Life history, reserve design and umbrella effects: grizzly bears and aquatic systems in western Montana

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Word count: 7186 including Tables and Appendix

Running Head: *Reserve designs for grizzly bears and aquatic systems*

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Abstract: *To investigate complementarity and the umbrella concept in conservation design, we compared spatial overlap and other similarities and differences between model-based conservation designs for grizzly bears (*Ursus arctos horribilis*) and aquatic biota in a case study region comprising Montana, U.S.A., west of the Continental Divide. We used previously-developed models that included the effects of habitat productivity, potential human activity, and access density on grizzly bears, and for aquatic systems, the stocking of nonnative fish, richness of native fish species, percent roadless area, and number of occurrences of aquatic and riparian- or wetland-depended taxa listed in Natural Heritage databases within each watershed. The indices of grizzly bear habitat suitability and aquatic integrity were both strongly negatively related to the respective measures of roadlessness used in each. We defined core grizzly bear habitat (CGH) and three tiers of aquatic integrity areas (AIAs) based on design criteria. Ninety-two percent of tier 1 (the best) AIAs occurred in CGH. When expanded to include an equal area (about 13,500 km^2), top-scoring AIAs overlapped only 55% with CGH. Together, CGH and top-scoring AIAs comprised about one-third of our study area. CGH was highly aggregated and restricted to broad tracts of wilderness. Top-scoring AIAs were spatially much more dispersed and often adjoined degraded watersheds. Despite extreme sensitivity to a common stressor (roads), designs for conservation of grizzly bears and aquatic integrity differed substantially because of differences in life histories of the related organisms. The umbrella effect engendered for aquatic systems by grizzly bear conservation declined as the area considered necessary to meet aquatic conservation goals increased. Our results demonstrate the need in conservation planning for design criteria to accommodate both terrestrial and aquatic biota.*

Resumen:

Introduction

The extent to which conservation of one species can serve the conservation needs of another is a basic question in conservation biology. This question typically falls under the rubric of "umbrella effects," although the concepts of flagship and keystone species are also invoked (Miller et al. 1998; Simberloff 1998). The question is motivated by pragmatic considerations arising from limited resources and limited socio-political attention to non-charismatic species. Even so, to date there have been few specific inquiries or the emergence of many generalizable concepts related to this issue (Andelman and Fagan 2000).

The life histories of organisms and related issues of body size and ecological scale are theoretically important considerations in answering the question of how well conservation of one species will serve the conservation of another (Calder 2000). Compared to large-bodied species, small species are predictably more fecund, exist at higher densities, and have greater genetic heterogeneity at broad scales, with these general expectations modified by whether the species is avian or terrestrial, volant or not, and carnivorous or otherwise (Peters 1983; Calder 1984). Given the typically different spatial configurations of freshwater (highly linear) and upland terrestrial (broadly two-dimensional) habitats and differences in the diffusion of human-related impacts into and through them, further differences would be expected in the design of conservation for terrestrial and aquatic vertebrates.

Grizzly bears (*Ursus arctos horribilis*) and aquatic integrity are important contemporary conservation interests in western Montana, U.S.A. Grizzly bears were listed as threatened under the U.S. Endangered Species Act (ESA) in 1975 and are managed for recovery in three official Recovery Areas partially or wholly west of the Continental Divide in Montana (U.S. Fish and Wildlife Service 1993; Fig. 1). The resident native bull trout (*Salvelinus confluentus*) and westslope cutthroat trout (*Oncorhychus clarki lewisi*) are also either listed or proposed for listing under the ESA (U.S. Fish and Wildlife Service 1999*a*, 1999*b*). Even so, grizzly bear conservation has received much more attention and many more resources. Large carnivores like grizzly bears have been proposed as umbrellas for other conservation needs (Noss and Cooperrider 1994; Noss et. al. 1996; Miller et al. 1998), including those of aquatic systems.

We compared conservation designs for aquatic systems and grizzly bears in western Montana to determine the extent to which differences were introduced by related differences in basic life histories and ecological geography. We also were interested in determining the extent to which the conservation of aquatic integrity might be served by overlap with areas prioritized for conservation of grizzly bears. We highlighted the effects of life history by comparing two biotic elements (grizzly bears and aquatic integrity) that were highly sensitive to the same environmental stressor – roads. Thus, we focused on distinguishing differences in design attributed to basic life history traits and habitat ecology, versus different vulnerabilities to primary environmental stressors.

Study Area and Methods

The 65,000 km^2-study area included all of Montana, U.S.A., west of the Continental Divide (Figure 1). This part of Montana consists of broad valleys ringed by rugged mountains mantled with mixed-conifer forest. The Flathead, Clark Fork, and Bitterroot valleys occupy most of the core and are transected by U.S. highway 93 along a north–south axis. The eastern portion is dominated by the main range of the Rocky Mountains and includes the Mission Mountain, Scapegoat, and Bob Marshal Wilderness Areas as well as most of Glacier National Park. The western portion includes the Cabinet Mountains and the eastern slope of the Coeur d’Alene and

Bitterroot Mountains. In the southeast, the continental divide runs along the crest of the Sapphire Mountains and Pintler Range.

Settlement of this region by Europeans began in the mid- to late-1800s (Malone et al. 1991). At that time grizzly bears and native fish like bull trout and westslope cutthroat trout occurred throughout the study area (Behnke 1992; Mattson and Merrill, In press). Declines in these species started shortly after settlement and were attributable to direct human-caused mortality and degradation of habitat (US Fish and Wildlife Service 1999*a*; Thurow et al. 1997; Young 1995; Mattson and Merrill, In press). There are currently 320,000 human residents of the study area, most whom live in the cities of Missoula, Kalispell, Butte, and Hamilton.

Modeling Grizzly Bear Habitat Suitability

We used a model developed by Merrill et al. (1999) to calculate grizzly bear habitat suitability for the study area at a resolution of 1 km^2. This model calculated habitat suitability from two primary indices: one of habitat productivity and the other of human activity. Habitat productivity – the availability and relative abundance of bear foods – was based on mapped vegetation types and estimated numbers of elk (*Cervus elaphus*). Merrill et al. (1999) used descriptions by Caicco (1989) to attribute the presence and abundance of vegetal bear foods, primarily fruits, to individual vegetation types. The vegetation types described by Caicco (1989) were not mapped for our Montana study area, but were mapped for the state of Idaho, immediately to the west.

The climate, topography, and vegetation of the study area are very similar to the climate, topography, and vegetation of northern Idaho (Peet 1988). Because of these similarities, vegetation types of the two areas have similar understory vegetation, including vegetal bear foods (Pfister et al. 1977, Cooper et al. 1991). On this basis, we extended habitat productivity values developed for Idaho to our western Montana study area.

Redmond et al. (1998) developed and mapped a vegetation type classification for northwestern Montana and northern Idaho. We overlaid this vegetation map on the map of grizzly bear habitat productivity developed for Idaho by Merrill et al. (1999). Each vegetation type was assigned a productivity value that was the area-weighted mean of intersected values. This value was then applied to the western Montana study area. Our confidence in this approach was increased by the uniformly high productivity of the unaltered vegetation of the region that was primarily due to a maritime climatic influence (Peet 1988).

In concept, the index of human activity corresponded to the probability that a grizzly bear would encounter humans or their developments and be displaced or killed. Given that almost all of the bears past the age of weaning that die do so because a human kills them (Mattson et al. 1996; McLellan et al. 1999), encounters with humans conceptually correspond to the odds of death for a grizzly bear (Merrill et al. 1999). This probability was modeled as a function of nearness to townsites, weighted by the number of resident humans, and density of roads and trails. We obtained data on location and numbers of humans from the 1990 U.S. Census (Dept of Commerce, U.S. Census Bureau). We obtained data on roads and trails from the U.S. Geological Survey (USGS) 1:100,000 digital line graphs supplemented with updated road coverages for lands administered by the U.S. Forest Service.

We defined core grizzly bear habitat (CGH) as those areas where suitability scores exceeded one standard deviation above the study area mean and that were of sufficient size to contain a female life range (Merrill et al. 1999). We made this determination after generalizing suitability values from the resolution of our calculations (1 km^2) to the scale at which bears live and die (450 km^2) by averaging values over an area of the latter size for each pixel. The resulting map was much smoother than the original and aggregated areas of highly suitable and highly unsuitable habitat.

Modeling Aquatic Integrity

Recently, several studies have shown the feasibility of partitioning regions into watersheds of differing aquatic biological integrity based on indicators of status of multiple taxa and indicators of the principal stressors of those biota (e.g., Reeves and Sedell 1992; Henjum et al. 1994; Frissell et al. 1995; Moyle and Randall 1998.). The common principle of all of these efforts (and others) is that if long-term conservation of freshwater biodiversity is to be successful, protection of the best remaining ecologically intact watersheds and aquatic communities is necessary. Ideally these areas are identified using multi-species and ecosystem criteria that reflect overall ecological integrity. For the present study we used a model and prioritization developed by Frissell et al. (1996) and Hitt and Frissell (1999) to rate aquatic ecological integrity of sub-watersheds (6-code hydrological units with spatial extent ranging from ca. 10-25 km^2) in the western Montana study area. The model, originally called the Aquatic Diversity Area model but here referred to as the Aquatic Integrity Area (AIA) model, was based on four ecological criteria reflecting threats and status: (1) the proportion of the drainage area that was roadless; (2) the frequency of fish stocking; (3) an index of the richness and integrity of native fish species assemblages ("fish quality"); and (4) known occurrences of sensitive or rare aquatic or riparian-dependent species other than fishes from the Montana Natural Heritage database. Data for each criterion were normalized and integrated into a simple algorithm to calculate an aquatic integrity score. Details of this calculation are presented in Appendix 1 and by Frissell et al. (1996).

Sub-watersheds are an appropriate scale for synthesizing existing biophysical data for aquatic systems because at finer scales survey effort and biological data become extremely patchy and the resolution of existing data bases (e.g. fish distribution or stocking records) is exceeded.   We also assumed that sub-watersheds are of sufficient size and internal diversity to support self-sustaining populations of most aquatic species, whether fish, plants, or invertebrates (Moyle and Sato 1991; Frissell et al. 1995; Frissell and Bayles 1996).   A typical sub-watershed includes a diversity of habitat ranging from small, steep headwater streams to larger, more gently sloping meandering streams, ponds or lakes, or river reaches at lower elevations. Each sub-watershed typically includes several kilometers of perennial streams capable of supporting fish year-round. Given the typical observed density of trout in streams, a watershed of this size with habitat in good condition potentially supports a fish population of several hundreds to thousands of mature adults – likely of sufficient size for demographic persistence, barring loss or deterioration of habitat, isolation from adjoining habitats, or displacement by nonnative fishes (Reiman and McIntyre 1995; Shlosser 1995; Shephard et al. 1997; Dunham et al. 1997, 1999). We also assumed, without systematic examination, that aquatic-habitat-dependent organisms other than fish are smaller in body size, generally shorter-lived, and thus more abundant than fish in a given area. In effect this remains an unexamined umbrella assumption embedded within our aquatic model that begs examination. However, data for taxa other than fish have been insufficient for quantitative assessment of this assumption.

Hitt et al. (1999) divided aquatic integrity scores from all 924 sub-watersheds in western Montana into 3 categories or tiers. Tier 1 aquatic integrity areas (AIAs) retained the highest aquatic integrity, were typified by having large areas in relatively pristine condition, accounted for about one-quarter of the area studied, and were of the highest priority for conservation. The aquatic integrity of sub-watersheds in tiers 2 (an additional one-quarter of the study region) and 3 (the remaining half of the region) was moderately and severely impacted, respectively, by humans.

Comparing Aquatic Integrity and Grizzly Bear Habitat Suitability

To compare grizzly bear habitat suitability and aquatic integrity we translated the resolution of the former measure to that of the latter. Aquatic integrity was calculated for sub-watersheds which are much larger than the 1-km^2 resolution of grizzly bear habitat suitability. Therefore core grizzly bear habitat (CGH) was scaled down to the resolution of sub-watersheds by labeling all of those sub-waterheds that were more than 50% CGH at the resolution of 1-km^2 as wholly CGH. The remaining sub-watersheds were treated as being wholly outside CGH.

We quantified the association between different tiers of AIAs and CGH in terms of relative and absolute areas of overlap. We considered both tier 1 AIAs, alone, and top-scoring tier 1 and 2 AAs that together equaled the extent of CGH in the study area. We estimated the probability that observed overlap between tier 1 AIAs and CGH was a random outcome. We did this by recording the extent of overlap between CGH and 100 sets of an equivalent number (69) of randomly selected sub-watershed and the proportion of those trials that resulted in overlap greater than or equal to what we observed.

To describe relations between aquatic integrity and grizzly bear habitat suitability, among variables used in each model, and between integrity or suitability and the variables that were used to calculate each of them, we drew a random sample of 1000 points from our GIS. These values were then used in regression and correlation analyses to describe relations. We interpreted the strength of relations between either the index of aquatic integrity or the index of grizzly bear habitat suitability and the variables used to calculate each as a measure of sensitivity.

Results

Overlap between core grizzly bear habitat and high integrity sub-watersheds

Tier 1 aquatic integrity areas (AIAs) overlapped almost wholly with core grizzly bear habitat (CGH). There were 4,438 km^2 of tier 1 AIAs distributed in 69 sub-watersheds in the study area as well as 14,411 km^2 of CGH at a 1-km^2 resolution (Fig. 2a). Ninety-two percent (4,089 km^2) of all AIA-1's were in CGH and comprised 31% of the latter. The mean area of overlap between 100 sets of randomized AIA's and CGH was 957 km^2 (SD = 242, Range = 451 – 1622 km^2). The probability that the observed overlap between AIA-1's and CGH was a random event was less than 0.01.

Core grizzly bear habitat and tier 1 AIAs also overlapped extensively with currently designated grizzly bear Recovery Areas. Seventy one percent of CGH and 92% of tier 1 AIAs occurred within Recovery Areas. Conversely, CGH accounted for 44% or 9,534 km^2 of the total 21,694 km^2 within grizzly bear Recovery Areas in Montana west of the Continental Divide.

This extensive overlap was consistent with a strong positive relation between grizzly bear habitat suitability and aquatic integrity (Fig. 3). Even so, considerable variation in aquatic integrity was not explained by variation in grizzly bear habitat suitability. This suggested noteworthy differences in distributions of these two values within the study area, an expectation that was born out by comparing the distribution of high-value sub-watersheds equal in total area to that of CGH.

Core grizzly bear habitat contained only about one-half of an equal area of the highest-integrity AIAs in the study area (Table 1). After being transformed from 1-km^2 cells to sub-watersheds, CGH totaled 13,372-km^2 (Fig. 2b). The highest-ranking AIAs approximated, but did not exactly equal this area because different sub-watersheds of unequal sizes comprised the two designations (Table 1). Accounting for overlap, CGH and the highest value AIA's encompassed about one-third of the study area.

Relations between indices and the variables used in their calculations

There were strong relations between grizzly bear habitat suitability and the indices of habitat productivity and human activity used in its calculation. Relations were positive and negative for each, respectively (Fig. 4a and 4b). Each explained somewhat more than one-half of the variation in habitat suitability. Given the way that habitat suitability was calculated, this value should have been closer to one-half, with the discrepancy due to spatial correlation between productivity and human activity. Of the variables used to calculate the primary indices from which grizzly bear habitat suitability was derived, road density was most strongly related to the ultimate suitability metric (Fig. 4c). As expected, the relation was negative.

Aquatic integrity was more strongly related to the measure of roadless area than to any of the other metrics used in its calculation. In fact, the negative relation with roadlessness explained nearly three-quarters of the variation in aquatic integrity (Fig. 5). This far exceeded its putative contribution to the calculation of aquatic integrity and is explained by a high degree of spatial correlation with other metrics used in calculation of this index.

Relations among variables used for calculations

There was a strong relation between the roadless value used to compute aquatic integrity and road density used to compute grizzly habitat suitability (Table 2). There was also a strong relation between aquatic roadless value and the grizzly bear model index of human activity. The moderate relation (r^2 = 0.19) between aquatic roadless value and grizzly bear habitat productivity was probably coincidental. Relations between all other variables were weak, with r^2's < 0.1 (Table 2).

Discussion

The best grizzly bear habitat and the most pristine aquatic systems overlapped extensively in Montana west of the Continental Divide. This was evident in the strong correlation between grizzly bear habitat suitability and aquatic integrity scores at the scale of sub-watersheds. Moreover, sub-watersheds that scored the highest aquatic integrity (tier 1 aquatic integrity areas [AIAs]) occurred almost wholly within the best grizzly bear habitat (> one standard deviation above the mean; core grizzly bear habitat [CGH]). Given that most CGH identified in this analysis was contained within designated grizzly bear Recovery Areas (U.S. Fish and Wildlife Service 1993), on-going grizzly bear conservation efforts, together with revision of fish stocking practices (Adams et al. 2001), could protect the remaining most pristine aquatic systems of western Montana.

The joint distribution of CGH and tier 1 AIAs was largely attributable to the shared sensitivity of both to the presence of roads. Statistically, we could explain aquatic integrity scores largely by the amount of roading in a sub-watershed. We could similarly explain much of grizzly bear habitat suitability by road density. This was due only partly to the extent that measures of roadlessness explicitly factored into each of the models. Information about other spatially correlated human impacts was also conveyed by these measures of access.

The common importance of roads in defining aquatic integrity and grizzly bear habitat suitability is consistent with our knowledge of bears and fish as well as a growing body of knowledge regarding the generally negative impacts of roads on biological diversity. Roads are the primary vectors by which a host of destructive meso-scale human impacts are dispersed across landscapes (Trombulak and Frissell 2000). For grizzly bears, roads heighten the odds that they will encounter intolerant humans with guns or human-related food sources that will attract them to humans and mark them as a problem (McLellan 1990; Mattson et al. 1996).

For native fish, roads are problematic for even more reasons. They bring more anglers, facilitate the stocking of non-native species, and degrade the quality of spawning and feeding habitat by increasing sedimentation (Jones et al. 2000; Trombulak and Frissell 2000). Roads are also associated with timber harvest, which can further accelerate erosion and lead to detrimental increases in stream temperatures owing to the loss of vegetation cover (Chamberlin 1982).

However, inasmuch as the best aquatic and grizzly bear habitat overlapped extensively, there was much variability in both metrics that was not explained by the other. This disassociation of grizzly bear habitat suitability and aquatic integrity was most pronounced at moderate to low integrity values. Most tier 2 AIAs occurred outside of CGH. However, it was the dispersed and fragmented distribution of these intermediate-value watersheds that was most striking.

In contrast to the highly aggregated nature of CGH and tier 1 AIAs, the dispersed nature of tier 2 AIAs was attributable to the distribution of humans impacts and fundamental differences in life history traits of fish. By definition, tier 2 AIAs were moderately impacted by humans. It was thus intrinsically more likely that these AIAs would occur in a more degraded matrix outside of the large and contiguous roadless areas required for the maintenance of grizzly bear populations (Craighead et al. 1995). Moreover, because native fish can exist as self-sustaining populations at the scale of a the sub-watershed units we used (Dunham et al. 1997, 1999; Young 1995), individual AIAs could exhibit moderate to high levels of self-contained integrity despite potentially severe degradation of neighboring watersheds. This would be impossible for intrinsically wide-ranging low-density species like grizzly bears. Thus, it was predictable that tier 2 AIAs would be fragmented and located largely outside of CGH.

At the scale of our analysis, any conclusions regarding the extent to which conservation of aquatic systems could be achieved by managing for the conservation of grizzly bears in CGH depended on answering the question for both models: how much habitat is enough? Because any defensible answer to this question heavily entails human values and norms (Mattson et al. 1996; Noss 1996), as well as lingering uncertainties about extinction risk and recolonization rates, we could not provide an explicit answer in this paper. Nonetheless, if the answer is that tier 2 AIAs are needed to achieve aquatic system conservation aims, then managing for conservation of aquatic elements in CGH would clearly be insufficient.

Our results are consistent with estimates by Noss (1996) that achievement of conservation aims will typically require prioritization of conservation on 25–75% of the lands in a region like that of western Montana. Areas of potential importance to conserving grizzly bears and aquatic systems alone entailed one-third of our study area. This is probably conservative. Although we did not reach any conclusions about the total area needed to meet policy objectives for bears and fish, it is suggestive that core grizzly bear habitat as we defined it comprised a smaller area (14,411 km^2) than officially-designated Recovery Areas (21,694 km^2).

Relative to grizzly bears, it is likely that conservation of aquatic systems will require a finer-scale more spatially-dispersed conservation design that, in our study area, includes many tier 2 AIAs. The genetic heterogeneity of grizzly and brown bears world-wide has been ascribed to a mere five clades, or lineages (Waits et al. 1999). Grizzly bears in western Montana are wholly of one clade. For most native trout species, genetic diversity equivalent to that of grizzly bears worldwide can be found within our study area alone (Allendorf and Leary 1988). There is consensus that for fish, conservation of biodiversity at the subspecific level, at the scale of our study area, is important to preserving evolutionary potential and resilience (Allendorf and Leary 1988; Leary et al. 1993; Altukov et al. 2000; Young 1995). Moreover, in contrast to grizzly bears, fine scale conservation designed to embrace the spectrum of genetic diversity among fish stocks in western Montana is made possible by the much greater reproductive potential and population densities of fish. Consistent with theory (Calder 2000; Cyr 2000), this fundamental difference in life history and the spatial distribution of populations both engenders and facilitates a widely dispersed, fine-scale conservation area design for fish in contrast to a spatially aggregated design for bears.

The vectors by which threats are propagated across the landscape also differ between bears and aquatic biota, which together with life history determines how populations respond to human disturbance and the scale at which the effects of disturbance are expressed. Sedimentation, for example, affects a linear array of habitats potentially many km from the source, whereas human access to streams for fishing rarely extends more than 1 km from an access point (usually a road crossing). Because bears move widely over large areas, they may be highly exposed to even a small number of humans on the landscape. At the same time, bears may be less seriously affected by site-specific physical impacts analogous to the sedimentation of streams because of their mobility. Thus aquatic biota express the effects of biophysical disturbance on finer-grained scale than do bears, and conservation of patches of high-quality natural habitat on the 10-25 km^2 scale of sub-watersheds may be sufficient and important for fish, but not for grizzly bears, which require much larger contiguous blocks of land.

Our analysis affirms that scale-related constraints of life history are inescapable in conservation design. Achievement of conservation aims for fish and grizzly bears very likely entail protection of large contiguous blocks of roadless habitat for both grizzly bears and fish, together with numerous, widely dispersed sub-watersheds managed primarily for conservation of aquatic integrity. This is emblematic of the diverse scales at which conservation efforts need to occur to accommodate scale-related differences among different life histories rooted in different body sizes and habitat media (Lambeck 1997; Caldwell 2000) or, ultimately, in processes that fundamentally structure biotic systems (Holling 1992; West et al. 1999).

The importance of scale-related considerations arising from different body sizes and life histories is relevant to developing guidelines for the selection of umbrella species. Lambeck (1997) proposed suites of species selected on the basis of different sensitivities to environmental stressors or threats. In our analysis, models for the design of conservation areas for both fish and grizzly bears were highly sensitive to the presence of roads and the human-related impacts associated with them. Yet, despite this common sensitivity, designs for these taxa were potentially quite disparate, primarily because of differences in life histories. Our results affirm Lambeck's (1997) advise that selection of focal species should consider not only sensitivities to different threats, but also body size and related life history traits that entail scale-related consequences for conservation design.

The answer to the question "how much is enough?" also had considerable consequences to appraising potential umbrella effects. Relative to the umbrella effect of grizzly bear conservation, it mattered a great deal whether we concluded that tier 1 AIAs were sufficient or not to meet conservation goals for aquatic systems. If sufficient, then potential umbrella effects were substantial. If not, then umbrella effects were considerably diminished, even if the extent of prioritized grizzly bear conservation were reckoned in terms of official Recovery Areas rather than CGH. Short of the impractical model of reserving the majority of a landscape for conservation purposes, development of optimal design rules to accommodate the needs of all broad taxonomic groups is a necessary subject for continuing research.

In our study area, we found that separate conservation area design criteria were probably needed for effective and efficient conservation of freshwater fish and grizzly bears. Although one environmental metric (roads or roadless areas) factored strongly in both designs, two other factors caused significant departure in conservation designs: (1) differences of relevant scale as a consequence of life history, and (2) differences in the ecological processes that mediate the spatial propagation of human influences. We conclude that for conservation planning, analyses for these disparate taxa should proceed in parallel, with integration during final phases. Similar evaluations should be done before any taxon is assumed to provide sufficient umbrella functions for other biota of disparate ecological and evolutionary heritage.

Acknowledgements

This paper arose from a workshop at the Society for Conservation Biology Annual Meeting held in Missoula, Montana, in June 2000. Discussion at that workshop stimulated our thinking about this topic. We appreciate funding to support this project provided by the Yukon-to-Yellowstone Conservation Initiative as well as the encouragement and facilitation offered by Marcy Mahr of that organization. The Pacific Rivers Council provided support for development of the aquatic model and for C. Frissell's contribution to the present manuscript. Contributions by D. Mattson also were supported by the U.S.G.S. Forest and Rangeland Ecosystem Science Center and M. Collopy and C. van Riper III of that bureau.

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Table 1. The extent and percent overlap of core grizzly bear habitat (CGH) and an equal area of sub-watersheds that scored highest for aquatic integrity, distinguishing tier 1 and tier 2 aquatic integrity areas (AIA-1 and AIA-2, respectively), for Montana, U.S.A., west of the Continental Divide. Data for both grizzly bears and aquatic integrity are at the resolution of sub-watersheds

Type of conservation area	*Total area (km^2)*	*Percent of study area*	*Area of overlap wt. CGH (km^2)*	*Percent overlap wt. CGH*
Core grizzly bear habitat (CGH)	13,372	20	13,372	100
Total aquatic integrity areas (AIA)	13,623	21	7,549	55
AIA-1	4,438	7	4,089	93
AIA-2	9,185	14	3,460	38
Total CGH or AIA	19,446	30	13,372	–

Table 2. The strength of relations (r^2 values) at the scale of sub- watersheds between constituent variables of the grizzly bear habitat suitability and aquatic integrity indices in Montana, U.S.A., west of the Continental Divide.

Aquatic integrity index and constituent variables for the grizzly bear habitat suitability index	*Constituent variables for aquatic integrity index*			
	Roadless value	*Fish quality value*	*Fish stocking value*	*Heritage value*
Aquatic integrity index	**0.733**	0.108	0.283	0.002
Index of human activity	**0.675**	0.026	0.015	0.008
Road density	**0.669**	0.012	0.011	0.006
Index of potential human activity	0.071	0.026	0.006	0.002
Index of habitat productivity	0.191	0.014	0.006	0.006

Appendix 1

Description of the Aquatic Integrity Area (AIA) model

Roadless area metric

We used the proportate area of each sub-watershed in roadless condition as an integrated indicator of human disturbance (Trombulak and Frissell 2000). A previous study in one portion of the study area substantiated that biotic indicators of ecological integrity are generally associated with road density and roadless area (Frissell et al. 1995). Roadless area was delineated as all undeveloped lands >200 m from a road and > 400 ha in total size. Roadless areas were mapped using a roads map that was a composite of best available data (ca. 1998) and then intersected this map with the sub-watershed layer by S. Beckwitt of the Sierra Biodiversity Institute (North San Juan, CA). The roadless area metric had continuous coverage. This feature allowed us to use this metric as a predictor of biotic conditions in areas for which biotic data were not available.

Fish stocking metric

We obtained fish stocking histories for each sub-watershed from the Montana Fish, Wildlife and Parks (Helena, MT) Fish Stocking Records Database. These data reflected all authorized and recorded fish plantings from 1920 through March of 1995. Fish stocking is a threat to aquatic biota through several vectors, including predation, competition, and genetic introgression between native and the introduced fishes. Introduction of pathogens is a further risk, both to native fishes and amphibians (e.g., Blaustein et al. 1994). Each stocking episode may increase or add to the risk or impact, but stocking can cause permanent ecological harm if self-sustaining populations of the introduced species become established. The stocking history of each stream reach in the database was tagged to the sub-watershed in which it was embedded, and each sub-watershed assigned a score based on the number of stocking events. Unfortunately, fish-stocking data for lakes was not used because Montana lacks a hydrography layer linking lakes to stream networks or sub-watershed areas. We used two different models with different weighting schemes to reflect differences in the risk of permanent establishment of nonnative fishes versus the more direct effects of stocking events. Final model runs drew from one or the other of these two stocking effect models.

Metric for the quality of native fish assemblages

We derived the "fish quality" component from the Montana Rivers Information System database on fish species distribution and genetic condition, for late 1995 (Montana State Library, Natural Resources Information System, Helena, MT). Stream reaches were linked to the sub-watershed they were embedded in. The the occurrence of native and nonnative species within the sub-watershed was then tallied and the fish quality score calculated as a ratio of the two. Genetic evidence for pure (non-hybridized) native populations additively boosted the overall score.

Metric for the occurrence of Natural Heritage elements

We gave sub-watersheds an overall bonus score based on the documented presence of sensitive, rare, or protected species of any aquatic and wetland-associated plants or animals, not including fish. We obtained information for this model factor from the Montana Natural Heritage Program (Helena, MT) Element Occurrences database, ca. late 1995. Aquatic and wetland-associated species were gleaned from the overall database using a pre-developed list. We then tallied the number of records for each sub-watershed. Most subwatersheds had no records, and many probably had never been surveyed. For these reasons we used this component as a weak modifier of the overall AIA score, boosting the overall AIA score where multiple records existed.

Integration of metrics

We added the normalized scores for roadlessness, fish stocking, and fish quality and then multiplied this sum by the Natural Heritage score factor. Because no mathematical formulation was intrinsically superior or more justified, we developed four different models, each version varying in relative weights assigned to the different components and in the fish-stocking model selected. We calculated a final overall AIA score for each sub-watershed as the arithmetic average of the scores produced by these four models. This final averaged AIA score (Version 2.0, potential scores from 0-40, observed scores ranged from 0.0 to 31. 5) was used in the present analysis.

Figure captions

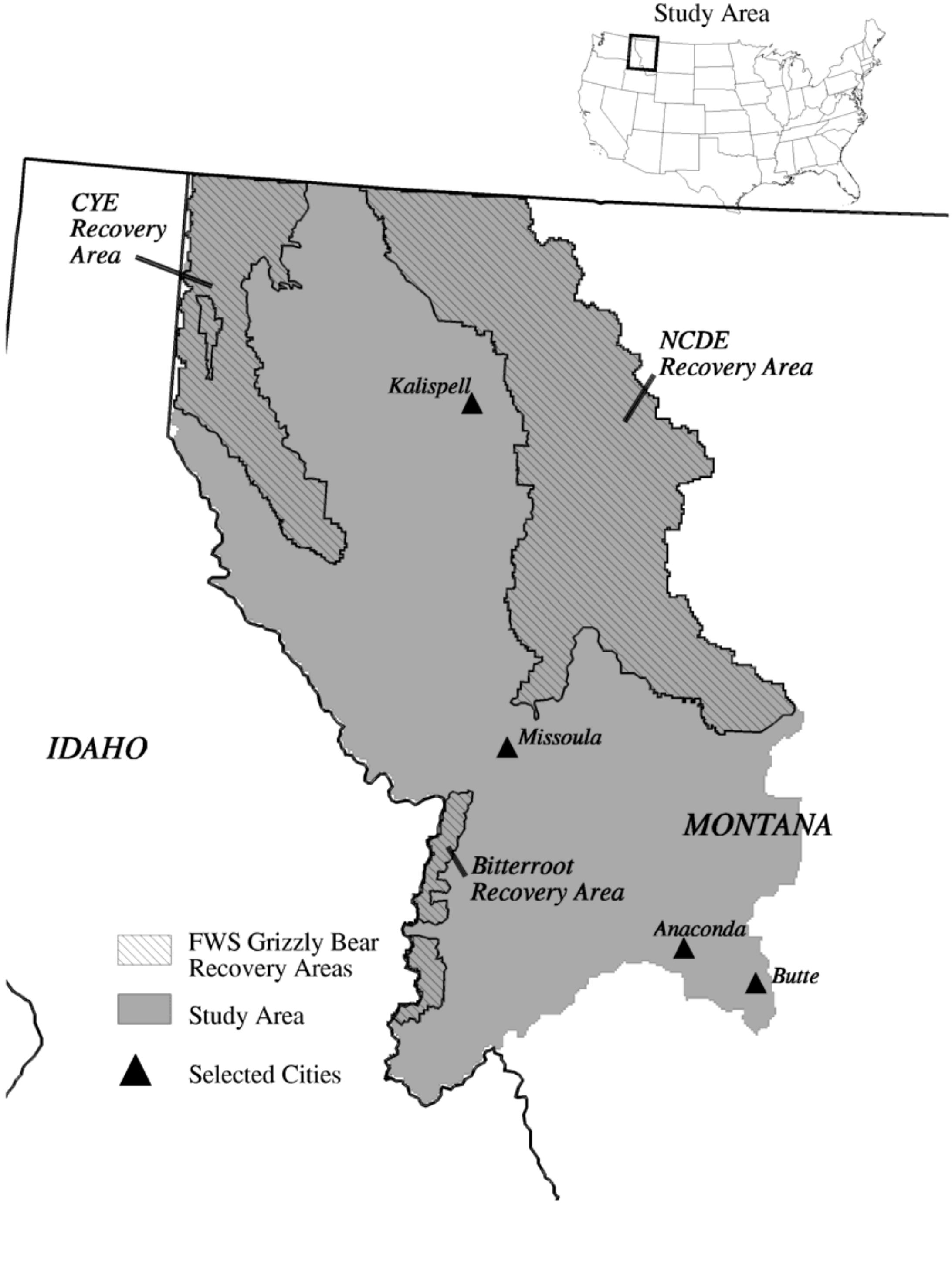
Figure 1. The Montana, U.S.A., study area west of the Continental Divide. Official grizzly bear Recovery Areas (RAs) are shown, including the Northern Continental Divide, Cabinet-Yaak, and Bitterroot RAs.

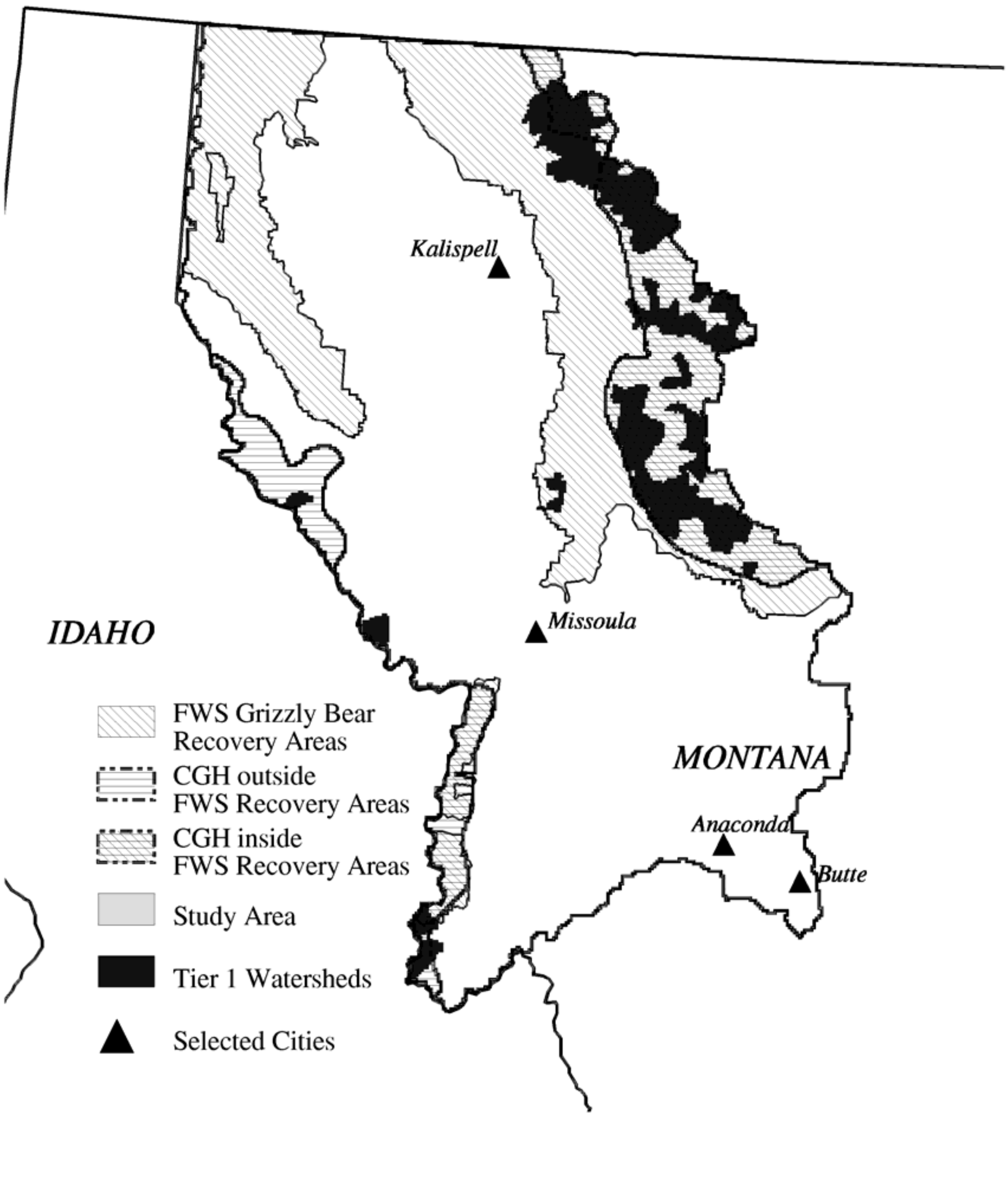
Figure 2. Distribution of core grizzly bear habitat (CGH) and (a) tier 1 aquatic integrity areas (AIAs) and (b) an area of tier 1 and tier 2 AIAs equal to that of CGH in Montana, U.S.A., west of the Continental Divide. CGH is shown with horizontal lines , tier 1 AIAs and tier 2 AIAs in solid black . Official grizzly bear Recovery Areas also are shown as by horizontal lines.

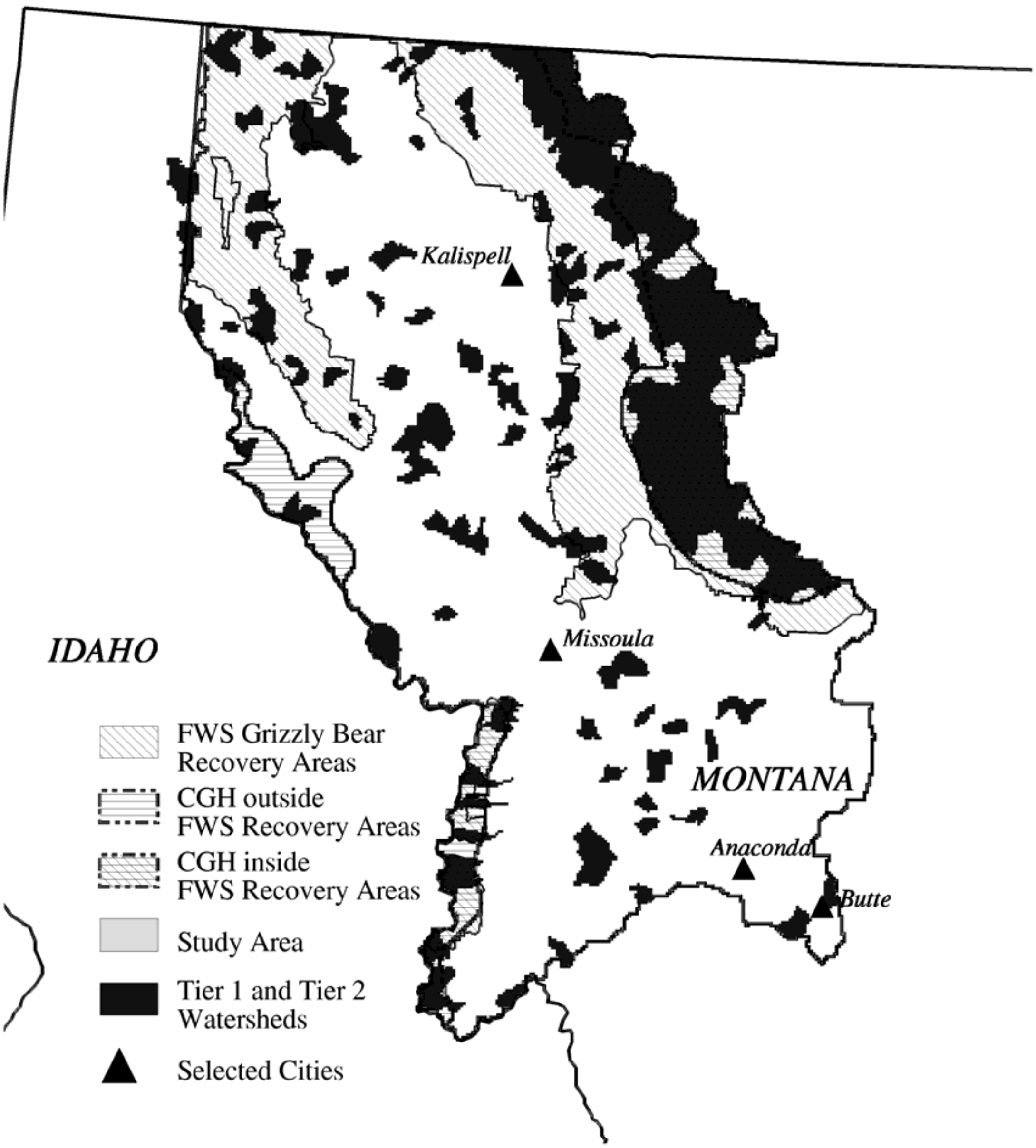
Figure 3. Relation between indices of grizzly bear habitat suitability and aquatic integrity at 1000 random points in Montana, U.S.A., west of the Continental Divide.

Figure 4. Relations between grizzly bear habitat suitability scores and constituent variables at 1000 random points in Montana, U.S.A., west of the Continental Divide; (a) index of habitat productivity, (b) index of human activity, and (c) road density.

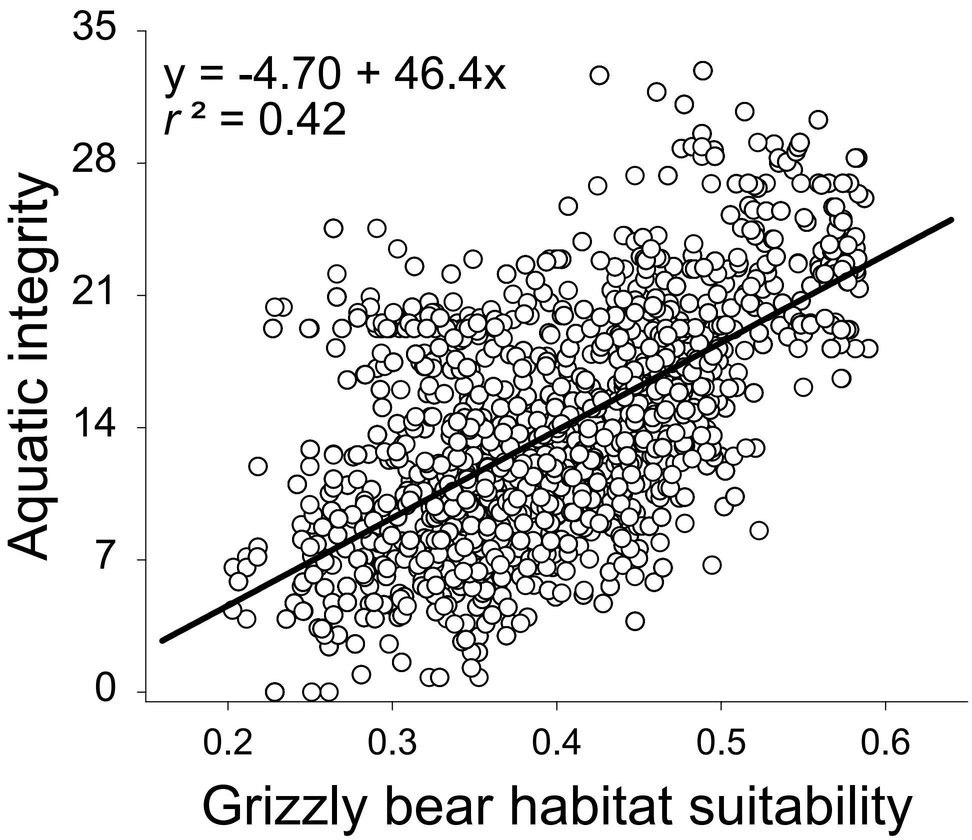
Figure 5. Relation between the index of aquatic integrity and roadless values used in its calculation at 1000 random points in Montana, U.S.A., west of the Continental Divide.


Study Area
CYE
Recovery
Area
NCDE
Recovery Area
Kalispell
IDAHO
Missoula
MONTANA
Bitterroot
Recovery Area
Anaconda
Butte
FWS Grizzly Bear
Recovery Areas
Study Area
Selected Cities

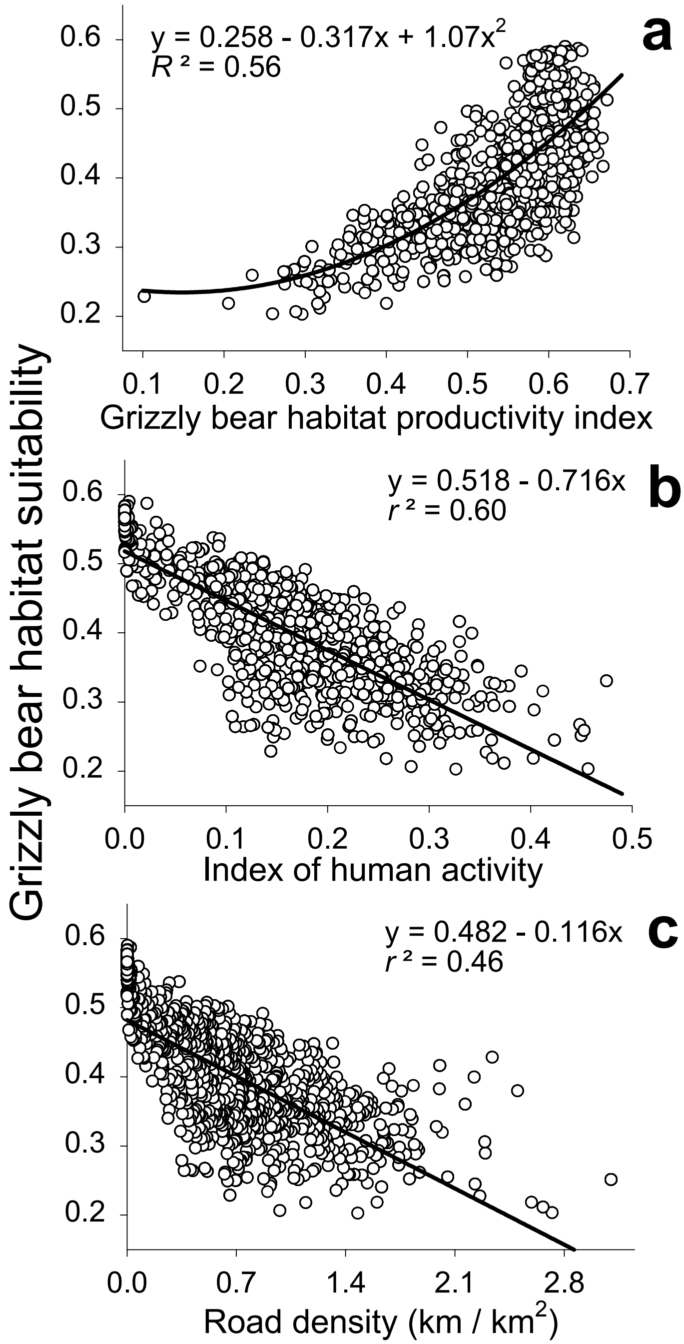

IDAHO
MONTANA
Kalispell
Missoula
Anaconda
Butte
FWS Grizzly Bear Recovery Areas
CGH outside FWS Recovery Areas
CGH inside FWS Recovery Areas
Study Area
Tier 1 Watersheds
Selected Cities

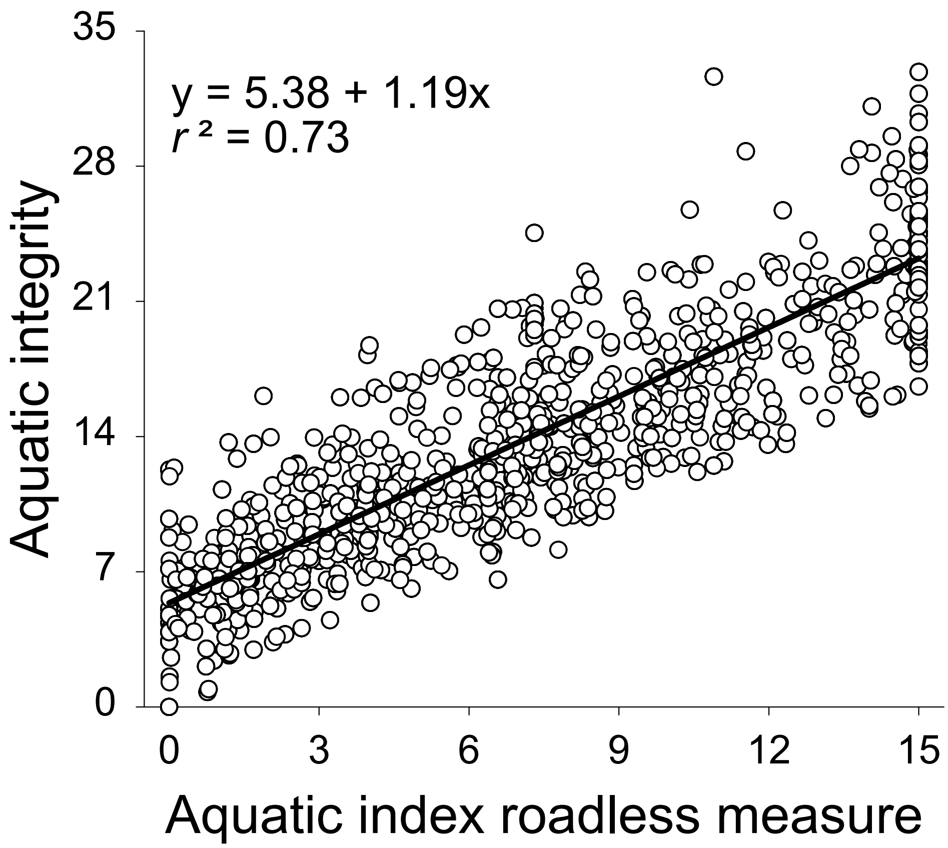


Kalispell
Missoula
IDAHO
MONTANA
Anaconda
Butte
FWS Grizzly Bear Recovery Areas
CGH outside FWS Recovery Areas
CGH inside FWS Recovery Areas
Study Area
Tier 1 and Tier 2 Watersheds
Selected Cities



y = -4.70 + 46.4x
r ² = 0.42
35
28
21
14
7
0
0.2
0.3
0.4
0.5
0.6
Aquatic integrity
Grizzly bear habitat suitability


y = 0.258 - 0.317x + 1.07x²
R ² = 0.56
a
0.6
0.5
0.4
0.3
0.2
0.1 0.2 0.3 0.4 0.5 0.6 0.7
Grizzly bear habitat productivity index
Grizzly bear habitat suitability
y = 0.518 - 0.716x
r ² = 0.60
b
0.0 0.1 0.2 0.3 0.4 0.5
Index of human activity
y = 0.482 - 0.116x
r ² = 0.46
c
0.0 0.7 1.4 2.1 2.8
Road density (km / km²)


y = 5.38 + 1.19x
r ² = 0.73
35
28
21
14
7
0
0
3
6
9
12
15
Aquatic integrity
Aquatic index roadless measure