicators of ecosystem health and integrity. The grizzly bear is one such species.

An addition to recovery planning is population viability analysis. A common benchmark for population management is a 95% or better probability of weathering the effects of demographic and environmental stochasticity, human-induced mortality, and adverse habitat modifications, and persisting over some discrete time frame (Allendorf & Ryman, In Press). Of related interest are estimates for the ratio of the effective population (N_e) to total population (N) size.

There has been considerable debate in the recent literature regarding the minimum effective population size needed to maintain genetic variation over the long term. Classically, minimum N_e has been set at 500 (Franklin 1980). However, Lynch & Lande (1998) suggest this number may be closer to 5,000, while Franklin & Frankham (1998) suggest minimum N_e in the range of 500-1,000 may be adequate. To be conservative in my spatial analysis for grizzly bears I use $N_e = 500$ for estimating spatial needs as well as for measuring the efficacy of U.S. Fish & Wildlife Service recovery goals and strategies.

This paper builds upon related work. I concluded in Bader (2000a) that unroaded wilderness habitats are a source habitat for grizzly bears while the roaded landbase is a sink. My analysis of mortality records found that ≈ 64% of all recorded grizzly bear mortalities in the Yellowstone and Northern Continental Divide areas occurred within 2 km of roads and 4 km of major developed areas. In Bader (2000b), I provide a current estimated distribution area for grizzly bears in the U.S. northern Rockies at ≈ 102,524 km^2 and I show that grizzly bear distribution greatly exceeds the areas delimited by the U.S. Fish & Wildlife Service as grizzly bear recovery areas. I recommend these recovery areas be significantly expanded.

Here, I submit that the essential building blocks needed for calculation of spatial needs for grizzly bears at the population or metapopulation level are: estimates of viable population size, mean density, area specific home range sizes, current and historic distribution areas including the locations of observations, habitat security and habitat productivity analysis. The major values of import I use are total area (A), density (D), total population size (N), effective population size (N_e), the ratio of N_e:N, habitat security (HS), and theoretical optimal carrying capacity (K). I present a proposed habitat network for grizzly bear recovery in a metapopulation context to accommodate the estimations for population and space.

I address four fundamental questions: 1) What are the spatial needs of grizzly bears in the U.S. northern Rockies?; 2)

How do U.S. Fish & Wildlife Service recovery goals and strategies match up with these requirements?; 3) Are suitable habitats within the range of spatial needs currently available?; 4) What might an adequate habitat network look like?

Methods

Study Area and Geographic Analysis

The area analyzed is the U.S. northern Rockies generally bounded by the 49° and 42° N. latitudes and 119° and 108° W. longitudes, shown in Figure 1. A Geographic Information System (GIS), Arc/Info 7.11 and ArcView 3.0 with Spatial Analyst (Environmental Systems Research Institute 1997) were used to plot digital information and for spatial analysis.

Density and Home Range Calculations

Reported densities from interior, non-coastal influenced grizzly bear populations were summed and averaged and expressed as D = bears/1000 km^2. Where a range was reported, a midpoint of that range was used. When a source identified marked only as well as marked and observed values, the higher densities derived from the latter were used. When more than one value was reported by different sources for the same area, a midpoint or a mean of those values was used.

Reported mean annual and life range sizes for adult grizzly bears were gathered from the literature, and when possible, were calculated from data in research reports by summing and averaging. Mean lifetime home range sizes were used with precipitation data for comparison of mesic and xeric systems. Overlap in grizzly bear home ranges was considered but excluded from calculations for total spatial requirements since it is implied within density estimates that overlap is a natural occurrence in grizzly bear populations. A review of the literature and a *delphi* approach revealed just one extensive effort to quantify home range overlap in grizzly bears (Mace & Waller 1997) and a few for black bears *Ursus americanus* (Rogers 1987, Powell 1987), although an exhaustive search for overlap studies in black bears was not undertaken. The literature shows that home range overlap occurs in virtually all studied grizzly bear populations (LeFranc, et al. 1987).

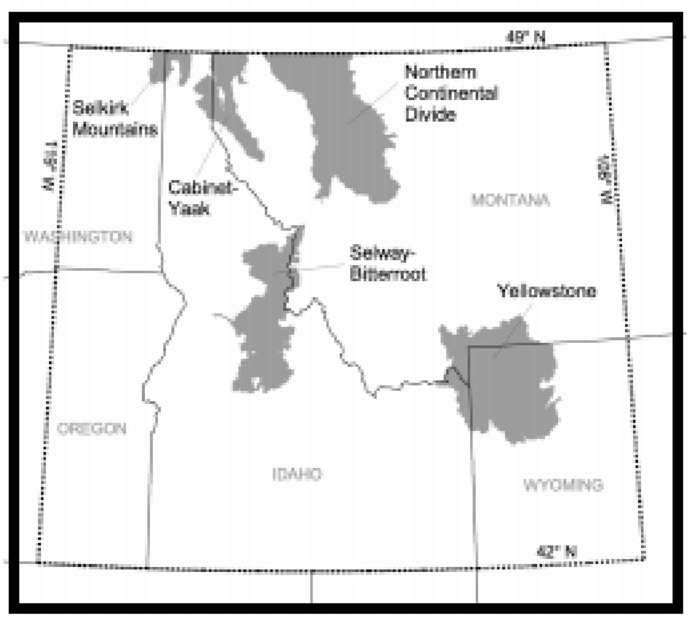


Figure 1 – The Northern Rockies analysis area and the locations of the five grizzly bear recovery areas developed by the U.S. Fish & Wildlife Service.

$N_e : N$ Ratios

A search of the literature revealed three estimates of N_e:N for grizzly bears. These were 1:5 (Allendorf & Ryman, In Press), 1:4 (Allendorf, et al. 1991) and 1:3 (U.S. Fish & Wildlife Service 1993). These ratios were used with the calculated value for D and the N_e = 500 baseline to estimate values for A.

Habitat Security Calculations

I calculated the size of current and proposed core recovery areas and the percentage that is currently secure habitat. I define secure habitat as lands formally classified as Wilderness, National Park, or inventoried roadless areas ≥ 2,833 ha (identified by Mattson [1993] as a minimum for micro-scale security areas for adult female grizzly bear/cub groups). Not all habitat within National Parks is secure. Thus, all areas ≤ 1.61 km from a road or major development were excluded. Some roads and developments have a greater zone of influence (Mattson, et al. 1987; Bader 2000a) and some roads less; I assumed this is balanced within the 1.61 km buffer. Area:perimeter ratios were calculated for each area. I used HS = 80% as a threshold value for adequate security. While this is a somewhat arbitrary measure, my review of grizzly bear populations indicates those in landscapes where HS < 80% have generally not sustained large populations, consistent with the findings of Mattson, et al. (1995). This threshold was used to calculate the total area which would need to be restored to secure habitat condition in order to meet total spatial needs.

I have provided a coarse definition of security since these figures do not account for habitat productivity. For example, the Beartooth and Pitchstone Plateau areas in the Yellowstone region are very secure as designated wilderness and national park areas, yet support minimal use levels by grizzly bears (Blanchard & Knight 1991). The former is mostly alpine tundra above treeline while the latter is largely defined by sterile volcanic soils. This is somewhat balanced by the fact some areas outside this definition are low road density areas or uninventoried roadless areas. Thus, the security results may somewhat understate overall security since my definition excludes low road density areas which may in fact be relatively secure, and also does not include roadless areas and other remote forested lands in tribal and private ownership. The security results also do not factor in spatial distribution. Fragmentation lowers the actual effectiveness of the habitat.

For example, in the Cabinet-Yaak and Selkirk Mountains areas, currently secure areas are small and spatially disjunct.

Habitat Productivity

I used average annual precipitation data from 1961-1990 (Daly, et al. 1994, Daly, et al. 1997, shown in Figure 4, appendix) as a rough proxy for productivity. Current and proposed recovery areas were ranked as percentages among precipitation categories, measured in 25.4 cm increments. This data was used with the home range data to scale the dimensions of linkage habitats and for comparison of mesic and xeric systems.

Estimated Distribution

I used estimated distribution of grizzly bears based on locations from > 10,000 grizzly bear observations (Bader, 2000 b). The distribution data were used for comparison with U.S. Fish & Wildlife Service recovery area totals and for development of the proposed habitat network.

Analysis of Potential Linkage Habitats

I reviewed the literature on linkage corridors pertaining to grizzly bears and identified, mapped, analyzed and ranked potential linkages considered for between-population function.

Identification

Potential between-population linkages for grizzly bears in the Northern Rockies include those identified by Picton (1986), Bader (1991); U.S. Fish & Wildlife Service (1993); (American Wildlands 1997).

Design and Mapping

Design and mapping of corridors generally followed the recommendations of Noss (1992) who suggests functional linkage corridors for grizzly bears should be about twice the width of the mean life range of an adult male, expressed as a rectangle twice as long as wide. Additional considerations include those described by Beier and Loe (1992).

Mattson (1993) first introduced the concept of scaling grizzly bear habitat area requirements according to habitat productivity. Thus, the precipitation data, in conjunction with Noss' formula and the data from Table 3, provide minimum linkage width values for two habitat categories:1) xeric types similar to conditions found in the Yellowstone and Rocky Mountain Front areas; 2) mesic types similar to conditions found in the South Fork Flathead, Selkirk and Cabinet-Yaak areas.

Thus, minimum corridor width for the mesic type is 27.8 km for males and 17.4 km for females, respectively. For the xeric type, minimum widths are 43.5 km for males and 21 km for females.

Corridors were mapped by using straight lines to connect secure areas, which were then buffered on either side to represent the widths determined for male and female needs (Figure 2, page 11). Whenever possible, the larger widths associated with the needs of male grizzly bears were used. These were adjusted when necessary to exclude areas overlapping residential townsites and extensive agricultural valleys, and to include opportunities to expand beyond the minimum width to incorporate public lands and roadless areas and to compensate for bottlenecks as per Noss (1992).

While I do not argue for use of minimum values in designing habitat systems, my analysis of potential corridor habitats was also guided by the reality that townsites and highways are more or less permanent landscape features.

Analysis and Ranking

The effectiveness analysis and ranking of the linkage habitats was based on the following factors:

- total distance between core population areas
- percent of state and federal public land
- percent currently secure
- distances between currently secure areas ≥ 2,833 ha
- productivity rank
- maximum and minimum width
- area:perimeter
- current and historically occupied habitat

Table 1 – Area Required to Support N_e = 500 at Varying Densities and N_e:N Ratios

Density	Area (km²) (N_e:N, 1:5) N = 2,500	Area (km²) (N_e:N, 1:4) N = 2,000	Area (km²) (N_e:N, 1:3) N = 1,500
13.5/1000 km²	184,919	147,883	110,995
15.4/1000 km²	161,869	129,495	97,121
17.4/1000 km²	143,884	115,106	86,329
19.3/1000 km²	129,495	103,596	77,697

USFWS
56,043 – 71,098

Note: The totals of the U.S. Fish & Wildlife Service grizzly bear recovery areas fall below the range of values estimated for spatial needs.

Table 2 – Reported Densities from Interior, Non-Coastal Grizzly Populations

Area	Source	Bears / 1000 km²
Selkirk Mountains	Wielgus, et al. (1994)	
	(a) US only	14.1
	(b) Canada Only	23.3
Cabinet-Yaak	Kasworm & Manley (1988)	3.3 – 4.0
	Calculated from Minimum Population Estimate *N* = 29-34 (W. Kasworm, pers. comm.)	4.3 – 5.1
Northern Continental Divide		
Rocky Mountain Front	Aune et al. (1986)	
	(a) marked only	13.5 – 14.0
	(b) marked & observed	19.6
Mission Mountains	Servheen (1981)	20.4
South Fork Flathead	Mace & Waller (1997)	
	(a) marked only	10.0
	(b) marked & unmarked (*N* = 7/year)	20.3
Yellowstone	Craighead, et al. (1995)	15.4
	Eberhardt & Knight (1996)	14.0
	(Mean Population Estimate *N* = 344)	
	Boyce (1999) population estimate *N* = 420	17.1
Selway-Bitterroot	Boyce & Waller (2000) *K* = *N* = 321	14.4 – 15.0
Northwest Territories	Miller, et al. (1982)	11.6
Canadian Rockies		
Swan Hills	Nagy & Russell (1978)	
	(a) marked only	7.92
	(b) marked & estimated	9.6
West Central Alberta	Nagy, et al. (1989)	4.4 – 4.7
Jasper National Park	Russell, et al. (1979)	9.8 – 11.7
Interior Alaska*	Miller, et al. (1997)	3.2 – 26.0

U.S. Populations only, $\bar{x}$ = 13.7/1000 km² All interior populations, $\bar{x}$ = 14.1/ 1000 km²

For total mean density calculations, a mean of the ranges were used. When more than one source appears for each area, a midpoint or a mean of the values was used.

*From interior, non-coastal influenced populations as per pers. comm. with H. Reynolds.

Table 3 – Mean Annual and Lifetime Home Ranges in the U.S. Northern Rockies

Xeric	Annual Range (km²)	Life Range (km²)
Yellowstone 1	281.0 (F) 874.1 (M)	883.9 (F) 3757.9 (M)
Yellowstone 2	395.7 (F) 365.7 (M)	– –
Northern Continental Divide 3 (East Front)	159.5 (F) 319.7 (M)	– –
Mesic		
Cabinet-Yaak 4	285.4 (F) 1271.9 (M)	606.3 (F) 1535.6 (M)
Selkirk Mountains 5	– –	319.9 (F) –
Selkirk Mountains 6	– –	296.5 (F) –
Selkirk Mountains 7	402.0 (F) –	608.9 (F) –
Northern Continental Divide 8 (South Fork)	120.9 (F) 767.9 (M)	– –

MCP = Minimum Convex Polygon; AK = 95% Adaptive Kernel; M = male; F = female

1 Blanchard & Knight (1991) 1975-1987, MCP.
2 calculated from data in IGBST reports (1988-1997), n = 74 calculated ranges for females, n = 29 ranges calculated for males, MCP.
3 calculated from Aune, et al. (1986), MCP.
4 calculated from Kasworm & Servheen (1995), AK.
5 calculated from Wakkinen & Kasworm (1997) AK, U.S. bears only.
6 calculated from Wakkinen & Kasworm (1997) AK, U.S. & Canadian bears.
7 Almack (1986), MCP.
8 Mace & Waller (1997), AK.

Review of FWS Recovery Goals

U.S. Fish & Wildlife Service recovery areas were analyzed for their ability to sustain a grizzly bear population using the $N_e = 500$ baseline. Using the D value, K was estimated for each U.S. Fish & Wildlife Service recovery area. While K is a relative concept and changes from year to year (Mattson 1998), it is used here to present a theoretical upper range, assuming effective and secure habitat. U.S. Fish & Wildlife Service estimates of N per recovery area were also used to estimate D and compared to D at U.S. Fish & Wildlife Service recovery goals for each recovery area.

Proposed Grizzly Bear Recovery Area

I used current distribution, historic distribution (Merriam 1922), habitat productivity information, the spatial estimates reported in this paper, and the analysis of potential linkage habitats to map a proposed habitat network. My review was also informed by habitat analyses performed by Merrill, et al. (1999) and Craighead, et al. (2000).

The proposed habitat network is based primarily on federal public lands where the public has more control over management and where legal mandates give priority consideration to recovery of threatened and endangered species.

Results

Estimated Density and Spatial Requirements

Estimated densities for interior, non-coastal influenced grizzly bear populations in North America are summarized in table 2. Summing and averaging of densities reported for lower 48 grizzly bear populations yielded $D \approx 13.7$. Including the densities reported for interior, non-coastal populations in Canada and Alaska, $D \approx 14.1$. A weighted mean based on land area would probably lower this value since two of the largest areas, the Yellowstone and south-central Idaho, are also among the more xeric. Therefore, a conservative value for regional mean density is $D \approx 13.5$. At $D = 13.5$, A = 147,883 km² when N = 2,000 and $N_e{:}N$ = 1:4, with A in-

Table 4 – Security Results by Area

Area	Total Area km²	% Secure	Area / Perimeter Ratio km²/km
Northern Continental Divide			
FWS	23,133	62.2	12.4:1
Proposed	24,273	61.1	11.6:1
Yellowstone			
FWS	23,957	80.5	12.2:1
Proposed	53,981	73.7	10.3:1
Cabinet-Yaak			
FWS	6,679	40.7	4.9:1
Proposed	14,573	25.6	6.6:1
Selkirk Mountains			
FWS	2,274	42.0	4.5:1
Proposed	6,299	22.8	5.0:1
Selway-Bitterroot			
FWS	15,128	100.0*	5.3:1
Proposed	52,565	76.4	15.0:1
Totals for Core Recovery Areas			
FWS	71,171	73.7	8.4:1
Proposed	151,691	65.9	10.6:1

* The FWS recovery zone includes the Magruder Corridor, which legally splits the Selway-Bitterroot from the Frank Church-River of No Return Wilderness Areas. Thus, actual security is slightly < 100%.

creasing to 184,919 km² when N = 2,500 and N_e:N = 1:5. A range of area requirements at varying N_e:N and D are summarized in table 1.

Home Range Sizes

Mean annual and life range sizes for grizzly bears in the U.S. northern Rockies are summarized in table 3. Both mean annual and home range sizes for males are significantly larger than those of females, in both mesic and xeric systems. There is an obvious, though unquantified, inverse relationship between home range sizes and density and these appear to be a function of habitat productivity and habitat security. Populations in xeric systems with lower food productivity typically show larger mean home range sizes and lower bear densities (Blanchard & Knight 1991, Aune, et al. 1986). Conversely, high productivity habitat areas show smaller mean home range sizes and higher bear densities (Mace & Waller 1997).

Linkage Analysis and Ranking

The detailed results of the linkage analysis and ranking are shown in Table A of the Appendix. The linkage between the Cabinet Mountains and the northern Bitterroot Mountains appears to represent the most promising opportunity for linkage management for grizzly bear use. It is > 97% public land, has the highest productivity score and it contains numerous verified observations of grizzly bears. Its current low $HS \approx 33\%$ may be somewhat mitigated by a low mean distance between secure areas and a relatively low distance between core population areas. Its width design can accomodate use by both adult males and females. It has by far the least amount of land area (658 km²) required for restoration in order to achieve an overall $HS = 80\%$ throughout the linkage area to serve a residential function. The major choke point limiting its viability is Interstate 90 at Lookout Pass.

Under current conditions, the corridors in the xeric type only marginally satisfy the width requirements for residential use by adult males, serving a primarily migratory function. Opportunities for expansion to the greater width will be limited in many cases. In the mesic types, where productivity results in smaller spatial requirements, corridors can serve both residential and migratory functions for both adult males and females.

Table 5 – Theoretical *K* at Mean Density of 13.5 Bears/1000 km²

Area	FWS Area	Proposed Expanded Area
Yellowstone	323	834
Northern Continental Divide	312	375
Selway-Bitterroot	203	812
Cabinet-Yaak	90	225
Selkirk Mountains	31	97
Linkages*	0**	153*
Total	959	2,496

* Assumes a mean density of 3.9 bears/1000 km² due to low area:perimeter ratios, lower security, and expected higher mortality rates.
** USFWS has not formally identified linkages as part of the grizzly recovery strategy.

Analysis of U. S. Fish & Wildlife Service Goals and Strategies

Spatial Needs

Summing of U.S. Fish & Wildlife Service grizzly bear recovery areas yields a total of 71,082 km² including the Selway-Bitterroot area where reintroductions are under consideration. This figure is 48.1% of the lower end (147,883 km²) of spatial needs. Without the Selway-Bitterroot the total is 56,043 km², or just 37.9% of the lower end figure. Even under the most optimistic scenario, which assumes uniformly high habitat productivity and $D = 19.3$, N_e:N = 1:3, and $N = 1,500$ (table 1), the total U.S. Fish & Wildlife Service recovery areas, including the Selway-Bitterroot area, fall below the lower end estimates for spatial requirements.

Effective Population Size

Results from the analysis of U.S. Fish & Wildlife Service recovery goals are summarized in Table 6. Summing the U.S. Fish & Wildlife Service (1993, 2000) minimum recovery goals for each recovery area results in $N = 1,026$. However, the total N are comprised of isolates, and actual N_e for each isolate is much lower, ranging from 3.6%-15.6% of $N_e = 500$, assuming N_e:N = 1:5.

A qualifier is that the U.S. Fish & Wildlife Service assumes connectivity with grizzly bear populations in Canada for three of the five populations, which if true would raise N_e. However, populations in the border area are depressed and may function as a sink area for U.S. populations (B. Horejsi, pers. comm.). Moreover, the ESA only has legal effect within the U.S. so that U.S. Fish & Wildlife Service recovery goals must be viewed as if they were stand-alone efforts.

Captured Grizzly Bear Distribution

The percent of current estimated distribution area captured within U.S. Fish & Wildlife Service recovery boundaries (Bader, 2000b) by area are: Yellowstone ≈ 51.3%; Northern Continental Divide ≈ 69%; Cabinet-Yaak ≈ 44.7%; Selkirk Mountains ≈ 32.2%. In sum, total U.S. Fish & Wildlife Service recovery areas excluding the Selway-Bitterroot = 56,043 km², 54.7 % of the current estimated distribution area of 102,524 km².

Population Estimates, Recovery Targets, and Bear Density

The U.S. Fish & Wildlife Service (1999a) population estimate for the Yellowstone area (N = 400-600), divided into the 23,957 km² recovery area, results in D = 16.3-25.1. The high end D is approximately twice the Eberhardt & Knight (1996) $D = 12.0$ (as cited in Mace & Waller 1997). The Fish & Wildlife figure is comparable to some of the highest reported densities for interior populations, from areas with higher productivity than the generally more xeric Yellowstone area.

For the Northern Continental Divide area, the minimum recovery target of 391 divided into the 23,133 km² recovery area yields $D = 16.9$, compared to the literature reports of 16.6-25.5.

The Cabinet-Yaak (U.S. portion only) minimum recovery target ($N = 106$) divided into the 6,679 km² recovery area yields $D = 15.9$. The recent estimate of $N \approx$ 29-34 bears (W. Kasworm, pers. comm.) or D = 4.3-5.1, is more comparable to the Kasworm & Manley (1988) D = 3.3-4.0.

Approximately 44% of the Selkirk Mountains recovery area is within the U.S. Assuming equal distribution at U.S. Fish & Wildlife Service recovery levels ($N = 91$), the goal for the U.S. side is $N = 40$. This figure divided into the recovery area (2,274 km², U.S. portion only) yields $D = 17.6$ compared to the Wielgus et al. (1994) $D = 14.1$. Again, assuming equal distribution, the most recent population estimate ($N = 46$, U.S. Fish & Wildlife Service 1999b) leads to $N = 20$ on the U.S. side and $D = 8.8$.

Table 6 – Minimum Grizzly Bear Population Targets Using the U.S. Fish & Wildlife Service Criteria

Area	Minimum Goal	Percent of N_e=500 at N_e:N=1:5
Yellowstone	158	6.3
Northern Continental Divide	391	15.6
Cabinet-Yaak	106	4.2
Selkirk Mountains	91	3.6
Selway-Bitterroot	280	11.2
Total	1,026	

Habitat Security

Security results for current and proposed core areas are summarized in table 4. The proposed areas show lower secure habitat as percentages of the whole than the U.S. Fish & Wildlife Service areas. This shows that current recovery areas have been largely restricted to National Park and Wilderness areas. The proposed areas have a larger total area of secure habitat due to their much larger size.

Habitat Productivity

The results from the analysis of habitat productivity are shown in Table B in the Appendix. As expected, these results are consistent with the differing density and home range estimates reported for mesic and xeric systems (table 3). The Cabinet-Yaak and Selkirk areas show productivity comparable to that found in the South Fork Flathead and Glacier National Park areas, but support much lower *D*. The most reasonable explanation for these differing densities are the extensive road networks and timber harvest programs which have depressed the populations far below optimal *K*.

My review of productivity indicates that in general, grizzly bear distribution is restricted to areas with > 50 cm annual precipitation. Picton (1986) noted a precipitation-density relationship exists in grizzly bears.

Proposed Grizzly Bear Recovery Area

I propose the habitat network for grizzly bear recovery comprising ≈ 190,777 km^2, shown in figure 3. In sum, this proposed habitat network could support a theoretical $K = N = 2{,}496$ (Table 5), with regional $N_e = 624$ when $N_e{:}N = 1{:}4$, and $N_e = 499.2$ when $N_e{:}N = 1{:}5$, assuming effective connectivity among subpopulations.

This proposed habitat network marginally satisfies the spatial needs of a demographically sound and genetically diverse metapopulation. The results of the security analysis suggest that to achieve $HS = 80\%$ of core areas, 21,411 km^2 of habitat must be reconstituted as secure, (either roadless or with low total roads/trails density). By management area these totals are: Yellowstone, 3,401 km^2; Northern Continental Divide, 4,587 km^2; Cabinet-Yaak, 7,928 km^2; Selkirk Mountains, 3,603 km^2; Bitterroot Mountains, 1,893 km^2. Including these totals, ≥ 36, 259 km^2 will need to be reconstituted as secure habitat assuming design of linkages for residential use, and ≥ 28,489 km^2 assuming design of corridors for migratory or genetic functions. Corridors were assumed to be capable of supporting $D = 3.9$ ($N = 151$) based on expected elevated mortality risk and low area:perimeter, although if restored to $HS = 80\%$, portions of these linkages could support $D > 3.9$.

There is ≈ 99,949 km^2 of currently secure habitat within this proposed habitat network, ≈ 68% of the 147,883 km^2 minimum *A* required to support $N = 2{,}000$ at $D = 13.5$. Therefore, with restoration of habitat security in key areas, this proposed habitat network would fall within the range of estimations for population and space.

Three additional areas, the Hells Canyon/Wallowa, Kettle Range, and Bighorn Mountains, are proposed for further study. The Kettle Range and Bighorns were historically occupied (Merriam 1922) and there have been recent observations from the Kettle Range (Washington Department of Wildlife 1998), which may serve as a potential link with the small population in the North Cascades.

Discussion

What are the Appropriate Temporal, Population and Spatial Scales for Grizzly Bear Persistence?

U.S. Fish & Wildlife Service recovery strategy (1993) is predicated on providing a 95% probability of population persistence over a 100 year time horizon. However, Shaffer & Samson (1985) found that while all of their simulated grizzly bear populations with an initial $N = 50$ persisted for 100 years, just 6% persisted for 300 years and 56% of all the populations went extinct in less than 114 years.

Another factor arguing for management over larger temporal and spatial scales is an analysis by Mangel & Tier (1994) which found that most population viability analyses do not incorporate the potential for catastrophic events, even though they are known to occur in the real world. Their analysis found that mean time to extinction was greatly reduced when catastrophes were included in persistence models, concluding existing populations are more at risk genetically than previously thought. While our ability to accurately model catastrophes is limited, a few real-life examples of catastrophic events relevant to grizzly bear persistence include periods of extended drought and major food source failures (Mattson & Craighead 1994), large habitat disturbances such as fires (Mattson 1998), war, and epizootic outbreaks.

Thus, the 100 year time horizon seems an inadequate standard for management performance, particularly for small populations. The timeframe of interest for conservation biology is over several generations to several hundred generations (Frankham 1995). With the generational interval for grizzly bears estimated at ten years (Harris & Allendorf 1989) and a very low reproductive rate (U.S. Fish & Wildlife Service 1993) I believe an appropriate temporal scale is more likely to be in the hundreds of years.

Population size is of critical concern to grizzly bear managers. Extinction risks become severe whenever $N_e < 50$ (Shaffer & Samson 1985) and if populations become too small, they can enter into an irreversible decline or "extinction vortex" (Gilpin & Soule' 1986). The ratio of $N_e{:}N$ is also of direct relevance.

Frankham (1995) found fluctuations in *N* result in lower $N_e{:}N$. This is important for two reasons. First, grizzly bear populations do fluctuate, according to the availability of major food resources (Mattson 1998). Second, if $N_e{:}N = 1{:}5$, then managing for long-term persistence ($N_e = 500$) would lead to a minimum recovery goal of $N \approx 2{,}500$. As shown in Table 1, a 5% decrease in $N_e{:}N$ leads to an increase of 500 in *N*, with corresponding increases in *A*.

In assessing $N_e{:}N$ ratios for conservation purposes, Nunney & Campbell (1993) suggested total *N* should be 5-10 times the value for N_e. Moreover, Lynch & Lande (1998)

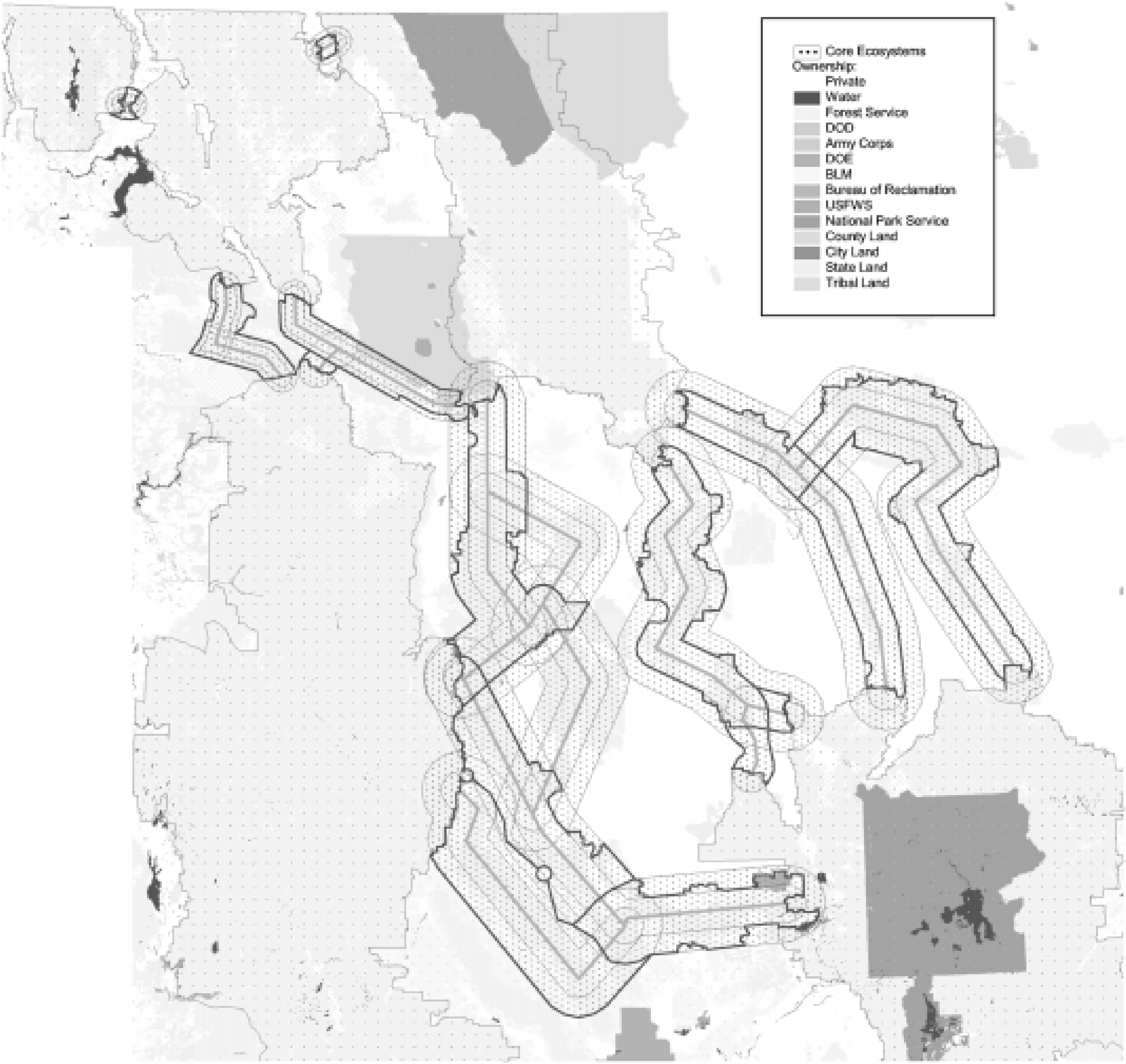


Figure 2 - Potential linkage corridors in the U.S. Northern Rockies for Grizzly Bears.

suggest minimum N_e is closer to 5,000 while Franklin & Frankham (1998) suggest minimum N_e ranges from about 500-1,000. Lynch, et al. (1995) conclude that populations < 1,000 face serious threats of "mutational meltdown" from harmful accumulation of genetic mutations.

I believe my use of $N_e = 500$ is conservative and appropriate in this instance, since the current state of knowledge regarding grizzly bears does not allow for pinpoint precision. These rules and relationships have received some empirical support (Westemeier, et al. 1998) and some theory suggests they may be conservative.Thus, I believe that $N_e = 500$ provides a reasonable measurement for assessing the efficacy of grizzly bear recovery programs and the figures I present are intended to serve as guideposts rather than absolutes. Based on the literature, I argue that the appropriate population scale for grizzly bear persistence lies within the range of N = 2,000-5,000.

Descriptions and prescriptions for spatial needs and habitat security for grizzly bears at the population level are exercises in risk management, and should be scaled to capture the full range of known bear behavior. Mattson (1993) suggested an appropriate scale for analysis in the Yellowstone ecosystem is approximately ten times the average life range size of adult females ($\bar{x}$= 884 km^2, Blanchard & Knight 1991) or 8,884 km^2.

Other investigators have suggested the appropriate scale for capturing broader environmental phenomena may be 10-15 and as much as 50-100 times the size of the largest disturbance patch (Shugart & West 1981). In the northern Rockies, wildfires burned ≈ 10,460 km^2 in 1988 (National Interagency

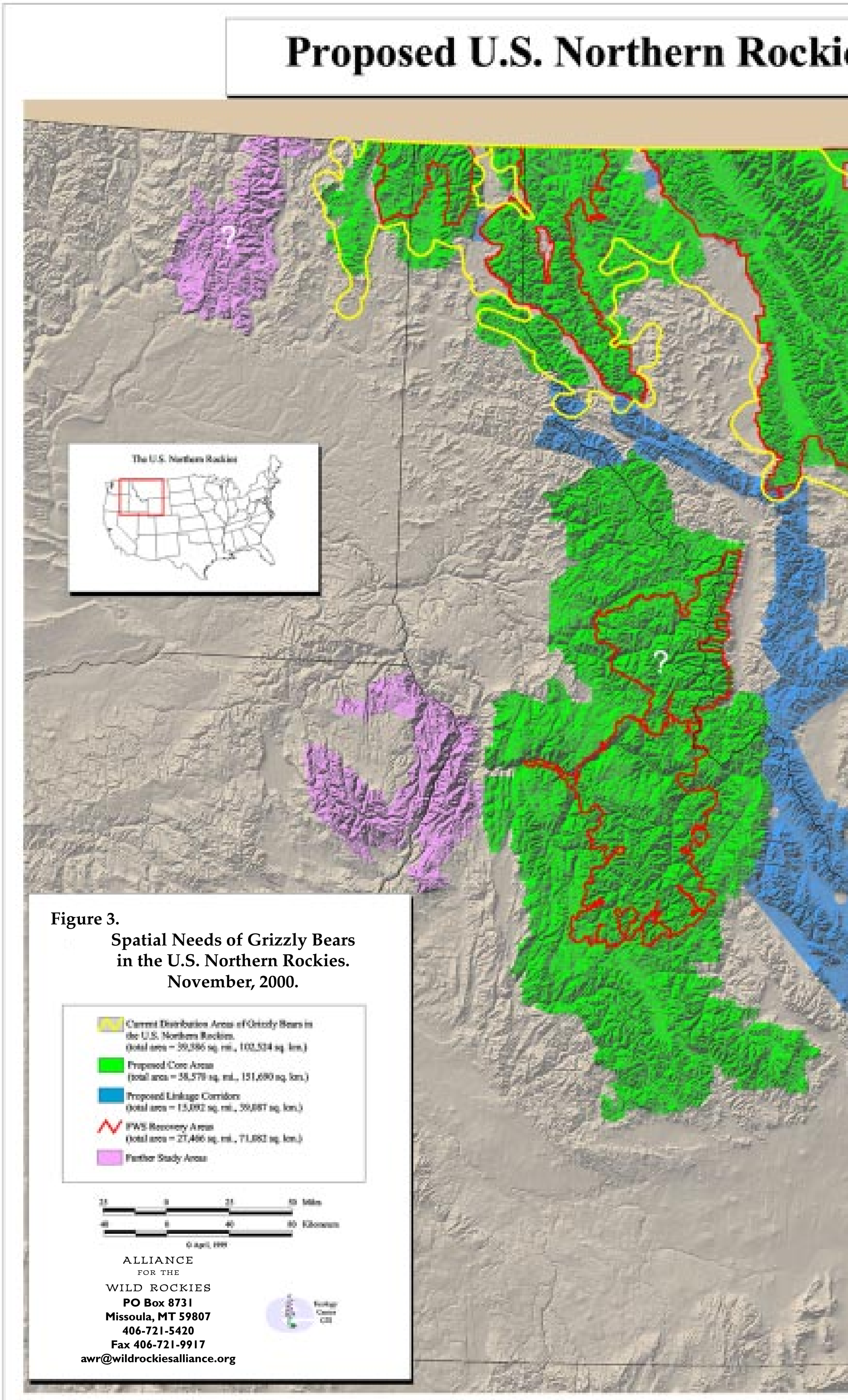
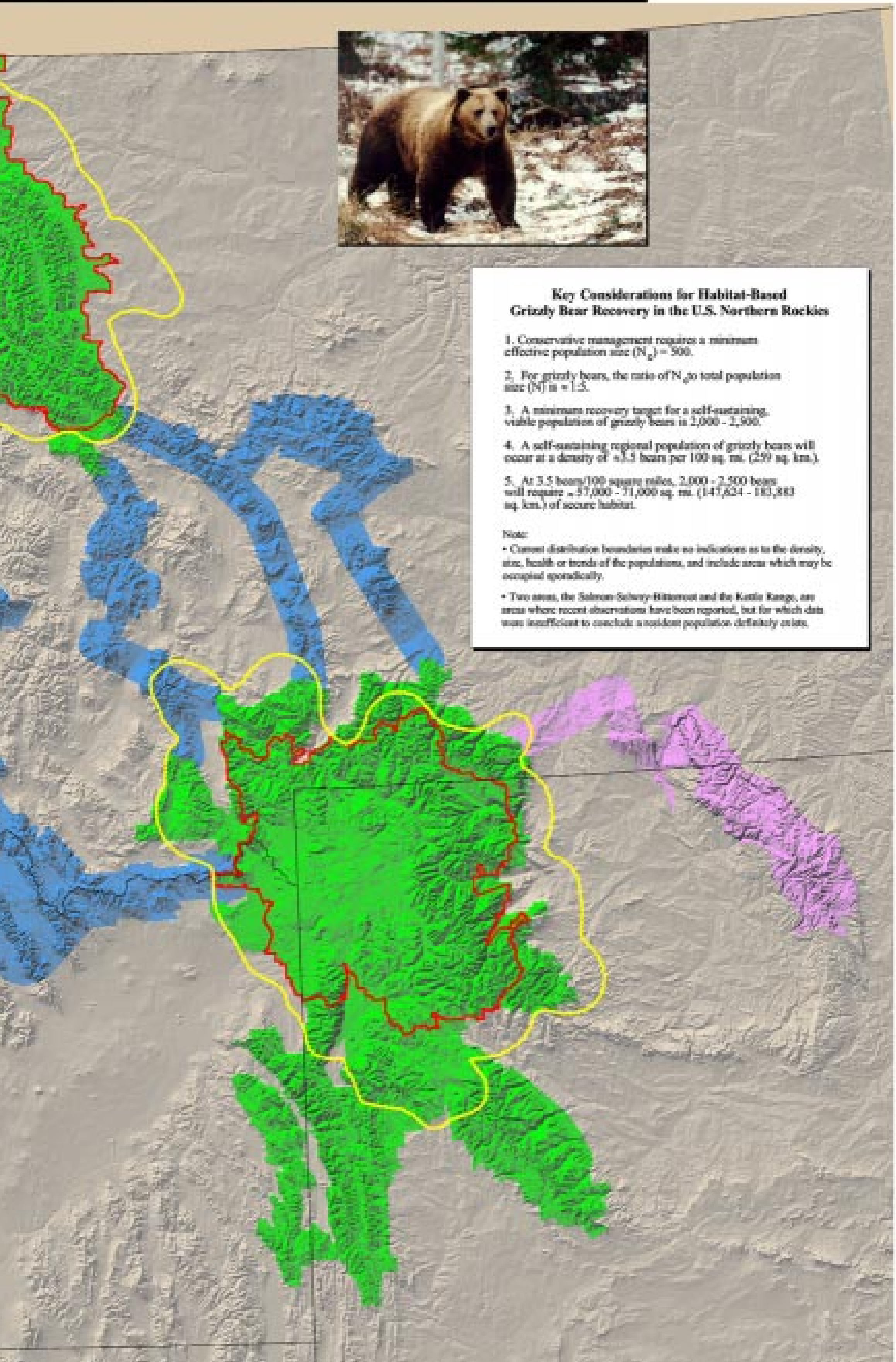


Figure 3.
Spatial Needs of Grizzly Bears in the U.S. Northern Rockies. November, 2000.

es Grizzly Bear Recovery Area



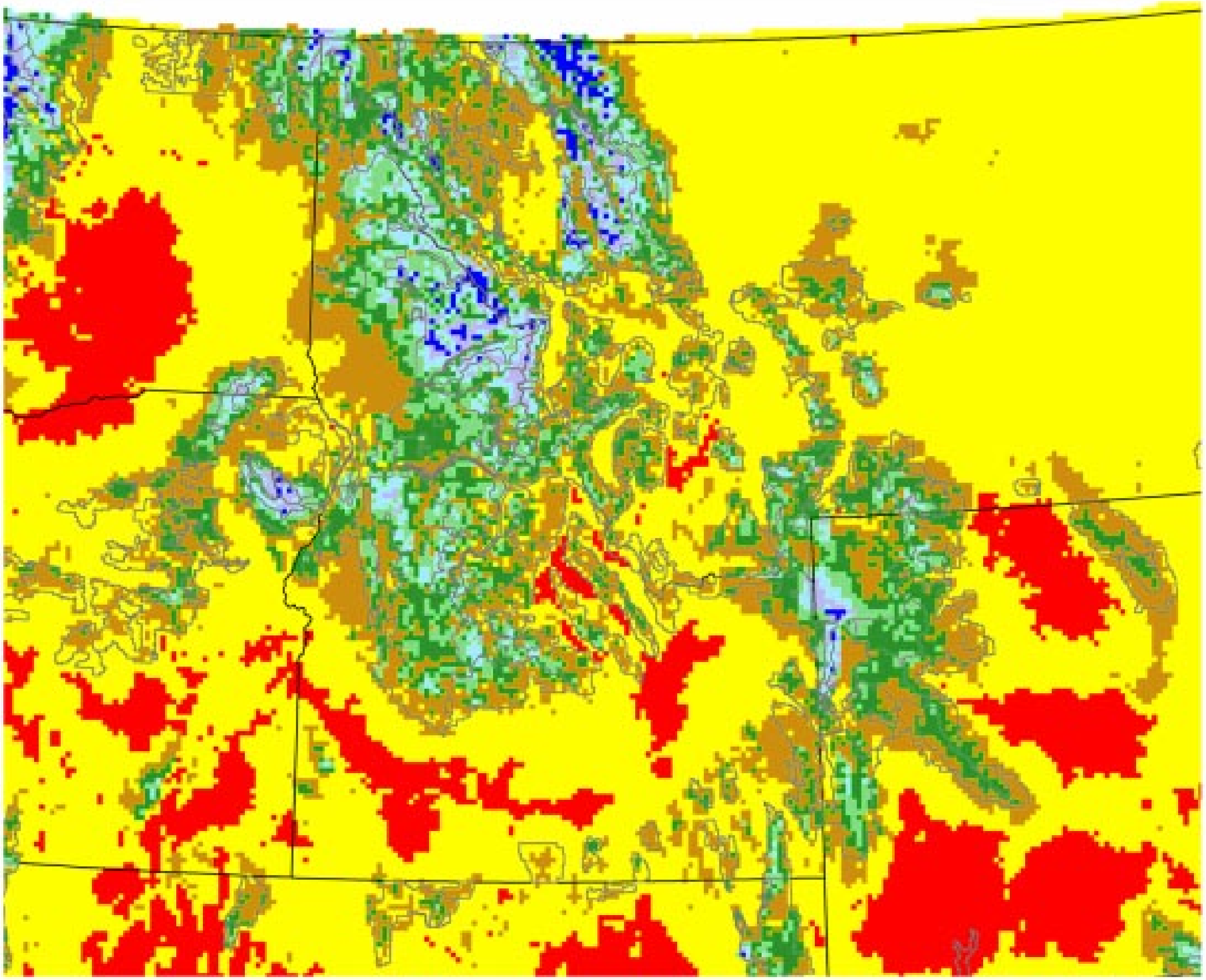


Figure 4

Mean Annual Precipitation

1961 - 1990

National Forests

Mean Annual Precipitation:

- 0 - 25.4 Centimeters
- 25.4 - 50.8
- 50.8 - 76.2
- 76.2 - 101.6
- 101.6 - 127
- 127 - 152.4
- 152.4 - 177.8
- > 178

Based on data in:

Daly, C., R.P. Neilson, and D.L. Phillips. 1994 A statistical - topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meterology 33: 140-158.

Daly, C., G.H. Taylor, and W.P. Gibson. 1997. The PRISM approach to mapping precipitation and temperature, In reprints: 10th Conf. on Applied Climatology, Reno, NV, American Meterological Society, 10-12.

Fire Center). Using this as the size of the largest disturbance patch, a minimum dynamic area (Pickett & Thompson 1978) in the U.S. northern Rockies may be ≈ 104,606-156,909 km^2, and possibly even > 500,000 km^2.

Based on the Allendorf, et al. (1991) estimate of grizzly bear N_e:N ≈ 1:4, and reported grizzly bear densities, Metzgar & Bader (1992) concluded that at a regional mean density of 4 bears/259 km^2, a distribution area of 129,495 km^2 of secure and connected habitats are required to support N = 2,000.

However, there are reasons to believe the earlier estimations for spatial needs may be too low. For example, Allendorf & Ryman (In Press) report that N_e:N for grizzly bears ≈ 1:5 and total N ≈ 5,000 may be required for long-term persistence. In Bader (2000b) I note that most grizzly bear study areas have been located within habitats with higher productivity and security, leading to potential sampling biases. Moreover, my review of habitat productivity indicates that vast areas of the potential habitat network are comprised of xeric habitats which will naturally support lower bear densities.

Taking the high end estimated N = 1,000 (U.S. Fish & Wildlife Service 1999a), divided into the A = 102,524 km^2 yields D = 9.8. This simple analysis indicates the D = 15.4 suggested by Metzgar & Bader (1992) as a reasonable approximation may have been slightly optimistic given the large amount of the total area that is comprised of generally more xeric habitats, extensive alpine areas above treeline and the total area required for restoration to secure habitat conditions.

It is clear that the size does count when designing effective habitat networks. For example, larger reserves are known to hold more species, better support wide-ranging species such as grizzly bears, and have lower extinction rates than smaller reserves (Meffe & Carroll 1994). In a review of western national parks, (Bekele 1980, cited in Harris 1984) found the two largest (Yellowstone and Glacier) had retained more large mammal species than any of the others. This is important for grizzly bears, which exhibit exploded home ranges in drought years and years with major food resource failure, leading to use of habitats seldom used during years of food abundance. For example, Mattson (1998) found a direct link between years of low whitebark pine production in the Yellowstone area, and elevated levels of mortality and management actions involving grizzly bears. Knight, et al. (1988) reported female mortality rates were inversely related to years of low natural food availability. The same trend has been documented in other ecosystems during years of poor huckleberry production or mast crops (Jonkel & Cowan 1971, Rogers 1976). Thus, K changes from year to year, and ecosystem to ecosystem, and even within ecosystems, greatly influencing spatial needs. Narrow or peninsular reserves will create "crammage" even in good food years, and elevate mortality risk and stress within bear populations in drought or poor food source years.

Wide-ranging species such as grizzly bears are especially vulnerable to sink habitats. These sinks exist across the landscape and virtually every bear has one or more major developments and roads within its home range (Knight, et al. 1988). They found that most eventually die in association with one of the sinks.

Habitat management and spatial needs for grizzly bears have traditionally focused on adult females for demographic reasons (U.S. Fish & Wildlife Service 1993, 1999a). However, Harris & Metzgar (1990) found that male grizzlies have value with respect to population growth rates while Shaffer & Samson (1985) reported that 58% of their simulated grizzly bear populations went extinct due to loss of adult males. Males have significantly larger home ranges (table 3) and dispersal distances (Table C. appendix) and hence may be the primary source of gene flow (Craighead & Vyse 1994). Adult males are also typically at the top of grizzly bear social hierarchies (Craighead, et al. 1995). Therefore, the needs of male grizzlies must be considered when attempting to preserve a behaviorally-structured, genetically-diverse population.

I argue that the appropriate spatial scale for grizzly bear persistence in the U.S. northern Rockies falls within my estimated range of 147,883-184,919 km^2, which I believe is responsive to the factors discussed above. Of course, if minimum N_e is > 500, spatial needs increase significantly.

Metapopulations or Isolated Reserves?

Grizzly bear habitat in the U.S. northern Rockies is not contiguous. Rather it occurs as a series of spatially disjunct and semi-isolated blocks, with none of the remaining blocks capable of supporting N = 2,000-2,500. Thus, they must either be connected with a system of habitat linkage areas, bears be mechanically translocated from one area to another, or the blocks be managed as non-viable isolates. Rather than discrete recovery areas, I suggest that the proposed habitat network shown in Figure 3 be formally adopted by U.S. Fish & Wildlife Service as the basis for its recovery strategy for grizzly bears.

The concept of the metapopulation, classically defined by Levins (1969) as a collection of populations, often occupy patches of source and sink habitats (see McCullough [1996] and Meffe & Carroll [1994] for more detailed assessments of metapopulation structures). Populations in sink areas avoid extirpations through demographic "rescue effects" (Brown & Kodric-Brown 1977), whereby immigrants from other patches prevent local extirpations or serve as a source of refounders for vacant patches. Source habitats allow and provide dispersing members of the species to replenish sink habitats.

Mangel & Tier (1994) suggest that metapopulation structures may be more resilient in the face of catastrophes, since there is less likelihood that all the habitat patches (subpopulations) would be wiped out by the same catastrophe, therefore spreading risk among populations (Rieman & McIntyre 1993). In modeling efforts, linked metapopulations have been shown to significantly increase the prospects for grizzly bear persistence in the northern Rockies (Boyce 2000). Grizzly bears are believed to have historically occurred as one contiguous population which has been fragmented by human settlement and activity into a potential metapopulation (Craighead & Vyse 1994).

Current U.S. Fish & Wildlife Service recovery policy fails to establish effective linkages although studies are in progress. Moreover, undersized recovery areas actually increase the distances between isolates, since grizzly bears do not receive priority consideration on public lands outside the recovery areas and face low habitat security conditions and higher mortality rates (Bader, 2000b). The low *N* in the isolates is of additional, non-genetic concern in light of the Allee effect (Allee, et al. 1949), defined by the occurrence of a low-density extinction threshold (Nunney & Campbell 1993) which can arise from the difficulty of locating suitable mates when populations are small. They believed this to be more of a factor in wide-ranging, territorial species.

Helicopters or Corridors?

There is general agreement amongst conservation biologists that connectivity confers numerous benefits to species conservation (Beier & Noss 1998). Therefore, the question relevant to grizzly bear management is whether connectivity should be maintained via linkage corridors or mechanical translocations.

There is debate regarding the efficacy of linkage corridor strategies in general (Simberloff, et al. 1992; Mann & Plummer 1995). However, corridor viability for mammals continues to gain empirical support (Laurance & Laurance 1999) and Beier & Noss (1998) found that evidence from a review of well-designed studies suggests corridors are valuable conservation tools.

Simberloff, et al. (1992) suggest corridors may be mechanisms for the spread of diseases. However, Mattson et al. (1996) noted there are no known catastrophic diseases affecting grizzly bears and they rejected this reason for dismissing the value of linkages. Beier & Noss (1998) place the burden of proof for corridor value on those who argue they are harmful to conservation.

Published research regarding corridor effectiveness for grizzly bears has been very limited. Picton (1986) concluded a functional linkage between the Yellowstone and Glacier National Park areas is possible, even though they are > 200 km apart. The U.S. Fish & Wildlife Service (1993) identified potential corridors for analysis although no results have yet been published.

My analysis of potential linkages (Table A, appendix) combined with the dispersal distances shown in Table C shows that secure areas ≥ 2,833 ha, ("demographic stepping stones," Mattson, et al. 1996) are spatially distributed within known dispersal distances for male and female grizzly bears. Moreover, Mills & Allendorf (1996) report as few as one immigrant per generation can suffice for maintenance of genetic variation within populations, with the generational interval of grizzly bears approximately 10 years (Harris & Allendorf 1989).

Craighead and Vyse (1996) concluded that male grizzlies, and particularly subadults, are most likely to use corridors for dispersal and can maintain genetic diversity. However, recolonization of empty habitat patches depends upon female dispersals, which are typically over shorter distances, requiring design of corridors which contain habitat capable of supporting several females through their lifetimes and the lifetimes of their offspring.

In reality, grizzly bear linkage corridors would likely function differently from the popular misconception of corridors supporting frequent migratory movements of grizzlies between distant core areas. Linkages, if effective, would serve to either grow the populations together (residential corridors) or provide demographic and genetic rescue through patches of secure habitat which may represent small islands of reproductive activity, spatially distributed within known dispersal distances (Mattson, et al. 1996). Elevated mortality risk and lower density are almost certain to be associated with corridors due to their peninsular configuration, isolation of secure areas, and low area:perimeter.

I argue that mechanical translocations as a connectivity strategy are problematic for numerous reasons. First is the low success rates associated with translocations. Servheen et al. (1995) report on four grizzly bears translocated from British Columbia to the Cabinet Mountains. Their results indicated poor survival for the four bears, which reared no cubs. Data from management relocations indicate adult females have just a 60% relocation success rate after coming into contact with humans (Montana Department of Fish, Wildlife & Parks 1992) and even lower success was reported in the greater Yellowstone area (Meagher & Fowler 1989).

To overcome very strong "homing" instincts in grizzly bears, minimum translocation distances must be ≥ 241 km (H. Reynolds, Alaska Department of Fish & Game, pers. comm.). This limits opportunities for mechanical translocations within the northern Rockies.

While empirical support for corridor linkages is limited, I argue that the available information shows effective linkages for residential use by grizzly bears are theoretically possible and would boost persistence probabilities. Support for linkage corridor management for grizzly bears has also gained the support of numerous professional scientific societies including The Wildlife Society, the American Society of Mammalogists, and the Montana Society for Conservation Biology. This points towards a metapopulation strategy for grizzly bear recovery in the U.S. northern Rockies. Ultimately, the only way to assess the efficacy of linkage corridor management for grizzly bear use is to establish and study them. Key to this strategy is protection of key linkage habitats now, before fleeting opportunities for their conservation are lost (Craighead, et al. 1995).

Bear Density

Density is one of the critical population statistics grizzly bear managers should monitor. Density ranges on a continuum from extirpation to optimal *K*, based on habitat productivity and security.

While $D = 13.5$ is an estimation and presented as a guidepost rather than an absolute, I believe it is not unduly conservative given that vast portions (> 103,000 km^2) of suitable and potentially suitable grizzly bear habitats occur within xeric, lower productivity areas such as the Yellowstone, Rocky Mountain East Front, and south-central Idaho. Areas on the fringe of the total recovery zone will likely support lower densities. Large areas are impacted by human developments, high road densities, livestock use, and extractive industrial activities, which can lower bear densities. Merrill, et al. (1999) predict that areas with high human population density and land use will be a limiting factor on grizzly bear recovery and habitat suitability and trends in the region are towards increasing human population. I argue that $D = 13.5$ is a conservative value. It is consistent with $D = 13.2$ reported by U.S. Fish & Wildlife Service (1993) from research in the Northern Continental Divide, Yellowstone, and Cabinet-Yaak areas, and $D = 14.1$ in the Selkirk Mountains. Using a Resource Selection Function method, Boyce & Waller (2000) estimated $K = N = 308$-321 for the most productive portion of the Selway-Bitterroot region. This results in $D = 14.4$-15.0. Incorporating the geographically larger and xeric southern portion of this region would most certainly lower the value for D. I found a basic uniformity to density estimates reported for interior populations, differing as might be expected based on variations in habitat productivity and security. Reported densities in the contiguous 48 states cluster around $D \approx 11.6$-19.3 and my review of habitat productivity supports a conservative view of regional mean density. I do not in any way suggest that $D = 13.5$ is a standard for managers to manage down to. Many productive habitats can and should support $D > 13.5$ and these areas can serve as source populations for areas with lower productivity and security. However, based on the literature, $D = 13.5$ is a reasonable approximation of a regional mean density for calculation of total spatial needs.

Recovery Targets and Population Viability

U.S. Fish & Wildlife Service grizzly bear recovery documents (1993, 1997, 2000) take into account genetic and demographic concerns by reference, but have implemented few actions to incorporate such concerns into active management.

While current U.S. Fish & Wildlife Service estimates for $N \approx 800$-$1{,}000$, summing the minimum recovery goals by recovery area yields $N = 746$ ($N = 1{,}026$ with the Selway-Bitterroot). Thus, de-listing and removal of ESA protections for grizzly bears could occur in the absence of a significant increase in total N. I argue that the grizzly bear recovery program exhibits a pattern similar to that detected by Tear, et al. (1993) who found that 28% of threatened and endangered species recovery plans identify population recovery targets at or below the number thought to exist when the species were listed. The Tear, et al. analysis also found that 37% of recovery plans call for the total number of populations to be at or below the number at the time of listing. In these cases, they suggested such species are "being managed for extinction." U.S. Fish & Wildlife Service is currently maintaining 4 grizzly bear sub-populations in the U.S. northern Rockies, the same number that existed at the time of ESA listing in 1975. While establishment of a fifth sub-population in the Selway-Bitterroot area is being contemplated (U.S. Fish & Wildlife Service 2000), it would be managed as an isolate, with none of the genetic benefits of a connected metapopulation. In fairness, it appears likely some gains in population have been made in the Yellowstone area, yet current FWS strategy would be predicated on the two largest recovery areas being isolated from the others.

Habitat Security

Human-caused or related mortality accounts for > 85% of recorded grizzly bear mortalities in the Yellowstone and Northern Continental Divide areas (Bader 2000a). The agent most associated with such mortalities are roads which allow access into grizzly bear habitat. Mattson & Knight (1991b) found that secondary roads presented a mortality risk five times that of roadless backcountry areas, ranked second only to primary developments in lethality. Telemetry locations of adult females over a ten year period coincided with the areas of lowest road and trail densities in the Yellowstone area. Bader (2000a) reports that ≈ 64% of all recorded grizzly bear mortalities in the Yellowstone and Northern Continental Divide areas occurred within 2 km of roads and 4 km of major developed areas. Several other studies documented that bears avoid roads at all road density levels. Bears generally avoided areas within 500 m of roads more than expected and this zone of avoidance ranges up to 3 km (see Mattson, et al. 1987; Kasworm & Manley, 1990; McLellan & Shackleton, 1988; Archibald, et al., 1987; Wakkinen & Kasworm, 1997; Schallenberger & Jonkel 1979). Recreational trails among unhunted populations also create displacement effects (Gunther 1990). Not all bears respond equally to these factors. Blanchard & Knight (1991) found indications that females with yearlings chose security over productivity in their use of habitats.

Grizzly bears generally occur in two distinct types of landscapes in the U.S. northern Rockies. The first type are characterized primarily by landscapes capable of supporting $N \geq 200$ over areas $\geq 23{,}000$ km^2. These landscapes contain large cores of Park, Wilderness, and roadless lands, and provide for short-term viability over a period of a few generations ($N_e \geq 50$). The second type consists of landscapes comprised chiefly of habitats which are highly fragmented, with small secure areas, and no large cores of park and wilderness lands. These landscapes are currently incapable of supporting $N_e \geq 50$ unless substantial blocks of type one landscapes are reconstituted through active management strategies. These lands may also be considered to be the matrix of lands heavily roaded, logged, etc. located within and between type one landscapes. In the U.S. northern Rockies, the Yellowstone, Northern Continental Divide and Selway-Bitterroot areas constitute type one habitat blocks and the Cabinet-Yaak and Selkirk Mountains are comprised of mostly type two. The absence of large secure areas helps explain the low bear densities in these areas relative to their productivity. These may also be characterized as source and sink habitats (Doak 1995, Bader 2000a). The Cabinet-Yaak and Selkirk Mountains results reveal densities for recovered populations far above recent estimates. Given current total road densities and habitat management direction, a four-fold increase in the bear population is extremely unlikely in the near future without an aggressive program of road obliteration, increased cover component, and reductions in illegal killings.

To address this problem, Mattson (1993) recommended open road densities of .42 km/km^2 to protect female/cub groups in the Yellowstone area. Craighead, et al. (1995) recommended maximum allowable road density of .40 km/km^2 for national forest lands containing grizzly bear habitat. With off-road recreational vehicle use on national forest lands burgeoning, a reasonable approach is to calculate total road and trails density. Priority allocation for road closures should focus on blocking up secure areas as well as achieving total road and trail density standards. Closures should further be prioritized based on actual bear locations and home range data (when available) and vegetative productivity based on satellite images ground-truthed according to methods described by Craighead, et al. (2000).

Bears can and do live in the matrix of sink habitats, but often at negative mean population growth rates, rendering them as mortality and habitat sinks for the source habitats. For example, one ten-year study of a grizzly bear population within a partially multiple-use landscape calculated a mean 2.5% annual negative population growth rate (Mace & Waller 1997), even though habitat productivity is very high in their study area.

Too Many or Not Enough?

Current U.S. Fish & Wildlife Service philosophy holds that grizzly bears outside the delimited recovery areas are "surplus" and thus not essential to achieving population recovery goals (U.S. Fish & Wildlife Service 1997, 2000), see also, Eberhardt & Knight (1996). Moreover, grizzly bear mortalities of all types which occur > 16 km outside the delimited recovery areas are subtracted from allowable mortality calculations, regardless of their reproductive status (U.S. Fish & Wildlife Service 1993, 1999a).

This view is contrary to an alternative view of expanding the active management area to allow both larger subpopulations and larger subpopulation habitat area, to accommodate basic principles of conservation biology and conservation genetics that larger is better.

Applied to a species listed as threatened under the ESA and managed as isolates at a small fraction of minimum N_e required for long-term persistence, the concept of "surplus" is confusing and contradictory. In Bader (2000b) I question the legality of this bifurcated management strategy, since bears outside the recovery zone are for all intents and purposes managed as if they were not an ESA listed species. Implicit in the current U.S. Fish & Wildlife Service management strategy is that what bears have now in terms of available habitat is all they will get. This strategy is inconsistent with the grizzly bear recovery plan (1993) investigation of linkages, and other research and discussion regarding genetic concerns (U.S. Fish & Wildlife Service 1997, 2000).

Another consequence of the "surplus" theory is that managers may relax their management tolerance for conflicts and kill more grizzlies (Mattson, et al. 1996), particularly outside recovery lines. In fact, a recent policy allows for more liberal killing of livestock depredating grizzly bears beyond recovery zone boundaries in Wyoming. Thus, recent gains in management which have reduced mortalities associated with management actions within Yellowstone National Park may be offset or reversed by increased mortalities outside the current recovery area. Indeed, mortalities in the Yellowstone area reached at least 19 in 2000, the most since 1981 (Peck, pers. comm.).

Conclusions and Recommendations

I conclude that the spatial needs of a genetically and demographically sound grizzly bear population in the U.S. northern Rockies ranges from 147,883- 184,919 km^2 and I recommend a habitat network comprising 190,777 km^2 to meet the estimations for population and space.

I conclude that the U.S. Fish & Wildlife Service recovery strategy for grizzly bears (1993, 1997, 2000) will not achieve demographic and genetic population viability and it exhibits a pattern detected by Tear, et al. (1993). At this time, the strategy lacks an adequate vision and accompanying regulatory framework. My analysis reveals that current grizzly bear recovery areas, in sum, are inadequate to satisfy the spatial needs of a viable metapopulation. The U.S. Fish & Wildlife Service, as well as other management agencies including the U.S. Forest Service, have embraced a management philosophy that treats current recovery area boundaries as hard. When grizzly bears attempt to exist beyond these delimited areas, they are often relocated or destroyed. Land management practices and activities often do not take into account potential adverse effects on grizzly bears and their habitat beyond the bounds of delimited recovery areas. Implied in this management strategy is that what grizzly bears have now in terms of available habitat is all they will ever get.

Minimum population recovery goals for each recovery area are far below optimal *K*. Moreover, in the Cabinet-Yaak and Selkirk Mountains areas, proposed recovery targets are not likely to be achieved under current habitat management strategies. Thus, neither the U.S. Fish & Wildlife Service population recovery targets nor the total recovery area are within the range of estimates we can infer from the literature.

While there have been real improvements and progress in grizzly bear management within the recovery areas (for example, better food storage regulations and bear-proof garbage containers, lower management mortality within the national parks, and removal of domestic sheep from some critical habitats), it appears that the U.S. Fish & Wildlife Service and other management agencies are imposing a biological cap on grizzly bear populations, preventing significant gains in both population numbers and distribution, two central goals of threatened and endangered species recovery planning. While it is unrealistic to expect to recover bears throughout their historical distribution, even over a temporal scale of several hundred years, current management direction is preventing effective gains in distribution and reductions in mortality on public lands, where the easiest gains are to be made.

The ESA does not recognize two classes of threatened species and my analysis suggests the U.S. Fish & Wildlife Service has made a *de facto* conclusion that grizzly bears outside the recovery zones are "not essential, surplus" populations. While the recovery targets have clearly been portrayed as minimums, they are levels which would satisfy legal mandates under the ESA. Thus, consequent removal of ESA protections for grizzly bears and their habitat could occur at significantly less than optimal *K*. This leaves room for substantial degradation of grizzly bear habitat, particularly in terms of habitat security, since lower recovery targets could translate into relaxed standards for habitat protection management.

Despite numerous attempts, accurate census of grizzly bears remains elusive (Mattson & Craighead 1994). I argue that protection of habitat is a more reliable method of achieving a self-sustaining grizzly bear metapopulation. Habitat-based recovery should provide for management of a sufficient number of individuals, over a sufficient area of land, with sufficient habitat security, such that significant management intervention is no longer necessary to prevent serious and prolonged downward trends in population growth. The analysis undertaken suggests an interim viability goal of 2,000-2,500, based on demographic and genetic considerations. This benchmark would guard against excessive rates of inbreeding depression and fitness effects as well as Allee and other demographic effects while other options are developed and implemented to enhance the probabilities of longer term persistence. The habitat needs of populations, including design of habitat networks which satisfy the requirements for spatial needs necessary to grow the population, must be incorporated into definitions of population viability.

My results suggest that recovery of grizzly bears in the U.S. northern Rockies is a daunting task requiring bold and decisive action on behalf of the U.S. Fish & Wildlife Service, the U.S. Forest Service and other land and wildlife management agencies, and should provide a sobering effect on unduly optimistic reporting of recovery achievements and proposals for de-listing of grizzly bear sub-populations.

The first necessary step is expansion and linkage of the current recovery area system. Bears on or beyond the fringes of currently inhabited core areas are likely to be important to grizzly bear populations since population and range expansion typically occurs at the outer bounds of populations. Not only are bears on the fringes the most likely individuals to spread genetic material from one subpopulation to another, these bears pioneer new territory, which must occur in order to achieve a linked metapopulation of 2,000-2,500 grizzly bears distributed throughout $A > 147{,}883\ \text{km}^2$.

A practical consideration is the land area that is currently available as suitable or potentially suitable habitats. Achieving higher goals, such as $N = 5{,}000$ (Allendorf & Ryman, In Press) will require maintaining current laws such as the Endangered Species Act. If similar laws were enacted for Canadian lands, connectivity with adjacent Canadian grizzly populations might allow this goal to be realized.

The strength of the proposed habitat network shown in Figure 3 is that it is based on actual, historic and reasonably projected distribution of grizzly bears in the U.S. northern Rockies, over an area sufficient to support a total population twice current estimates. Private lands are largely excluded from this proposed management area, since legal mandates and management control are lower or nonexistent in these areas and they are often mortality sinks for grizzly bears. However, some critical habitat components which occur on private lands can and should be secured through conservation easements, willing seller basis purchases, or land exchanges, in order of desirability, or privately developed management plans (example, the Nature Conservancy's Pine Butte Swamp Preserve). Private land trusts play a major role in successful efforts to secure important grizzly bear habitat within private land ownerships. These strategies will be particularly vital to establishment of effective linkage corridors.

Population viability analyses for grizzly bear suggest currently isolated populations face reduced probabilities of persistence unless they are linked through habitat corridors or replenished with immigrants via mechanical translocations. I conclude that restoration of functional between population linkage corridors for grizzly bears, serving both demographic and genetic functions, is possible. I argue that immediate action must be taken to restore and manage the linkages shown in Figure 3.

The alternative to the proposed course of action is highly intrusive and intensive management involving the mechanical translocation of bears from one recovery area to another. I argue that mechanical translocations take the easy way via a technological quick-fix. Translocations are costly, controversial and are largely unproven as a successful strategy. They would also be subject to continuing congressional appropriations of necessary funds, as well as public support. This strategy would also represent giving up on establishment and restoration of functional linkages before this approach has even been given a chance. The inconsistencies in U.S. Fish & Wildlife Service direction indicate the agency must now explicitly declare its operating strategy as to whether it will be comprised of linked or isolated reserves.

Ultimately, grizzly bears are likely to occur only where people allow them to live. That is, people will have to support having grizzly bears in a larger area in the U.S. northern Rockies in order to effectively manage a demographically and genetically viable, self-sustaining population. With clearly stated goals and scientifically sound methods, the necessary public support is possible.

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Table A - Linkage Results

Linkage	Total Area km²	Total Length (km)	% Public Land	% Secure	Min/Max width (km)	Mean (km) Distance[2] (range)	area: perimeter	Total Rank (1 = highest)
GYE/NCDE Route I	5,154	201.8	64.3	22.2	12.9/12.9	14.3 (3.7-20.8)	5.4:1	10
Route II	4,346	208.9	38.4	21.5	15.1/26.6	4.4 (0.2-32.7)	5.1:1	5
Route III	8,378	333.3	58.0	36.2	15.1/45.4	7.9 (0.2-32.7	5.8:1	6
GYE/GSSE Route I	8,479	261.5	79.6	38.4	21.1/47.5	2.9 (0.3-7.7)	6.0:1	7
Route II	9,458	266.4	83.6	37.4	21.1/43.0	4.8 (0.2-10.6)	8.0:1	8
NCDE/ GSSE	5,522	181.5	84.7	51.2	16.6/32.2	7.4 (0.5-32.7)	6.1:1	3
CYE/GSSE	1,409	76.9	97.4	33.4	17.4/21.9	5.8 (0.3-13.0)	3.9:1	1
CYE/NCDE Route I	1,961	117.3	82.5	23.8	14.2/17.4	7.9 (0.5-28.3)	4.1:1	2
Route II	106	9.5	15.4	0.004	10.8/10.8	7.9 (no range)	1.1:1	9
CYE/SE	122	5.5	18.6	0.002	17.4/17.4	3.2 (no range)	0.9:1	4

1- Security defined as Wilderness, Parks, and inventoried roadless areas ≥ 7,000 acres.
2- Mean distance between secure areas ≥ 7,000 acres.

Table B – Results of Habitat Productivity Analysis Using Annual Precipitation Data. Percentage of Total Area by Precipitation Class Measured in 25.4 cm Increments

Area	0 - 25.4	25.4 - 50.8	50.8 - 76.2	76.2 - 101.6	101.6 - 127	127 - 152.4	152.4 - 177.8	> 178
Selkirk Mountains								
a	0	0	5	22	24	26	15	8
b	0	0	15	38	21	16	7	3
Cabinet-Yaak								
a	0	0	21	38	21	8	7	5
b	0	2	37	30	17	7	4	3
Northern Continental Divide								
a	0	4	20	22	18	15	11	10
b	0	4	22	22	17	15	11	9
Yellowstone								
a	0	3	23	43	21	6	3	1
b	0	6	36	38	13	4	2	1
Selway-Bitterroot								
a	0	7	19	28	21	15	9	1
b	0	6	22	29	22	12	6	3

a – Recovery area delimited by U.S. Fish & Wildlife Service (1993, 2000)
b – Proposed areas.

Table C- Reported Distances of One-Way Grizzly Bear Movements in the Northern Rockies

Area	Source	*N*	Distance (km)
Yellowstone	Blanchard and Knight (1991)	5 (Males)	45 - 105
Yellowstone	Blanchard and Knight (1991)	1 (Female)	34.9
Yellowstone	IGBST (1998)	1 (Male)	≈ 161
Selkirk Mountains	Almack (1986)	1 (Female)	45.5
NCDE	Kasworm (pers. comm. 2000)	1 (Female)	≈ 150

Table D – Percent of Current and Proposed Core Recovery Areas with > 101 cm Annual Precipitation.

Area	Current	Proposed
Selkirk Mountains	73	47
Cabinet-Yaak	41	31
Northern Continental Divide	54	52
Yellowstone	31	20
Selway-Bitterroot	46	43