1. Introduction

This report focuses on human-built infrastructure—primarily roads and residences—and how these physical features directly or indirectly affect the behavior and demography of brown and grizzly bears (both the same species: *Ursus arctos*). Even so, these effects cannot be isolated from the choices people make not only about building and maintaining infrastructure, but also about behaving in human-impacted environs. Even more fundamentally, human choices and behaviors of relevance to bears cannot be divorced from peoples' underlying attitudes and perspectives regarding their relations with the natural world.

Human infrastructure, per se, has vagarious effects on bears. Many effects arising directly from physical roadbeds and the vegetation in peoples' yards are positive, whether by easing travel or as a source of food. On the other hand, effects arising from the behaviors of humans concentrated in human-built environs are usually negative. Tongue in cheek, roads don't kill bears, people kill bears. The problem is, though, that roads and residences almost invariably come with people. The two cannot be readily disentangled, with a resulting gradient of impacts on bears that largely vary with peoples' attitudes and behaviors.

Up front, this complexity debars any credible statements about fixed effects of human infrastructure on bears, with the proviso that certain issues such as impacts of heavily trafficked highways are more amenable to widespread extrapolation. Even so, the effects of traffic on main thoroughfares can be mitigated by changing speed limits, improving roadside visibility, and installing infrastructure to facilitate crossings by wildlife.

All of this foreshadows topics more comprehensively covered in the remainder of this report. My main introductory point is that people looking for simple answers or conclusions regarding how human infrastructure affects bears will not find them in the remainder of this report. The insights plausibly gained from close examination of ample evidence contained in numerous studies cannot be reduced to one or two sentences – other than, perhaps, that infrastructure impacts are contingent on context. That having been said, in the end, most impacts can arguably be attributed to human intolerance and behaviors arising from prejudice against bears.

1.1. People's Behavior as a Central Dynamic

Few researchers have explicitly investigated the manifold human-initiated dynamics that ultimately configure bear survival and behavior near human infrastructure. One could plausibly argue—or at least defensibly hypothesize—that bear-centric phenomena are largely derivative from dynamics entrained by people (e.g., Mattson et al. 1996a, Mattson 2021a). If so, then the innumerable studies focused on temporal and spatial responses of bears and bear populations to human-built environments are missing information essential not only for explaining study-specific results, but also providing context needed to locate a study in the larger universe of possibilities. Several researchers have undertaken literature reviews that broach complex dynamics involving people and bears organized around human infrastructure (e.g., Elfström et al. 2014a, Proctor et al. 2020), but these forays have been incomplete in terms of both conceptualization and coverage of relevant research. These limitations complicate or even debar extrapolation of their conclusions to specific situations.

This report attempts to provide a more replete view of not only research focused on how bear populations and individuals respond to the human-built environment, but also how variation in results from one location to another plausibly relates to differences in history and human behaviors. Unfortunately, information on human-specific aspects of any given study is almost invariably missing from peer-reviewed publications, perhaps because the institutions that direct, fund, and publish wildlife research do not adequately reward inquiry into site-specific complexities. One could argue, in fact, that these institutions often penalize researchers who stray too far from the confines of a narrow research agenda (e.g., Mattson 2022). The upshot is that human-specific information for most studies can only be guessed or crudely approximated.

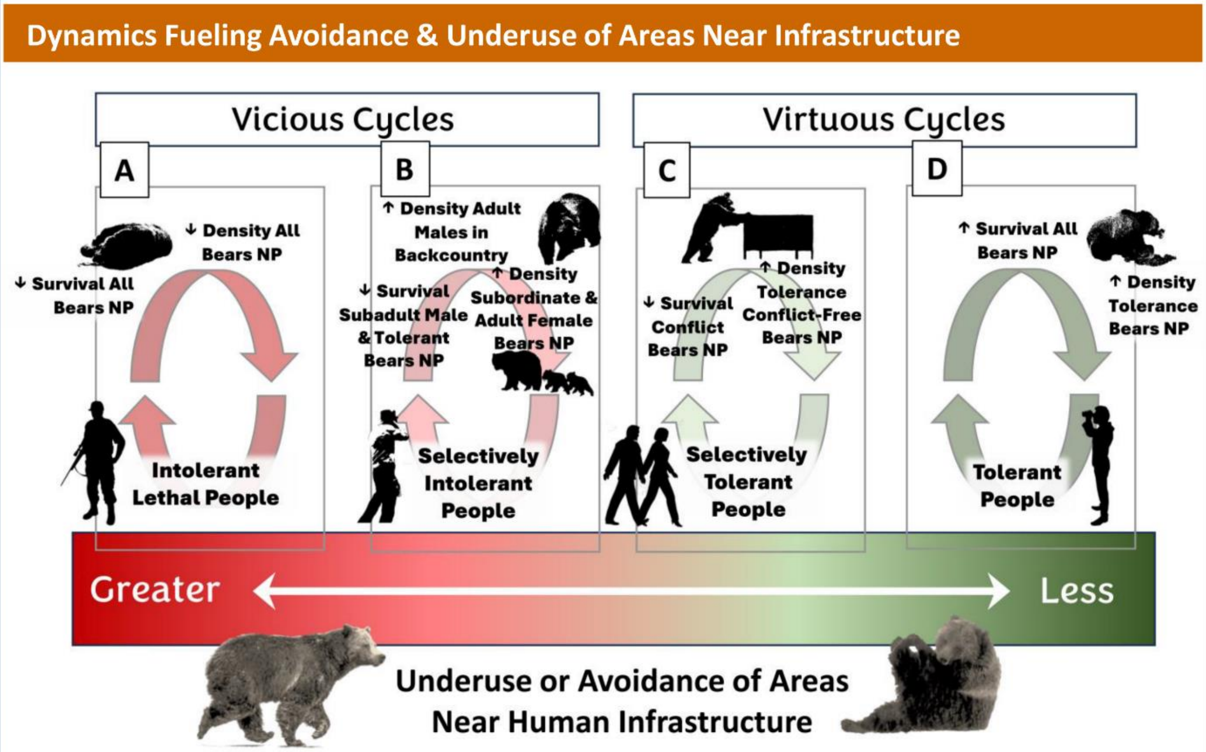

Figure 1. The conceptual graphic above attempts to capture in simplified form a gradient of dynamics entrained by human tolerances and behaviors that result in greater or lesser underuse of areas near human infrastructure by bears (near infrastructure in graphic labels is denoted by NP ≈ Near People). Underuse can either be the result of population-level demographic effects or changes in behaviors of individual bears. The four illustrative dynamics above are differentiated as either vicious (A & B) or virtuous (C & D) cycles. Vicious cycles result in greater death rates of bears near human infrastructure as well as increased intolerance and avoidance among bears that survive. Virtuous cycles result in lower death rates of bears near people and increased tolerance of humans, resulting in less overall underuse of areas near human infrastructure. The dynamic in (B) is perhaps the most complicated of all: tolerant as well as subadult male bears die at comparatively higher rates near human infrastructure, resulting in comparatively greater recruitment of adult male bears in the back country, in tun resulting in displacement of bears vulnerable to aggression from adult males to the front country, notably subadults and females with dependent young. The dynamic in (C) is characterized by comparatively higher death rates among bears involved in conflicts with humans, usually the result of bears becoming food-conditioned while seeking out anthropogenic foods.

1.2. A Conceptual Model

Figure 1 is a simplified visual depiction of a conceptual model I employ for interpreting study-specific results as well as the sometimes-substantial differences in findings among studies and study areas. This conceptualization is primarily based on models and reviews previously published in Mattson et al.

(1996a, 1996b) and Mattson (2004, 2021a). The model posits a gradient of avoidance or underuse of areas near people by bears, with "avoidance" of greater relevance to behaviors of individual bears and "underuse" of greater relevance to population-level phenomena such as differences in bear densities between front- and back-country areas. This gradient is premised on differences in human tolerance of bears, with derivative human behaviors promulgating lagged responses in bear demography and behaviors.

The root driver of variation in avoidance or underuse along this gradient is hypothesized to be levels of human tolerance for bears, especially individual animals using areas near human facilities. Greater intolerance predictably leads to higher deaths rates of bears exposed to people, with resulting lower densities of bears near human infrastructure and greater intolerance of people among bears that survive. Greater tolerance predictably leads to the opposite: lower death rates of bears near people, more uniform resulting distributions vis-à-vis human facilities, and higher levels of tolerance for and habituation to people among survivors. In the first case, investigators would likely have found that bears substantially avoided or otherwise underused areas near humans and, in the latter case, they would have likely found the opposite.

Figure 1 arrays these differences as four illustrative dynamics, with synergistic outcomes rooted in human intolerance characterized as "vicious cycles" (Figures 1a and 1b), and synergistic outcomes rooted in tolerance characterized as "virtuous cycles" (Figures 1c and 1d). Vicious cycles precipitate deleterious outcomes for bears, including a larger human footprint, whereas virtuous cycles alleviate human impacts and allow for greater accommodation of both bears and people. Parenthetically, the concept of virtuous and vicious cycles (or circles) first gained widespread popularity in the realms of economics and management where concerns focused on self-reinforcing dynamics that led to problematic outcomes for businesses or the broader public (e.g., Schlesinger & Heskett 1991).

One cycle of particular interest and complexity is illustrated by Figure 1b. In this cycle, contingent human intolerance manifests as comparatively high rates of human-caused death among human-tolerant bears and inexperienced adolescent males near people. There is consequently greater comparative recruitment of adult males in back- versus front-country areas. Given that adult males are potential predators on cubs and yearlings, and well-able to displace subordinate bears from richer food resources, females with dependent young as well as younger subordinate bears are displaced to areas near people, not only to escape threatening males, but also to access underutilized food resources. This potentially commonplace dynamic is perhaps best described by Mattson et al. (1996a: 137-141) and Mattson (2021a: Sections 4-6).

1.3. Scope of This Review

I bounded the definition of "infrastructure" primarily to make the scope of my analysis manageable. As a factual matter, almost all the investigations of how bears are affected by human infrastructure have focused on highways, roads, and permanent residences, including townsites and recreational developments built to accommodate substantial numbers of people (Section 3). Although some research has focused on hard-rock mines and extraction of hydrocarbons (e.g., Cristescu et al. 2016), most effects attributable to these specific types of infrastructure and associated human activities can be decomposed to effects of roads and permanent facilities with concentrations of people – the latter much like townsites or recreational developments.

As a corollary, I also did not cover effects associated with trains and railways, back-country campsites and trails, and people dispersed on foot, all of which I have previously covered in Mattson (2019a, 2019b). Nor did I cover impacts associated with peoples' landscape-level modifications of the environment – notably agriculture and timber harvest – which, although important to human-bear relations, are entangled with a broader gamut of topics such as thermal and hiding cover and effects directly attributable to availability of natural and anthropogenic foods. This report ended up being sprawling enough without tackling these additional topics.

Within the bounds of effects directly linked to highways, roads, residences, and recreational developments, I attempted to encompass all the documented variation attributable to differences in levels of human activity and proximal behaviors of bears. This scope included research that examined effects attributable to human densities, levels of traffic, vehicle speeds associated with different road surfacing, visibility along roads, and diel variation in human activity. Bear behavior was covered more directly by documented levels of nocturnality and exhibited tolerance of humans, as well as indirectly by the proxies of sex, age, and reproductive status.

As a final note, avoidance of humans and human infrastructure by bears is ultimately rooted in complex processes by which bears learn about the risks and rewards of their world. The cognitive and emotional dynamics entailed by bears interacting with their environment are in some ways central to understanding all the results presented in this report related to avoidance. There is little evidence to suggest that brown and grizzly bears are, as a species, intrinsically wary or fearful of humans. If anything, available evidence suggests the opposite and that wariness or intolerance among bears largely arises from adverse painful interactions with people (e.g., Stringham & Rogers 2017). As important as this topic is, I did not attempt to encompass the extensive body of research and theory related to learning in bears and other animals here but instead rely heavily on a previous synthesis published by Mattson (2021a).

2. The Centrality of Human-Caused Mortality

Humans cause most deaths of adolescent and adult grizzly and brown bears worldwide (e.g., McLellan et al. 1999, Bishof et al. 2009, Krofel et al. 2012). Depending on time and location, fractions of human-caused deaths range from plurality to near totality. Figure 2 summarizes fractions of human-caused deaths for a pooled sample of radio-marked grizzly bears from six study areas in the Rocky Mountains of adjacent Canada and the United States. (Using causes of death for only radio-marked bears guards against inflation of estimates arising from higher comparative odds of detecting human-caused versus natural deaths.) An estimate based only on bears where causes of death were known (left) is differentiated from an estimate that assumed unknown causes were attributable to humans—largely poaching (right).

Regardless of assumptions regarding deaths from unknown causes, humans caused nearly all adolescent and adult grizzly bear mortality in this region. Of the 186 radio-collared grizzly bears known to die during monitoring in the U.S. and Canadian Rocky Mountains, somewhere between 72 and 91% were killed by humans, with little difference evident between jurisdictions.

Cast against the background of history (e.g., Mattson & Merrill 2002, Albrecht et al. 2017), the magnitude of contemporary human-caused mortality emphasizes the extent to which humans dictate the fates of brown and grizzly bear populations—a conclusion underscored by several demographic analyses showing that a difference in one or two female bears killed by people every year can determine whether smaller populations grow or decline (e.g., Knight & Eberhardt 1985, Wiegand et al. 1998, Garshelis et al. 2005). Human-caused mortality can, moreover, have adverse indirect effects on bear populations, largely through disruptions of social organization that lead to an increase in infanticide by adult males (e.g., Frank et al. 2017, Van de Walle et al. 2021).

This corpus of research highlights the extent to which humans and human behaviors are central to conservation of bear populations, as well as the need to account for all major factors driving levels of human-caused mortality and resulting behavioral responses of bears to humans and human facilities (Sections 1.1-1.2).

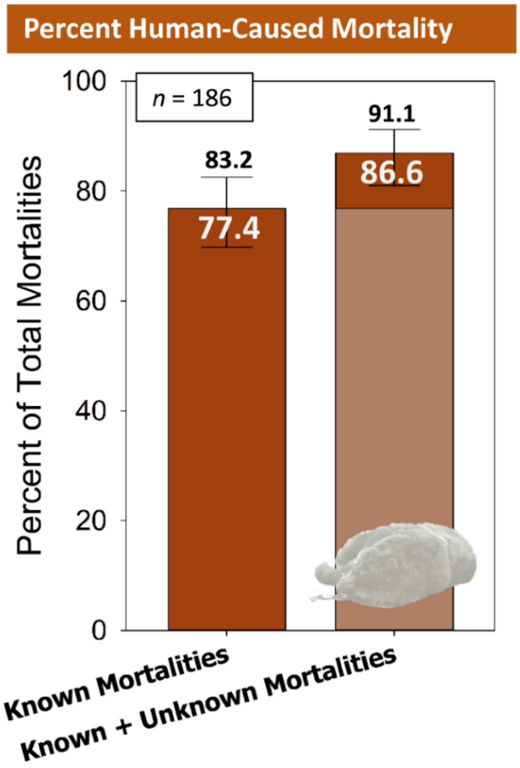

Figure 2. Humans cause almost all deaths of adolescent and adult grizzly bears in the Rocky Mountain of North America. The bars above show proportions of known human-caused deaths at left (mean = 77.4%) and known plus possible deaths at right (mean = 86.6%) calculated from a pooled sample of radio-marked grizzly bears from study areas in the Rocky Mountains for which cause of death was documented (*n* = 186). Brackets shown 95% Confidence Intervals for each proportion. Data are from McLellan et al. (1999), Wakkinen & Kasworm (2004), Garshelis et al. (2005), Schwartz et al. (2006), Boulanger & Stenhouse (2014), and Costello et al. (2016).

2.1. Drivers of Human-Caused Mortality

By first principles, human-caused mortality is a joint function of two phenomena: the frequency with which bears encounter people (i.e., exposure), and the likelihood that these encounters will be lethal for the involved bears (i.e., lethality) – much like the classic components of risk (e.g., Pritchard 2014), but with humans being the focal hazard (Mattson et al. 1996b). By this construction, human-specific lethality replaces the more static notion of vulnerability used in most risk analysis. Several environmental as well as human- and bear-specific factors plausibly dominate the dynamics driving human-caused grizzly bear mortality, with some having a greater role in configuring frequency of human-bear contact and others a greater role in configuring lethality (Figure 3; Mattson et al. 1996a, 1996b; Mattson 2004, 2021a).

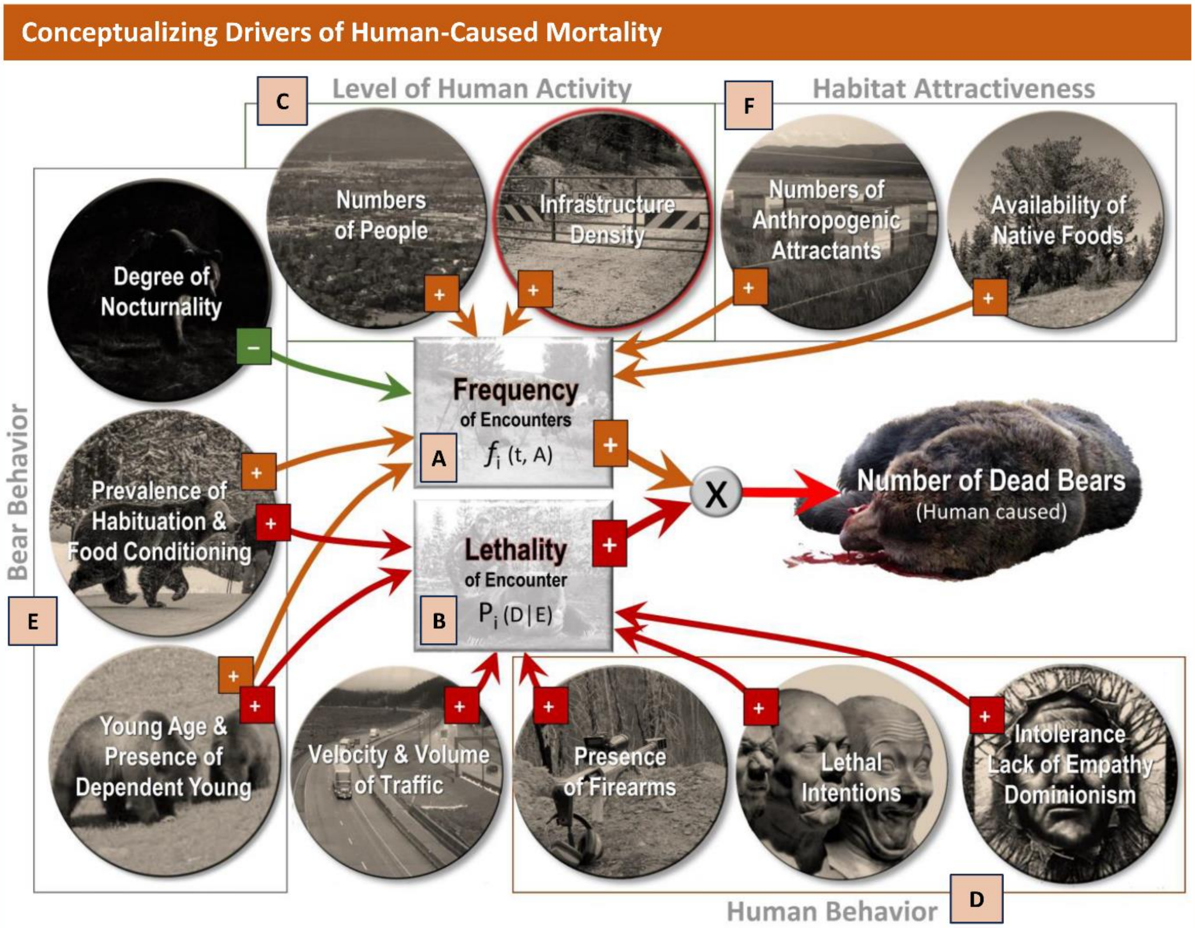

Figure 3. By first principles, numbers of human-caused grizzly bear deaths are a function of how often bears encounter humans (frequency of encounter [A]), and given an encounter, how likely it will result in a bear's death (lethality of encounter [B}). The conceptual model above decomposes frequency and lethality of encounter into various drivers of each dynamic related to human numbers (C) and behaviors (D), bear behavior (E), and factors intrinsic to habitat near or far from humans (F). Each labeled circle denotes a factor, with factors logically grouped in boxes. Arrows labeled with pluses denote effects that exacerbate or increase frequency or lethality of encounters. Arrows labeled with minuses denote effects that ameliorate. Red arrows and boxes denote effects on lethality of encounter; orange arrows and boxes denote effects on frequency of encounter.

Frequency of contact is axiomatically a function of the joint likelihood that bears and people will be present at a given time and place. Figure 3 parses the factors governing this dynamic into those related to levels of human activity (Figure 3c), attractiveness of local habitats for bears (figure 3f), and bear behaviors (Figure 3e). Human activity is manifestly a function of human numbers and the access that people have to a given locale. Bear activity is plausibly a function of the extent to which local habitats are attractive because of anthropogenic and natural foods, the prevalence of behaviors that allow bears to better accommodate people (increased nocturnality or tolerance), and other behaviors that motivate bears to actively seek out human-impacted areas (conditioning to human foods and avoidance of threatening conspecifics, especially on the part of females with dependent young; Mattson 2021a).

Human lethality is arguably determined largely by human behaviors, most of them directly or indirectly rooted in human attitudes, worldviews, and choices (Figure 3d). Prospectively the deadliest situations for bears arise from when people arm themselves (choice) and go into grizzly bear habitat with the intent of killing a bear (intention), as commonly happens during a regulated bear hunt or in cases of poaching (Mattson 2020). Less perniciously, people who are unwilling to accommodate or otherwise be tolerant of bears (attitudes and worldviews) will likely respond to conflicts by killing the involved animals or calling upon government officials to do the same (Mattson 2022). Bears predictably elevate the odds of lethal outcomes by engaging in behaviors that are seen as threatening by affected people, notably through becoming conditioned to eating human foods or merely more tolerant of nearby people (Mattson 2021a). Fatal outcomes arising from encounters with large numbers of speeding vehicles do not fall neatly into any overarching category and are uniquely attributable to a specific kind of human infrastructure (i.e., major highways).

There are two important conclusions that can be drawn from this conceptualization of human-caused mortality. First, bears can likely survive in human-affected environs despite numerous encounters with people, but only if interactions are benign – not lethal – as in many National Parks where bears are afforded high levels of protection. By contrast, even rare encounters with people who are highly lethal (e.g., hunters) can debar coexistence of humans and bears in areas where access to humans is facilitated by roads, trails, or residences (Mattson 2020). The second main conclusion is that human infrastructure, as such, is only one of several factors determining levels of human-caused bear mortality.

2.2. Drivers of Avoidance and Underuse

Population-level underuse and individual-specific avoidance of areas near human infrastructure by grizzly bears is the ostensible focus of this report. Yet, as with human-caused mortality, infrastructure per se is likely to be only one of several drivers for these phenomena at any given time and place. Figure 4 conceptualizes underuse and avoidance as the outcome of factors grouped into the higher-order categories of bear behavior (Figure 4a), habitat attractiveness (Figure 4b), pressures attributable to bear populations (Figure 4c), and levels of human activity and disturbance (Figure 4d) – with many of these same factors at play in dynamics driving human-caused bear mortality.

Consistent with effects driving greater frequency of contact between bears and people (Figure 3), increased nocturnality, food-conditioning, tolerance, and vulnerability to aggression from adult males predictably lead bears to seek out and use areas near humans and human infrastructure (Mattson 2021a). The same is true of increased availability of natural and anthropogenic foods near people. Conversely, increased levels of highway traffic, numbers of people, and densities of roads and buildings plausibly increase the likelihood that bears will avoid human-affected areas, both because of learned behaviors and visual and audio disturbance (Mattson 2021a). More opaquely, higher population densities relative to carrying capacity likely lead bears to use human-impacted area as a means of alleviating competition with conspecifics, prospectively countered by intolerances arising from past negative experiences resulting from human persecution (Mattson 2021a). Here again the effects of human infrastructure, as such, are likely to be conditioned on other environmental and behavioral factors.

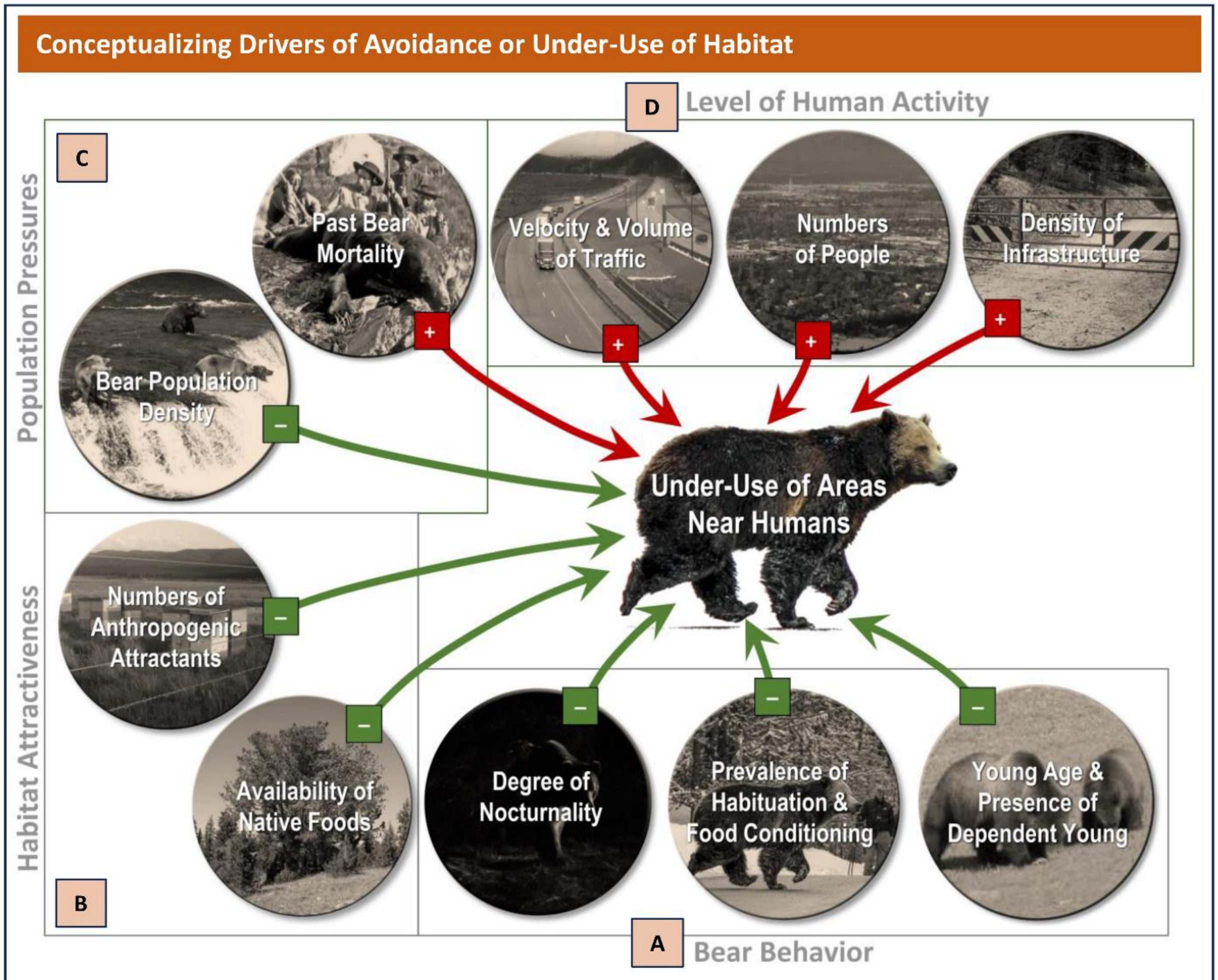

Figure 4. Grizzly bears avoid humans or underuse habitat near human facilities for several reasons related to bear personality and learned behaviors (A), the attractiveness of habitats near people (B), pressures related to numbers and distributions of other bears (C), and level and nature of human activities (D). Each of the labeled circles above denote a factor related to one of these broader groupings. Red arrows labeled with pluses denote effects that accentuate avoidance or under-use. Green arrows labeled with minuses denote effects that diminish avoidance. Humans have indirect effects not shown here on past bear mortality (see Figure 1) and numbers of anthropogenic attractants (see Figure 3).

2.3. The Complex Contingencies of Human Impacts

Throughout the previous two sections I have highlighted the extent to which the effects of humans and human infrastructure on grizzly bear demography and behaviors are contingent on diverse factors. Even more complicated, the effects of these factors at any given time and place are predictably a result of several amplifying or tempering interactions. Figure 5 attempts to capture some prospectively more important interactions among factors operating in a constellation configuring direct effects of each on bear mortality and behavior featured in Figures 3 and 4. As in the previous two figures, individual factors are grouped into the higher-order categories of localized human activity (Figure 5a) and behaviors (Figure 5b), bear behaviors (Figure 5c) and population pressures (Figure 5d), and habitat attractiveness deriving from availability of anthropogenic foods (5e).

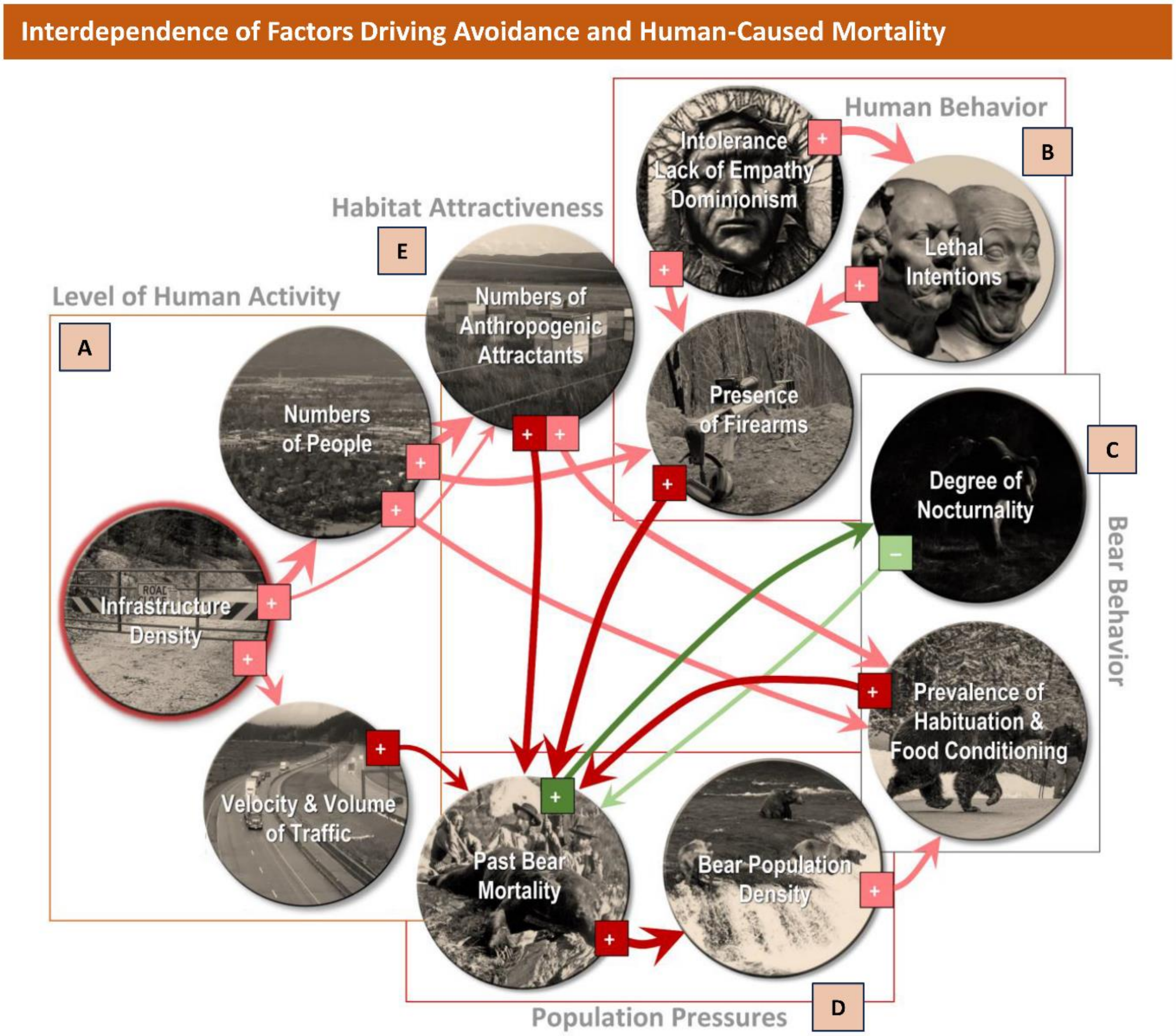

Figure 5. The factors driving grizzly bear avoidance of humans (see Figure 4) and levels of human-caused mortality (Figure 3) do not operate independently. This lack of independence introduces complex dynamics that produce highly variable outcomes depending on the nature and level of interactions among each factor. Each labeled circle here shows a factor from either Figure 3 or Figure 4. The arrows show documented effects of one factor on another. Arrows labeled with a plus sign denote effects that indirectly exacerbate avoidance or levels of human-caused mortality, with red denoting an effect that directly impacts grizzly bear demography. Green arrows denote effects that ameliorate avoidance or mortality, notably through the prevalence of nocturnal behavior among bears.

Emblematic of these interactions, a history of exploitable anthropogenic foods predictably leads to increased levels of food-conditioning among bears, leading in turn to higher levels of human-caused bear mortality – with derivative effects on bear population density and the related drive among individual bears to seek out human environs in pursuit of food (Mattson 2021a). Another prospective web of interactions involves the facilitation of increased levels of human activity by increased human infrastructure – entailing increased volumes of traffic and amounts of anthropogenic foods – with resulting effects on levels of human-caused bear mortality; ad nauseum. As an upshot, self-reinforcing dynamics can be entrained by these interactions that either exacerbate or alleviate the isolated effects of any given factor on bears and bear populations, as per the notion of vicious and virtuous cycles introduced in Section 1.1 and Figure 1.

Put simply, it is reasonable to assume that human infrastructure will not affect grizzly bears in isolation, but with effects likely to vary from one time and place to another depending on the nature and magnitude of individual drivers and interactions among them.

3. A Research History

Some of the earliest grizzly bear research perhaps inadvertently focused on the effects of human infrastructure—specifically, the effects of garbage dumps on bear behavior and demography. The most notable example is the pioneering work of Frank and John Craighead between 1959 and 1970 in Yellowstone National Park (e.g., Hornocker 1962, Craighead et al. 1976). Garbage dumps became a natural focus of investigations prior to the advent of radio-telemetry-based methods primarily because they offered some of the only opportunities to observe numerous bears at close range. Natural aggregations of bears fishing for anadromous salmonids in coastal spawning streams were the only other settings offering similar opportunities (e.g., Troyer & Hensel 1964, Egbert & Stokes 1976).

The Craighead's coined the term "ecocenter" to describe the remarkable dynamics created by bears concentrating at garbage dumps to feed on anthropogenic foods. The demographic effects of these dumps were debated for several decades (e.g., Craighead et al. 1974, Cole 1974, Picton 1978, Stringham 1986), although there was undisputed evidence that numerous grizzly bears traveled long distances to eat human refuse for much of the summer, with resulting amplified social interactions among the concentrated bears (Craighead et al. 1995). Importantly, these dumps inside Yellowstone Park were characterized by comparative isolation from major highways and recreational developments, in contrast to other dumps in the Yellowstone Ecosystem that spawned high levels of human-bear conflict because of nearness to towns and highways (Schullery 1986).

Two of the earliest landscape-level investigations focused on how human infrastructure might affect dispersed brown bears were published by Franco Zunino and Stephen Herrero in 1972 and Káre Elgmork in 1978 - the first focused on bears in the Apennine Mountains of Itay and the second on a remnant population of bears in Norway. Both relied on historical bear observations to establish relations between human infrastructure and bear distributions, with predictably strong negative correlations despite the likely positive bias introduced by reliance on bear observations resulting from encounters with people.

The advent of methods based on radio-telemetry developed by Frank Craighead, Jr., during the 1960s allowed researchers to reliably track bears without depending on visual observations, albeit still contingent on having opportunities to trap and radio-collar bears in convenient places (Craighead & Craighead 1965). Although early uses of radio-telemetry did not explicitly focus on effects of human infrastructure, investigations featuring the impacts of roads and townsites followed during the next 20 years.

These later investigations relied on ground-based triangulation and aerial overflights to locate radio-marked bears, both of which introduced substantial geospatial error and a strong bias towards daytime locations. Mattson et al. (1987) and McLellan & Shackleton (1988) were among the first to analyze spatial distributions of telemetry locations relative to roads and townsites, with underuse of areas near infrastructure estimated vis-à-vis patterns expected by random occupancy. Both analyses partitioned results by sex, age, and reproductive status of radio-marked bears, although Mattson et al. (1987) was the first to additionally look at how distributions of bears were configured by habitat productivity. Knight et al. (1988) and Mattson et al. (1992) subsequently addressed, first, the spatial footprint of human-caused mortality centered on settlements and, second, effects of tolerance and food-conditioning on distributions of radio-marked bears vis-à-vis roads and townsites.

3.1. Revolutions in Technology: A Personal History

It is probably difficult for those who take the performance of current computers and software for granted to imagine the state of technology available to wildlife researchers during the late 1970s and early 1980s. GIS software was essentially non-existent. Primitive versions of ESRI's ARC/INFO only became available in 1981, followed shortly by the U.S. Army Corps of Engineers' GRASS program in 1982. Desktop computers capable of even basic geospatial calculations were also essentially non-existent. The first Hewlett-Packard computer to grace my research office in 1982 cost >$30,000 and featured a feeble 18MHz of speed and 512kB of RAM. Current laptop computers used for basic computational research typically have >18,000,000 MHz of speed, >30,000,000 kB of RAM, and cost closer to $1,000-2,000.

As an upshot, the geospatial analyses I undertook in the early 1980s required that I use a terminal connected to a mainframe computer and collaborate with a programmer named Bill Hoskins to develop software that could undertake basic geospatial calculations such as nearest-neighbor distances and areas of overlap based on various types of buffers. There was, moreover, the additional major challenge of developing a GIS consisting not only of geospatial coordinates for bear telemetry locations, but also vector- and raster-based renderings of environmental features. The latter required hand-digitizing hard-copy maps of point and linear human features along with habitat polygons obtained by dint of considerable field work (e.g., Mattson & Despain 1985, Dixon 1997). Developing the requisite GIS and software took four full years and, when finally ready, entailed mainframe calculations lasting an entire night.

Meanwhile, field investigations remained limited by dependence on VHF technology for radio-tracking, and paper maps for on-the-ground navigation. Even when GPS technology became available for field work in 1989, I have vivid memories of carting around a device weighing 1.5-lbs, with a battery life of 2-hours, offering locational accuracy of around 100 meters—but only when I had a clear sky window—and costing around $3,000 (e.g., Ardö & Pilesjö 1992). As a practical matter, GPS technology remained unavailable for wildlife applications until around 2000 when the U.S. Government ended a program that deliberately degraded performance of GPS for non-military purposes, and technology had advanced enough to allow for installation of long-lasting light-weight batteries and GPS devices on collars for radio-tracking larger wildlife species.

On-going limitations of telemetry-based studies during the 1980s and 1990s led me to collaborate with other researchers on alternative approaches focused on detecting durable bear sign along transects concentrated in areas with high-quality food resources likely to be exploited by any bears that were present (e.g., whitebark pine [*Pinus albicaulis*] seeds, spawning cutthroat trout [*Oncorhynchus clarkii*], and carrion from large ungulates). These kinds of studies were not contaminated by diel bias and, moreover, allowed us to precisely locate sites where bears had fed for significant periods of time. An additional advantage of this approach was the explicit focus on high-quality foods and derivative opportunities to determine likelihood of exploitation as a function of environmental features – including nearness to human infrastructure (e.g., Reinhart & Mattson 1990, Green et al. 1997, Mattson & Reinhart 1997).

With the post-2000 advent of widely available GPS technology, accuracy of telemetry locations increased dramatically, at the same time as diel bias in locations was essentially eliminated. As battery and receiver technology continued to improve, intervals between location fixes dropped from hours to minutes (see

Tomkiewicz et al. 2010 for a review). All of this allowed for dramatic advances in analytic techniques (e.g., Katzner & Arlettaz 2020), with a resulting shift from concern about temporal and spatial autocorrelation of telemetry locations during the 1980s and 1990s (e.g., Swihart & Slade 1985, Otis & White 1999) to frames emphasizing time series of spatially explicit movements during the 2010s and 2020s (e.g., Roever et al. 2010).

Another revolution pioneered by Michael Proctor and others emerged during the late 1990s, organized around the use of genetic techniques for broader-scale geospatial analyses (e.g., Proctor et al. 2002, 2004, 2005, 2010). This methodology was widely employed in Canada to estimate not only bear numbers and densities, but also, of greater significance here, spatially explicit patterns of population isolation and fragmentation. Researchers led by Clayton Lamb (e.g., Lamb et al. 2017a, 2019) further refined use of genetic-tagging in finer-scale geospatial analyses that allowed for greater insight into how roads and townsites affected distributions and survival of grizzly bears, again with a focus on Canadian study areas.

These improvements in technology and analytical techniques during the last 40 years are starkly evident in the research reviewed in this report. Insights into how humans and human infrastructure affect bear movements and demography have clearly benefited from access to temporally and spatially finer-grained data reckoned against evermore replete digital representations of human and natural environments. That having been said, conceptualizations of bear-human relations have lagged far behind, and in some key regards remain underdeveloped. A glut of data combined with computational and statistical sophistication is not equivalent to conceptual adequacy.

3.2. A Burgeoning of Conceptually Limited Research

Advances in technology and techniques together with mounting concerns about wildlife conservation (e.g., Dunlap & Mertig 1991) fueled burgeoning research focused on habitat selection and spatially explicit survival of brown and grizzly bears, featuring the effects of humans and human infrastructure. Figure 6a shows the number of published papers, summed by 5-year increment, that reported research either focused on or secondarily addressing geospatial effects of humans and human infrastructure on grizzly bears. These numbers sky-rocketed after 1999, coincident with the maturation of tracking technology, genetic techniques, and long-term field studies.

Interestingly, the average number of human-related factors addressed in any single publication (as per Sections 2.1-2.3) has remained relatively static, as denoted by the height of brown-shaded bars in Figure 6a. Moreover, there has been sustained neglect of factors rooted in human attitudes, intentions, and behaviors (purple-colored bars in Figure 6b), in contrast to factors related to physical features such as road densities or rote numbers of people (brown-colored bars). The roles of habituation and food-conditioning in configuring geospatial distributions of bears vis-à-vis human infrastructure have also been given scant attention.

This collective as well as study-specific inattention to the broad suite of factors likely configuring effects of humans and human infrastructure on bears poses problems as well as questions. For one, it complicates or even debars extrapolation of results from a given study to other times and places. For another, it bedevils reaching higher-order conclusions about the comparative importance of different factors. Ultimately, this failure to embrace complexity deprives people who care about or manage bears and bear habitat of the information they need to adequately address local challenges and opportunities.

I can only speculate about why the scientific community has failed to address the complexity that attends effects of humans and human infrastructure on grizzly bear survival and behavior, but a lifetime of professional experience offers some clues. For one, I suspect there is a pervasive tendency among researchers to conflate advances in statistical methods and high-end technology with insight into the complexities of real-world systems. For another, I think this tendency both feeds and is fed by the nature of research that manages to pass muster in peer reviewed scientific journals. Length and comprehensiveness are rarely rewarded in scientific manuscripts, as is true for the articulation of replete conceptual models that frame complexities. My experiences in academe and government research emphasize the extent to which students graduating with doctoral degrees are statistical technicians more than philosophers of science.

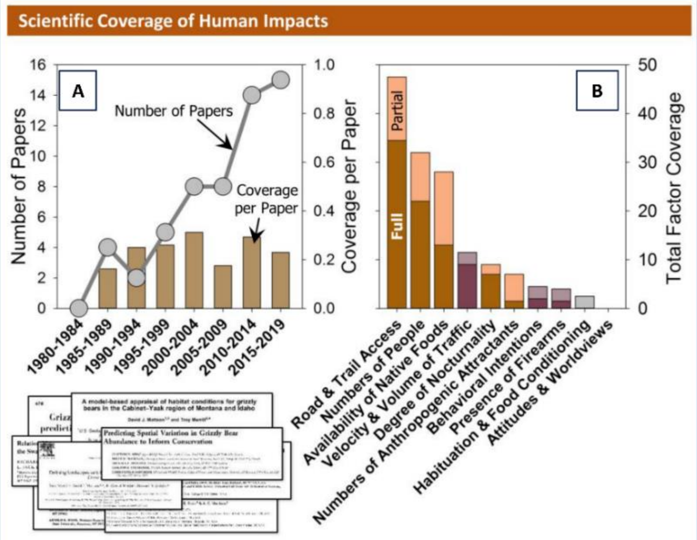

Figure 6. The impacts of humans on grizzly bear behavior and demography have received increasing attention by researchers during the last 40 years. The gray dots in (A) show numbers of published papers addressing human impacts by 5-year increments. The brown bars show average number of factors identified in Figures 2 and 3 that individual papers addressed during each period, suggesting that coverage of multiple factors in each paper has not increased over time. The bars in (B) show cumulative coverage of factors summed over all research papers. Darker shading indicates more complete coverage of a factor in individual papers whereas lighter shading indicates parenthetical or partial coverage. Brown-shaded bars relate to factors primarily affecting grizzly bear avoidance of humans (Figure 3) whereas purple-shaded bars denote coverage of factors primarily affecting human lethality. Avoidance by bears has received far more attention than human lethality.

Regardless of the reasons why research and synthesis have remained bounded, my intent here is to remedy some of this deficiency by not only marshalling the available published research, but also synthesizing this research through a replete and *prima facie* plausible conceptual framework. This latter consideration leads me to devote considerable up-front text to conceptualizing (Section 2) as well as contextualizing (Section 3, here) the problem of how humans and human infrastructure likely affect grizzly bear behavior and demography.

4. Effects on Bear Demography

Human-caused mortality has perhaps the most dramatic and demonstrable effect of any phenomenon on grizzly bear demography (Section 2). Here I use the term demography to encompass individual survival rates, presence versus absence of bears, bear densities, and growth and persistence of bear populations. Population growth and persistence are ultimate reckonings of individual survival rates. Bear densities also reflect survival – as well as female reproduction – but with human impacts more overtly conditioned on environmental productivity (Mattson 2021b). Presence versus absence is perhaps the crudest demographic metric, but nonetheless an axiomatic derivative of whether bears survive and reproduce in an area.

In this section I focus on how humans directly affect bear demography through the mediating effect of human infrastructure as an overt consequence of peoples' intentions and choices (Section 2.1), whether in immediate interactions with bears or through configuring the human environment. This encompasses malicious killing, defense of life and property, responses to depredation and exploitation of human foods, and actions by bear managers. All these phenomena are implicit to analyses that investigate relations between grizzly bear demography and human features such as management jurisdiction, road density, visibility along roads, human density, presence of residential areas, and levels of human activity on roads – but only up to a point.

I make a distinction in this report between impacts attributable to people on industrial or lightly trafficked secondary roads and impacts attributable to collisions between bears and vehicles on heavily trafficked high-speed highways. Researchers routinely make this distinction in reporting results on road and highway impacts. Perhaps more importantly, there are substantial differences in human motivation and choice between when bears die from a lethal injection or a bullet wound, and when they die from accidently colliding with a vehicle acting as a *de facto* lethal projectile, with implications for how people associated with human infrastructure affect bear demography and behavior. Nonetheless, because high speed primary highways have major impacts on bear demography and behavior, I cover these human-related features in Section X.

4.1. Complexities of Spatial Grizzly Bear Demographic Analyses

Compared to spatially indeterminate analyses of survival, geospatial analyses of are much more complex simply because spatial and temporal dimensions need to be simultaneously considered. Compounding this dimensional complexity, researchers must assemble geospatial data, account for the grain of these data, determine how to treat spatial correlation of grizzly bear location data, and furthermore determine the grain and extent of the spatial frame. Whether using densities or distances, researchers ideally need to make defensible choices regarding the grain of calculations, which are inescapably related to spatial extent of the analysis area and grizzly bear movements (e.g., Boyce 2006). These specifications are rooted in assumptions about the spatial footprint of risks associated with humans and human infrastructure, often codified in the extent of areal buffers attached to individual bear locations.

Plausible choices for the geospatial resolution of analyses include arbitrary units such as km^2 or, more defensibly, a grain based on the average extent of movements by bears during different periods of time, including 24-48 hours, a given season, or the entirety of a year. The first emphasizes exposure of individual bears to human infrastructure during a typical foraging bout (Haroldson & Mattson 1985, Mattson 1993, Gibeau et al. 2001, Schwartz et al. 2010) whereas definitions based on seasonal or annual ranges emphasize cumulative exposure of individuals at a temporal scale that more directly correlates with annual survival. At the coarsest grain, a focus on hazards accumulated over average lifetimes or generations logically entails using a spatial grain of grizzly bear lifetime ranges as well as data aggregated over populations or demographic classes (Mattson & Merrill 2002, Merrill & Mattson 2004).

Although spatially indeterminate approaches to survival analysis are well developed (e.g., Lebreton et al. 1992) and commonly used in bear research (e.g., Schwartz et al. 2006, Mace et al. 2012), these methods do not eliminate the need to define compatible time units and geospatial grains when undertaking spatially explicit analyses (e.g., daily survival x extent of 24-48-hour movements, or seasonal survival x cumulative seasonal exposure to various road densities; Boyce [2006], Ciarniello et al. [2007]). Schwartz et al. (2010) provide a good example of mismatch between spatial and temporal grains (in their case matching daily foraging area with seasonal survival). Choices regarding the geospatial scale of calculations almost always introduce an element that is more about convenience of calculations than it is survival, persistence, or density of bears (e.g., Wheatley & Johnson 2009, Wheatley 2010). Analyses of *human* survival typically obscure this issue by focusing on data aggregated for permanent residents of jurisdictions such as counties, municipalities, or neighborhoods that have shared risk features (e.g., Banerjee 2016), whereas *bear*-focused demographic analyses are inescapably faced with more complex choices regarding spatial and temporal grain, especially when examining movements and fates of individual bears.

Methodological complexities, subjective choices, differences in response variables, and constraints imposed by temporal and spatial resolutions of data complicate any straight-forward comparison of results from the different studies synopsized here (e.g., Mayer & Cameron 2003, Wheatley 2010). For example, relationships between road density and grizzly bear survival, density, or persistence may vary simply because of differences in data resolution and the spatial-temporal grain chosen by researchers – as well as because of differences in the strength of environmental processes operating at different spatial and temporal scales. Even so, landscape features that exert a powerful influence on survival or reproduction predictably manifest in broadly similar although not exactly comparable relations regardless of scale (e.g., Nisi et al. 2021), as might be expected with geospatial relations between grizzly bear demography and human infrastructure.

4.2. Secondary Roads and Grizzly Bear Demography

Road densities and the related extent of lands remote from roads have become proxies for almost all human impacts on public lands in North America. In an apparent quest for simplicity, federal agencies with authority over grizzly bear management in the contiguous United States have established fixed standards for allowable road densities and derivative calculations of “secure” habitat on public lands that do not vary regardless of roadside visibility, juxtaposition with attractive habitats, local human lethality, levels of human traffic, or vulnerability of local bear populations – in other words, without regard for most factors identified in Section 2.1 as plausibly governing human-caused grizzly bear mortality (U.S. Fish & Wildlife Service 2007, Greater Yellowstone Ecosystem Grizzly Bear Subcommittee 2016, Northern Continental Divide Ecosystem Grizzly Bear Subcommittee 2019).

This quest for simplicity has resulted in a *de facto* presumption by bear managers that human effects on grizzly bear security are non-existent if certain fixed geospatial thresholds attached to roads are not exceeded[1]. Various researchers have obliged this logic by publishing conclusions such as: "industrial road management would be a useful tool if…(b) open road densities exceed 0.6 km/km^2; (c) less than at least 60% of the unit's area is >500 m from an open road in patch sizes of ≥10 km^2 [sic]" (Proctor et al. 2019). Regardless of the nuance or proviso attached by researchers to such statements, managers have historically seized on them to justify an abridged and oversimplified approach to managing grizzly bear habitat security.

4.2.1. Concentrations of Grizzly Bear Deaths Near Roads

The proportional concentration of documented bear death near roads is perhaps the crudest reckoning of how human infrastructure affects grizzly bear survival. The box-and-whisker diagram in Figure 7 summarizes these proportions from seven studies in the Rocky Mountains of Canada and the United States, with proportions standardized to distances of 500 and 1000 m from roads to facilitate comparison of results reported for zones varying from 100 to 1600 m. Given that the exact relation between distance and concentration of deaths is not known, these standardized proportions are only rough approximations.

Most grizzly bear deaths occurred within 500-m (0.3 mile) of roads, and nearly all within 1000-m (0.6 mile) – regardless of study area. Outliers in Figure 7 are attributable to historical patterns of mortality in the Northern Continental Divide Ecosystem associated with grizzly bear sporting-hunting largely concentrated in remote Wilderness Areas (Dood et al. 1986, Aune & Kasworm 1989, Mattson 2019:36).

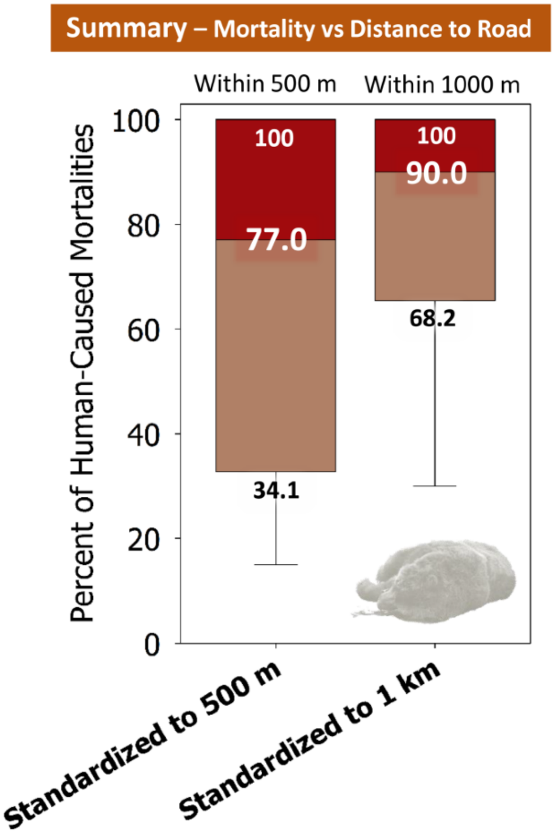

Figure 7. The box-and whisker plots above summarize results from 7 different studies that estimated the proportion of human-caused grizzly bear mortalities occurring near roads (Dood et al. 1985, Aune & Kasworm 1989, Nagy & Gunson 1990, Mattson et al. 1996, Benn & Herrero 2002, Wakkinen & Kasworm 2004, Boulanger & Stenhouse 2014, McLellan 2015, Stenhouse unpublished). These studies reported fractions for binary distance thresholds varying from ~100 (N = 2), to 500 (N = 3), to 1000 m (N = 3), to 1600 m (N = 1). The box plots above show estimated fractions standardized to 500 m (left) and 1000 m (right) based on asymptotically pro-rating fractions to 100-m increments. Most bear mortalities occurred within 500 m of roads, whereas almost all occurred within 1000 m.

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[1] Evidence for this phenomenon can be found in numerous decision documents by the U.S. Forest Service. Noteworthy examples include decisions related to the Black Ram project on the Kootenai National Forest and South Plateau Landscape Area Treatment project on the Custer-Gallatin National Forest.

These results suggest that bears using areas within 500-m of industrial and other secondary roads are highly vulnerable to lethal interactions with people, especially in jurisdictions where bears are not strictly protected. This conclusion is reinforced by the fact that proportional deaths near roads are *greater* for results based exclusively on fates of radio-marked bears compared to results including observations of unmarked dead animals. Deaths of the former were likely to be documented regardless of nearness to roads whereas deaths of the latter were biased towards detection in areas where people were active – near roads and residences (Mattson 1998).

4.2.2. Grizzly Bear Demography versus Road Densities

Road density is invariably negatively related to grizzly bear demographic performance regardless of study area location, design, scale, or response variable. This holds for annual survival rate (Figures 8a and 8b), population growth rate (Figure 8c), population density (Figure 8d), and crude presence-absence (Figures 8e and 8f). Importantly, the relation between road density and demographic response is consistently monotonic, with variation in the magnitude and exact nature of responses varying by habitat matrix; study area; analytic method; independent variable; and sex, age, and reproductive status of affected grizzly bears.

Of relevance to grizzly bear conservation, these monotonic negative responses suggest that any increase in road density will have adverse effects on demographic performance of grizzly bears. There is no intermediate optimum for bears. Instead, the available evidence suggests that the most favorable conditions for grizzly bears occur when there are no roads at all.

Even so, configurations of demographic responses by grizzly bears to road density offer opportunities to harmonize human access and bear conservation. These optima logically derive from demographic thresholds for bears that include sustainable annual survival rates for adult females (s = 0.91-0.94; Schwartz et al. 2010a), sustainable population growth ($\lambda = 1.0$; Boulanger & Stenhouse 2014), and a greater than 50:50 chance of being present versus absent (Merrill et al. 1999, Mattson & Merrill 2004). Of further relevance, thresholds for survival and population growth roughly correspond with inflections where negative responses to increases in road density intensify (Figures 8a, 8b, 8c).

These thresholds derived from sustainability criteria for grizzly bears correspond with a wide range of road densities depending on the study and whether factors such as uncertainty of estimates (e.g., Figures 8a and 8b), reproductive status (e.g., Figure 8a), or security of the larger matrix (e.g., Figure 8b) are accounted for. The results shown in Figure 8 as well as the scale-dependent results from Mattson (1993) and Lamb et al. (2017a) yield a median threshold for road densities of around 0.7 km/km^2 (1.1 mi/mi^2), but with an interquartile range of 0.4 km/km^2 (0.6 mi/mi^2) to 1.0 km/km^2 (1.5 mi/mi^2) – the former less risky for bears and the latter more hazardous.

Depending upon how a transportation system is laid out, road densities of around 0.7 km/km^2 would result in patches of habitat around 30-40 ha in size outside the 500 m hazard zone of roads (see Section 4.2.1) – roughly 4 to 30 times smaller than the average size of areas used by grizzly bears in interior areas for foraging during a 24-48-hour period (110-150 ha [Schwartz et al. 2010]; 290 ha [Schleyer et al. 1984, Haroldson & Mattson 1985]; 910 ha [Gibeau et al. 2001]) and roughly 29 times smaller than the recommended size of core security areas (1,012 ha) in the Northern Continental Divide Ecosystem of the contiguous U.S. (Northern Continental Divide Ecosystem Subcommittee 2019). This disparity suggests that grizzly bears would need to venture near or across roads multiple times during a 1-2-day foraging period if road densities were around 0.7 km/km^2, with resulting heightened exposure to potentially lethal encounters with humans.

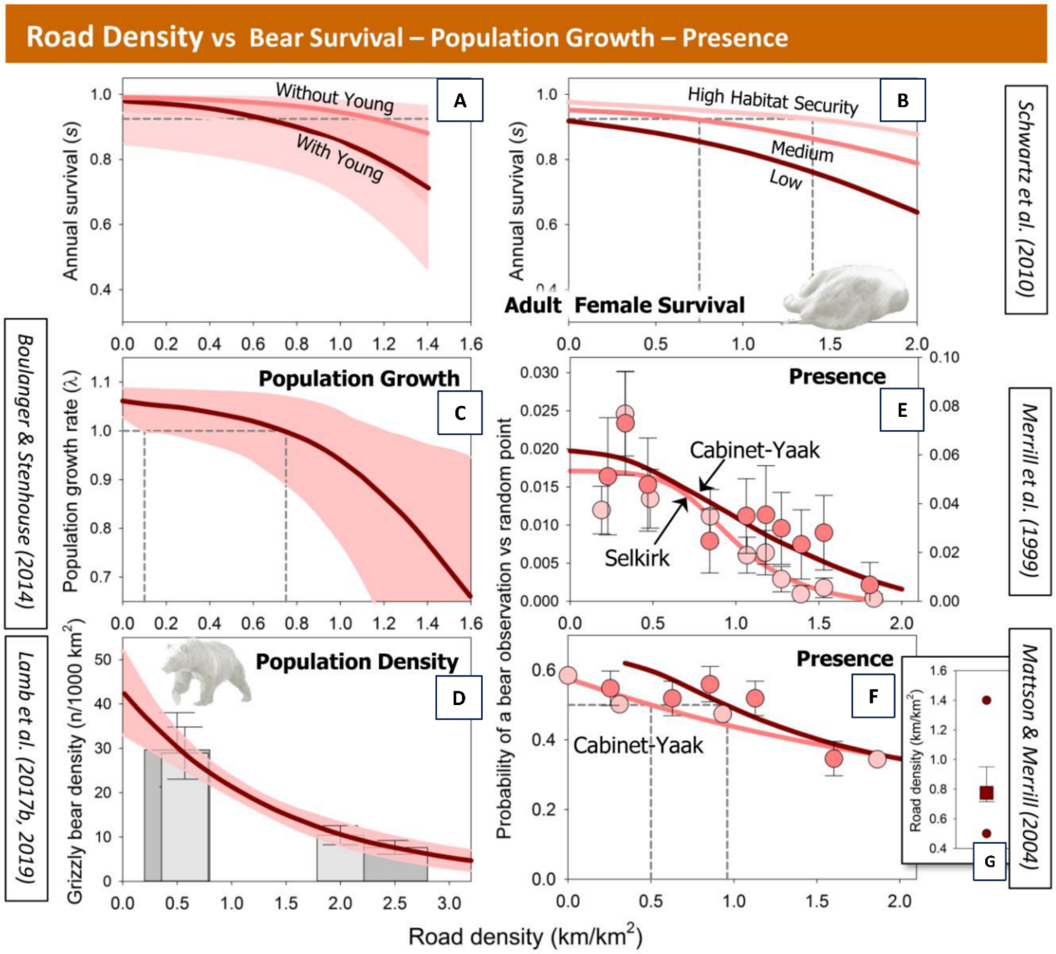
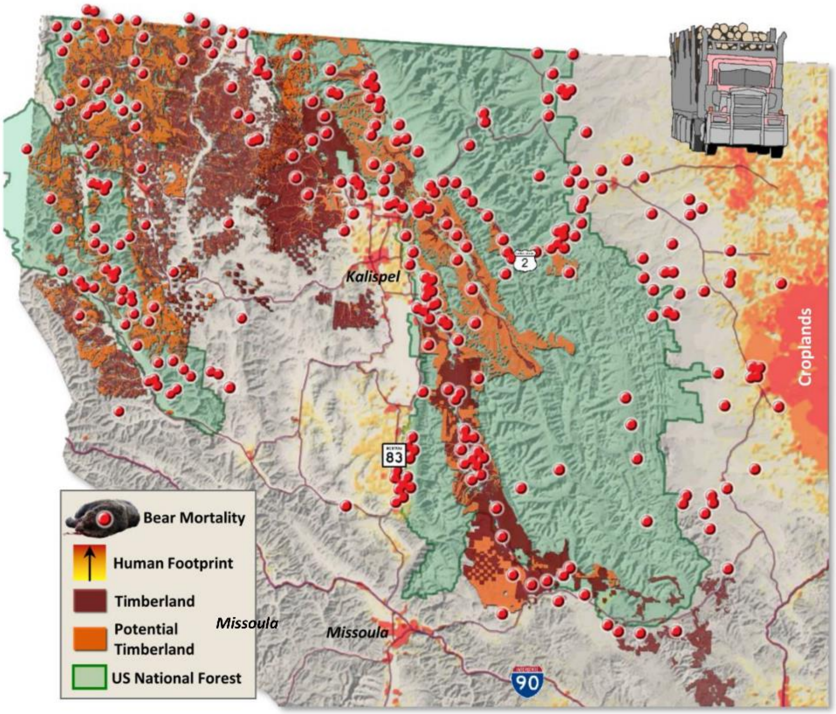


Figure 8. These figures provide a synopsis of research that investigated relations between road density and various demographic measure for grizzly bear populations in North America. Figures (A) and (B) show variation in annual survival rates of adult females bears in the Yellowstone Ecosystem as a function of road density, with lone females distinguished from females accompanied by dependent young in (A), and bears living in areas with different levels of habitat security differentiated in (B), where habitat security is defined in terms of core areas far removed from any roads (Schwartz et al. 2010). The threshold of sustainable female annual survival ($s = 0.925$) is shown as a horizontal dashed line. Figures (C) and (D) show variation in bear population growth (Boulanger & Stenhouse 2014) and density (Lamb et al. 2018, 2019) as a function of road densities for study areas in southern Canada. The threshold of stable population growth ($\lambda = 1$) is shown as a horizontal dashed line in (C). Figures (E) and (F) show the likelihood of grizzly bears being present as a function of roads densities for study areas in northern Idaho and northwestern Montana (Merrill et al. 1999, Mattson & Merrill 2004). The horizontal dashed line in (F) show a threshold above which grizzly bears were more likely present than absent ($p = 0.5$). All these relations show monotonic non-linear declines in demographic measures for grizzly bears as road densities increase. Depending on stratification and whether uncertainty is accounted for, road densities associated with sustainability thresholds varied from 0.1 to 1.4 km/km^2 (0.2-2.0 miles/mile^2), with most thresholds between 0.4 and 1.0 km/km^2 (0.6-1.6 miles/mile^2).

Box 1: Timber, Roads & Grizzly Bear Mortality

US Forest Service

High-density road systems on multiple-use public lands in the U.S.-Canadian Rocky Mountains are almost invariably associated with commercial extraction of resources, typically timber (e.g., Proctor et al. 2019). Areas devoted to timber production, whether under express government management or management of private companies with tenure, have extensive permanent and temporary road systems devoted to the conveyance of logs or the transport of people and machinery needed to cut and plant trees. The map below shows lands on Forest Service and State jurisdictions in northwestern Montana and northern Idaho that are dedicated to timber production in burgundy. Areas colored rusty orange have less extensive road systems but are reserved for prospective future harvest. Red dots show documented grizzly bear mortality, most of it post 1998. Visually, the positive correlation between grizzly bear mortality and industrialized roaded landscapes is striking – as well as consistent with results summarized in Sections 4.2.1 and 4.2.2. The only exceptions to this spatial correlation between timberlands and bear deaths are mortalities associated with vehicle strikes along highways such as US2 on the southern edge of Glacier National Park and conflicts on agricultural lands to the east and south. Despite being so closely identified with geospatial patterns of grizzly bear mortality, disentangling road building and maintenance from timber harvest is politically and legally virtually impossible (Havlick 2002, Nie 2008). Nonetheless these entangled human phenomena are critical to understanding the effects of secondary road systems on grizzly bear behavior and demography.



This map provides a visual synopsis of the association between grizzly bear mortalities and industrial-scale timber extraction or other permanent conversions of the natural landscape by humans (the "human footprint"; Leu et al. 2008). Both are intimately associated with dense road networks that compromise grizzly bear survival (see Figure 7). The map encompasses the Northern Continental Divide and Cabinet-Yaak grizzly bear ecosystems of northwestern Montana. US Forest Service jurisdictions are shown in green and areas within these jurisdictions designated for industrial-scale timber extraction are shown in dark brown. Dusky orange areas are candidate for timber extraction and road building. The heaviest human footprint is shown as dark orange, including croplands of grasslands to the east and areas around Missoula, Kalispel, and in the Mission Valley along Highway 83. Grizzly bear mortalities are shown as red dots, most of which are concentrated in either roaded timberlands on Forest Service jurisdictions or along major highways such as US Highways 2 and 83. Mortality data are from annually-published reports summarizing grizzly bear research in the NCDE and Cabinet-Yaak ecosystems as well as from Costello et al. (2016). Areas designated by the US Forest Service for timber harvest are from Forest Plans for the Flathead, Kootenai, and Helena-Lewis & Clark National Forests.

4.2.3. Road Densities: Confounding Scale and Management Mismatches

The issue of security at large scales confounds any reckoning of how various road densities might affect grizzly bear demography. Researchers have almost invariably addressed the finer-grained effects of roads in the context of habitat security at scales of 1,000 to >30,000 ha. This invocation of areas larger than the conventional scale at which road densities are calculated (0.25-km^2 to 1-km^2) is both tacit as well as explicit acknowledgment that grizzly bear demography is affected by cumulative exposure of individuals to hazards at the scale of daily, seasonal, and annual movements (see section 4.1), often manifest in landscape-level source-sink population dynamics (e.g., Knight et al. 1988; Doak 1995; Carroll et al. 2003; Merrill & Mattson 2003; Naves et al. 2003; Johnson et al. 2004; Nielsen et al. 2006; Falcucci et al. 2009; Schwartz et al. 2010a; Apps et al. 2016; Lamb et al. 2017a, 2017b, 2019, 2020; Boulanger & Stenhouse 2018).

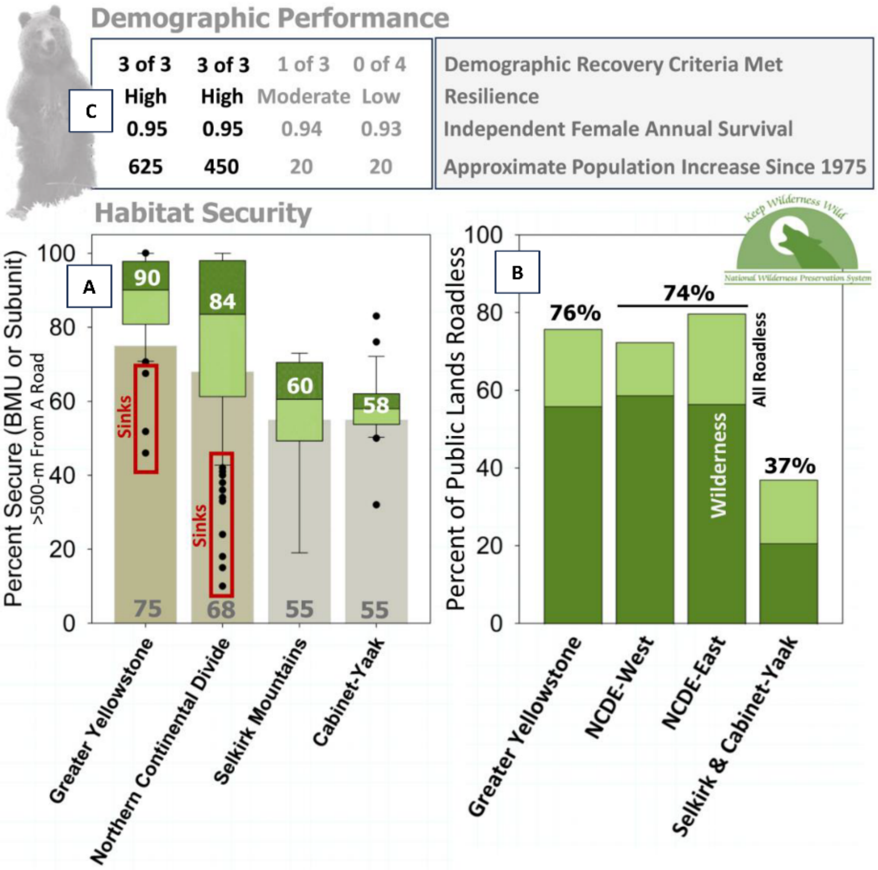
Various researchers have attempted to explicitly account for spill-over effects of security in the larger matrix on realized security at the scale of most road building and maintenance activities by recommending that larger-scale levels of security exceed what would be realized solely through finer-scale limits on road densities. Proctor et al. (2019) recommended that habitat >500-m from a road comprise >60% of 10-km^2 project areas whereas, more conservatively, Mattson (1993) recommended that habitat >2500-m from a road or human development comprise >57% of 28-km^2 analysis areas. Either one of these recommendations based largely on infra-seasonal bear movements far exceeds the ca. 30% levels of security that limiting road densities to <0.7-km/km^2 would provide for grizzly bears, especially if this limit was propagated over large areas.

Even so, the effects of security over large spatial extents on bears at the scale of seasonal or annual ranges is perhaps most convincingly manifest in demography within areas delineated for population management or surveys. At the most extensive, bear densities in Alberta have been shown to vary annually and with configurations of source and sink habitats at the scale of Bear Management Areas ranging in size from 2,800 to 19,000-km^2 (Morehouse & Boyce 2016, Boulanger et al. 2018). Apps et al. (2016) similarly found that bear densities in an overlapping study area were strongly correlated with habitat security and productivity at the scale of survey areas averaging 3,500-km^2 in size. At a smaller scale, Naves et al. (2003) showed that presence versus absence of brown bears in Spanish Cantabria varied among spatially uncorrelated areas 225-km^2 in size, implying a decay of demographic effects that comports with the *ca*. 200-km^2 scale at which road densities affected brown bear mortality on the Kenai Peninsula of Alaska and Granby-Kettle region of British Columbia (Suring & Del Frate 2002, Lamb et al. 2017) as well as the >200-km^2 spatial scaling parameters used by Bischof et al. (2020).

These last results are consistent with the scale at which the U.S. Fish & Wildlife Service assesses the totality of human impacts on grizzlies in various ecosystems of the contiguous United States. During the 1980s, Recovery Areas in the contiguous United States were stratified by Subunits roughly the size of female grizzly bear annual ranges (*ca*. 300-km^2) nested within larger Bear Management Units (BMUs) approximately the size of cumulative female life ranges (*ca*. 900-km^2; Weaver [1986], Blanchard & Knight [1991], Dixon [1997]). These delineations were premised on the notion that fates of individual bears are determined primarily by cumulative exposure to hazards and foods at the scale of areas used during a year or lifetime.

Security standards evolved for BMU Subunits in various grizzly bear Recovery Areas of the contiguous United States over a period of decades, culminating in a decision by the U.S. Fish & Wildlife Service to establish a no-net-loss policy for grizzly bear security at the Subunit level in two ecosystems, with security defined in terms of >500-m distance from roads and other human infrastructure. Baselines for calculation of no-net-loss in the Greater Yellowstone and Northern Continental Divide Ecosystems were set as conditions existing during 1998 and 2011, respectively, based on the premise that preceding increases in grizzly bear populations (Eberhardt et al. 1994, Mace et al. 2012) were a result of concurrent security levels (U.S. Fish & Wildlife Service 2007, Northern Continental Divide Ecosystem Grizzly Bear

Large-Scale Security vs Demography



3 of 3	3 of 3	1 of 3	0 of 4	Demographic Recovery Criteria Met
High	High	Moderate	Low	Resilience
0.95	0.95	0.94	0.93	Independent Female Annual Survival
625	450	20	20	Approximate Population Increase Since 1975

Figure 9. Extensive areas of secure roadless habitat at the scale of 300-900 km/km^2 are demonstrably important to sustaining grizzly bear populations in the Rocky Mountains. The bar graph in (A) shows the percent of Bear Management Units (BMUs) or BMU Subunits >500-m from roads as green box-and-whisker plots for four grizzly bear Recovery Zones in the contiguous United States; outliers are shown as black dots (U.S. Forest Service 2006, 2011; Van Manen et al. 2019). BMU Subunits that have independently been shown to be populations sinks in the Greater Yellowstone and Northern Continental Divide Ecosystems are delineated by red boxes (Johnson et al. 2004, Schwartz et al. 2010, Mattson 2019c). Median percent security in each Recovery Zone (RZ) is shown as a white number. The bars shaded dusky green are proportional in height to security standards set for BMUs or BMU Subunits in each of the four RZs, with standards shown as numbers at the base of each bar (Greater Yellowstone Grizzly Bear Subcommittee 2006; U.S. Forest Service 2006, 2011). The dark green portion of the bars in (B) are proportional to the percent of public lands that are Wilderness Areas, recommended as Wilderness, or Inventoried Roadless Areas in which no road-building is allowed in different RZs. Total bar height and associated percentages are the total of all roadless areas (https://www.fs.usda.gov/detail/roadless/2001roadlessrule/maps/statemaps/?cid=stelprdb5400185). The table in (C) shows demographic performance for grizzly bear populations in each RZ, including number of demographic recovery criteria met, estimated population resilience (U.S. Fish & Wildlife Service 2021), and recent estimates of annual survival for adult female bears (Wakkinen & Kasworm 2004, Schwartz et al. 2006, Costello et al. 2016). Populations in RZs with realized levels of security >75% have fared better than populations in other RZs. Similarly, almost all BMU Subunits with <70% security are rated as population sinks.

Subcommittee 2019). Regardless of whether this premise is defensible or not, the resulting relationship between codified levels of habitat security at the Subunit level and population trajectory in these and other ecosystems is instructive.

Figure 9 summarizes some key aspects of habitat security, demographic performance, and progress towards recovery for grizzly bear populations in four ecosystems of the contiguous United States. The range of values for all parameters is both substantial and telling. Median levels of core security defined largely in terms of distance to human infrastructure ranges from >80% in the Greater Yellowstone and Northern Continental Divide Ecosystems (GYE and NCDE, respectively) but nearer 60% in the Selkirk Mountains and Cabinet-Yaak Ecosystems (SE and CYE, respectively; Figure 9a). Median percentages of BMUs or BMU Subunits with open road densities >0.6 km/km^2 correspondingly range from 6-9% in the GYE and NCDE to 30-33% in the SE and CYE – a 4-5-fold difference. These levels of security closely track proportions of public lands in each ecosystem that are classified as being roadless (roughly 75% in the former and 37% in the latter; Figure 9b) and a >2-fold difference in ecosystem-wide average road densities in the GYE (<0.4 km/km^2; Schwartz et al. 2010a) versus the CYE (*ca*. 0.8 km/km^2; Figure 8g, Mattson & Merrill 2004).

It is thus not surprising that resilience is judged to be low-moderate for the SE and CYE grizzly bear populations and that few demographic criteria for recovery have been met (U.S. Fish & Wildlife Service 2021; Figure 9c). The problematic status of these populations stands in clear contrast to that of more robust bear populations in the GYE and NCDE where annual survival rates of adult female bears are also estimated to be higher (Figure 9c). It is telling, moreover, that almost all BMUs or BMU Subunits in the GYE and NCDE with <70% core secure habitat are likely to be population sinks (Johnson et al. 2004, Schwartz et al. 2010a, Mattson 2019c). Taken together, these results suggest that grizzly bear populations can only be sustained if the totality of distributions governing source-sink dynamics are >70% secure, with <19% of these areas impacted by road densities >0.6 km/km^2 – at least under conditions that have prevailed in the contiguous United States during the last several decades.

Given this conclusion and observations by others such as Lamb et al. (2017b, 2019, 2020) and Boulanger & Stenhouse (2018), it is paradoxical that the laxest habitat security standards adopted for Recovery Zones in the contiguous United States have been applied to the CYE and SE. Standards in the GYE and NCDE call for 68-75% core security in BMU Subunits (Figure 9a), with no more than 19% of each Subunit impacted by >0.6 km/km^2 of open roads. By contrast, standards for the SE and CYE call for 55% core security and <33% of each BMU impacted by >0.6 km/km^2 of open roads. This amounts to 23% less security and 74% greater allowable impacts from high densities of open roads in the latter two Recovery Zones, both with precarious grizzly bear populations. Standards applied to the SE and CYE clearly have little evidentiary support, especially at scales meaningful to population-level demographic performance.

As a bottom line, research from multiple study areas suggests that it is possible to locally sustain grizzly bears in areas with open road densities of around 0.4 to 1.0 km/km^2, but with the important proviso that bears in these locally impacted areas be augmented by emigration from productive and long-lived individuals occupying most of (e.g., >70%) adjacent or surrounding landscapes >900-3,000 km^2 in size. As a corollary, there is no evidence to suggest that propagating open road densities of approximately 0.6 km/km^2 over extensive areas (e.g., >15-20% of life-range-sized areas) is compatible with sustaining grizzly bear populations in North America.

However, even this conclusion comes with several important caveats. First, almost all the results reviewed here have been obtained from data gathered largely on multiple-use public lands, some under long-term tenure of private companies, with most access devoted to industrialized extraction of resources – less often to recreational traffic. Private lands typically comprise a small portion of the studied landscapes, and strictly protected areas rarely have extensive road systems. Second, fine-grained effects of roadside cover, juxtaposition with attractive habitats, local topography, and types or levels of vehicular traffic (see Section 2.1) are rarely integrated into spatial analyses of how secondary road systems affect grizzly bear demography (although see Nielsen et al. [2004a], Lamb et al. [2020] and Parsons et al. [2021]). Finally, perhaps most important, none of these studies has explicitly addressed variation in lethality of humans to grizzly bears – i.e., the deadliness of people who use roads in different regions or areas (Section 2.1, Mattson 1996b).

4.2.3. Grizzly Bear Demography versus Human Populations and Activity on Roads

Given that physical infrastructure such as roads doesn't by itself kill grizzly bears, a key factor in judging effects on bear demography is the extent to which this infrastructure correlates with or expedites the activities of people who directly or indirectly cause bear deaths (Section 2.1, Figure). As a case in point, McLellan (2015) postulated that high densities of grizzly bears were sustained in his 2,800-km^2 study area despite an average open road density of 0.74 km/km^2 because very few people used this access, in part because the nearest human settlement was >75 km (47 miles) away. Roads without any people on them are self-evidently not problematic for bears, but roads with people on them almost invariably are, especially if a significant portion are armed, intolerant, or causing human-bear conflicts.

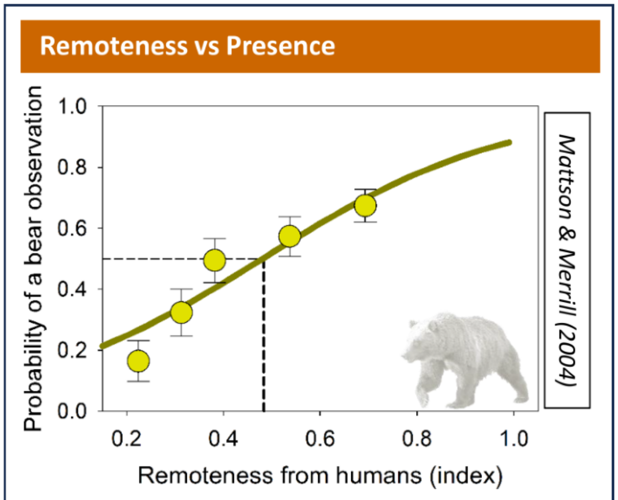


Figure 10. The figure above shows the effect of remoteness from humans on the likelihood that a grizzly bear would have been present and documented in the Cabinet-Yaak Ecosystem of the U.S. (Mattson & Merrill 2004). Remoteness incorporates both local road density and likelihood that people would be active on roads as a function of distance from population centers. The horizontal dashed line is calibrated to the probability that a bear was more likely to have been present than absent ($p > 0.5$) in any given 30-km^2 grid cell.

Several researchers have attempted to integrate the presence of roads with levels of traffic to better represent the effects of site-specific human activity on bear demography. The earliest of such efforts by Merrill et al. (1999), Naves et al. (2003), Merrill & Mattson (2003), and Apps et al. (2004) indexed levels of human activity on roads by introducing a decay function that inversely weighted numbers of people in censused locales to approximate human activity on local road networks – a method that was adopted by Carroll et al. (2001, 2003) to model regional habitat suitability for grizzly bears in the Rocky Mountains of Canada and the United States. Lamb et al. (2020) developed a similar approach that more reliably weighted site-specific roads with traffic levels extrapolated from highway and road counters (Figure 11c). Even more abstract, Lamb et al. (2020) also employed an index (Human Influence Index or HII) that integrated human-associated linear features, human population densities, the extent of settled and 'built up' areas, and human land use at a 1-km^2 resolution (WCS & CIESIN 2005).

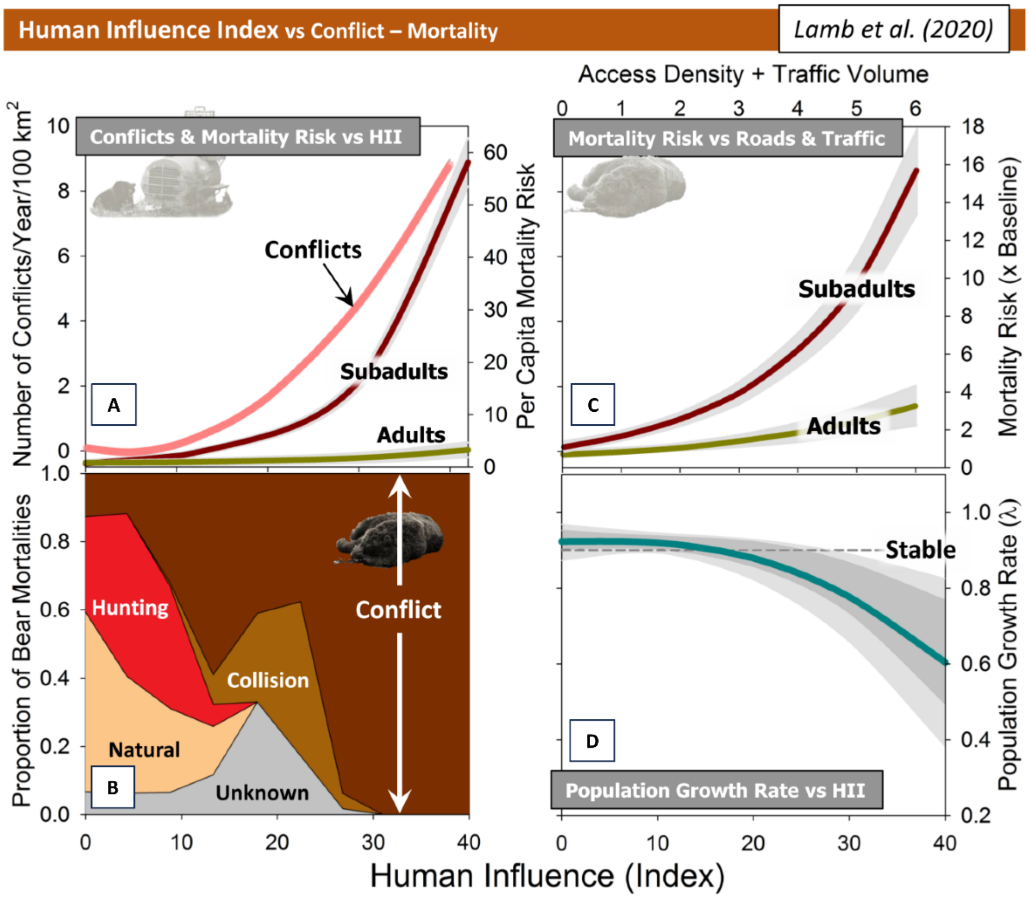


Figure 11. Lamb et al. (2020) developed a synthetic Human Influence Index (HII) that they used to integrate local levels of road access, residences, and other aspects of the "human footprint." Relations between HII and human-bear conflicts or indicators of grizzly bear demography in southeastern British Columbia are shown in the four figures above. Figure (A) shows total numbers of human-bear conflicts per year (in pink) in addition to mortality risk for adolescent (burgundy) versus adult (green) bears as a function of HII. The stack diagram in (B) similarly shows trends in proportional causes of grizzly bears deaths, with conflicts accounting for nearly bear deaths at high levels of HII and collisions with vehicles peaking at intermediate levels. The relations in (C) show per capita mortality for adolescent versus adult grizzly bears relative to a measure integrating access density and levels of human activity, similar to "remoteness" in Figure 10, yielding results resembling those in (A) modeled for HII. The trend line in (D) shows the modeled decline in growth rate for grizzly bear populations with increasing levels of HII. The horizontal dashed line corresponds with a threshold for population stability (λ ≈ 0.9).

All these synthetic measures exhibited strong relations with some aspect of grizzly bear demography, including presence versus absence of bears (Merrill et al. 1999, Merrill & Mattson 2003, Mattson & Merrill 2004; Figure 10). But the strongest and most comprehensive relations with demography were demonstrated for the Human Influence Index by Lamb et al. (2020), including human-bear conflicts and mortality risk for bears (Figure 11a); causes of grizzly bear deaths (Figure 11b); and population growth rate (Figure 11d). As might be expected, conflicts escalate, bears are at greater risk of dying, a greater portion of these deaths are attributable to human-bear conflicts, population growth declines, and bears are more likely to be absent as road access, road traffic, human populations, and other aspects of the human footprint increase.

As strong and plausible as these relationships might be, translation into ameliorative management action is problematic largely because synthetic indices of human activity are intrinsically abstract and dimensionless – which means that teasing out the effect of any one human-related feature is difficult. For example, the intrinsic nature of relationships described by Lamb et al. (2020) provide little concrete guidance for managers or planners interested in furthering grizzly bear conservation other than to reduce road densities, levels of traffic, number of residences, and land uses that create human-bear conflicts. In the end, these synthetic indices affirm the perhaps self-evident proposition that humans, human infrastructure, and human-associated land uses have potentially major impacts on grizzly bear demography.

Other researchers have attempted to differentiate the effects of human numbers and human infrastructure (e.g., roads) by introducing these factors as suites of separate variables in statistical models. Martin et al. (2010) and Apps et al. (2004, 2016) dealt with resulting model complexities and covariance by statistically collapsing the human-related factors they considered into synthetic variables that consistently showed negative effects on bear demography. However, in common with *a priori* synthetic variables, these statistical constructs ended up being difficult to interpret or translate into actionable management recommendations.

More commonly, researchers have examined human-related features as individual effects in statistical models, but almost invariably as an eclectic collection specific to a given analysis. Any attempt to compare results among models and study areas thus quickly mires in inter-study variation. Human numbers have most commonly been treated as either local density of residences or residents and/or as nearness to townsites and recreational developments. Of the 10 of a total 11 analyses that considered these effects, nine showed a negative effect on some aspect of brown or grizzly bear demography (Figure 12 at right is illustrative) – none showed positive effects (Merrill et al. 1999, Kobler & Adamic 2000, Suring & Del Frate 2002, Naves et al. 2003, Johnson et al. 2004, Mattson & Merrill 2004, Posillico et al. 2004, Falcucci et al. 2009, Schwartz et al.

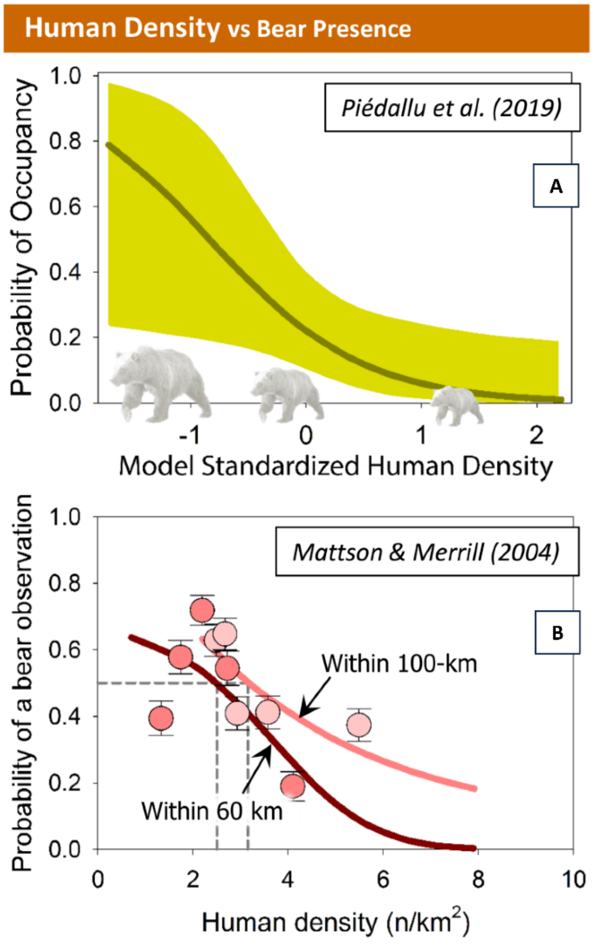


Figure 12. The x-y diagrams above are illustrative of the negative relationship between grizzly/brown bear demography and human density. (A) Shows the model-standardized effect of human density on presence of brown bears in the Pyrenees Mountains of France during 2008-2014. (B) Shows the likelihood that a grizzly bear would have been present as a function of human densities in the Cabinet-Yaak grizzly bear ecosystem, with human density reckoned at two different scales (within a 60-km and 100-km radius). The horizontal dashed line denotes a threshold at which bears were more rather than less likely to be present (p = 0.5). The relationship of bear presence to human density was stronger within a 60-km radius and more closely matched the relationship between human density and brown bear occupancy in the Pyrenees.

2010a, Peters et al. 2015, Steyaert et al. 2016, Piédallu et al. 2019). Of the 10 that considered some measure of road access, eight likewise showed a negative effect – and none likewise showed positive effects. However, none of the eight that considered both access and human numbers statistically addressed interactions between the two, which complicates reaching conclusions regarding how nearness to population centers explicitly affected the lethality of local road systems.

The main conclusion to be drawn from the results reviewed here is that human activities associated with residences and resident humans generally have a negative effect on grizzly bear demography, typically compounded by spillover onto accessible road networks. These effects can, moreover, be severe. Put another way, there is compelling evidence that, at a minimum, nearness to human residences, townsites, and population centers needs to be considered as effects that compound the potential localized impacts of road access on grizzly bear demography. The effects of road densities cannot defensibly be judged in isolation from this aspect of the human matrix.

The other important conclusion to be drawn is that almost all modeled effects of humans and human infrastructure on bear demography – at least at a population level (see Section) – are not only negative, but also monotonic, meaning that as the human footprint increases, demographic outcomes for grizzly bear populations worsen. Only one study exhibited a hump-bank or non-montonic relationship (Johnson et al. 2004) suggestive of an optimal level of human impacts. Although there is usually some level of human impact compatible with persistence of grizzly bears, at the same time the best situation for bears is unequivocally when there is no human infrastructure or local human population.

4.2.4. Grizzly Bear Demography versus Structural Configurations of Habitats

Any natural feature that either directly or indirectly reduces exposure of grizzly bears to people concentrated at or near human infrastructure also plausibly reduces associated levels of human-caused bear mortality (Section 2.1). The mechanisms behind this could include (1) decreased likelihood that people would detect nearby bears from a road or residence, (2) decreased human mobility because of greater resistance from vegetation or terrain, and (3) greater opportunity for bears to select secure microsites even while near people. Even so, there have been few investigations into this likely phenomenon explicitly focused on bear demography. Nonetheless, results of these investigations – all from Alberta – have affirmed the basic tenant that natural obstructions around human infrastructure reduce levels of human-caused bear mortality.

Nielsen et al. (2004) set the stage for this work by showing that distributions of human-caused grizzly bear deaths were not only concentrated nearer roads, but also in areas with less rugged terrain, nearer forest-nonforest ecotones, and dominated by deciduous vegetation (e.g., cottonwoods, aspens, and shrubs) – together defining a gradient of low- to high-risk habitats for bears (Figure 13a). Parsons et al. (2022) affirmed the credibility of this risk gradient by showing that bears spending more time in high-risk habitats ended up more often being killed by people, especially as the time frame for exposure to high-risk habitats was compressed from the period 2-4 years to 1-week prior to death (Figure 13b and 13c). As a corollary, Parsons et al. (2021) showed that concentrations of grizzly bear deaths were roughly 1.7-times greater in areas visible from and within 500-m of roads compared to what might be expected by concentrations of grizzly bear radio-telemetry locations (Figure 14a).

Of the mechanisms outlined above that potentially explain these patterns, there is evidence supporting all three, including behaviors of bears when near roads as well as behaviors of people – especially hunters – in the backcountry at large. Hunters are an especially useful focus because they are plausibly more motivated than other people to observe wildlife and pursue animals away from roads. Even so, hunters have almost universally been shown to distribute themselves nearer roads or other access, with maximum distances traveled from points of departure ranging from around 600 to 850 m (e.g., Thomas et al. 1976, Gratson & Whitman 2000, Stedman et al. 2004, Diefenbach et al. 2005, Jones et al. 2015, Lebel et al. 2012, Rowland et al. 2021). Other than this consistent and unsurprising result, behaviors of hunters have varied among study areas and types of big game being pursued, but with observed patterns generally what one would expect of people impeded by vegetation and terrain. Hunters did tend to see more big game in areas with less screening by vegetation and when on foot (Basile & Lonner 1979, Lebel et al. 2012), but were more variable in their use of areas with greater forest cover depending on the big game they pursued (Rowland et al. 2021). Increases in slope steepness generally reduced levels of hunter activity (Stedman et al. 2004, Deifenbach et al. 2005, Rowland et al. 2021), although certain kinds of hunters tended to use comparatively steeper slopes compared to others (bear vs other, archery vs rifle, successful vs unsuccessful; Jones et al. [2015], Rowland [2021]).

Documented bear behaviors predictably tended to magnify the screening effects of topography and vegetation within 500-1000 meters of motorized access (see

Habitat Risk vs Survival

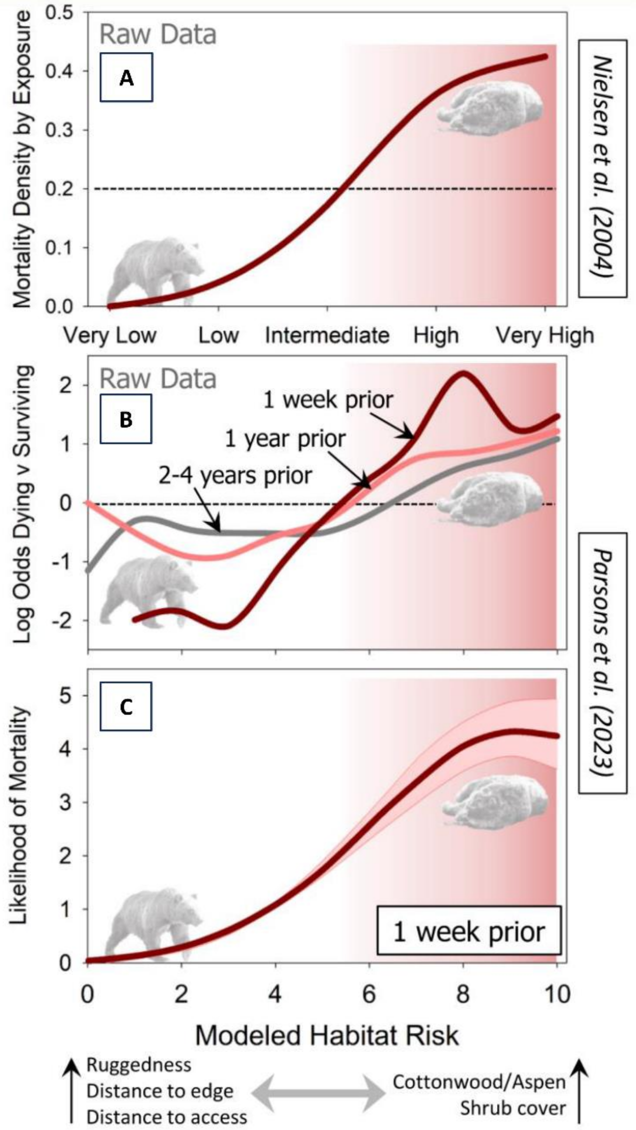


Figure 13. These graphics show relations between grizzly bear deaths and risk intrinsic to the habitats they occupied in southwestern Alberta. Habitat risk is an index that incorporates the effects of various factors affecting exposure of bears to humans, as per the variables identified immediately above. Greater ruggedness, distance to habitat edge, or distance to human access reduced risk for bears (Nielsen et al. 2004). Figure (A) shows the unit area level of mortality for grizzly bears as a function of risk categories based on raw data. The trend lines in (B) were estimated from raw data and show odds that a bear would die depending on the intrinsic risk of habitats occupied 1-week, 1-year, and 2-4 years prior to death. Risk of habitats occupied 1-week prior to death had the greatest apparent effect. The trend line in (C) is a modeled estimate of this relationship, controlling for other potential effects (Parsons et al. 2023).

Section). Although the body of research addressing the effects of vegetation and topography on behaviors of brown and grizzly bears near roads is not extensive, results are consistent. For one, bears tended to exhibit greater avoidance of roads wherever there was less audio or visual screening (Archibald et al. 1987, Parson et al. 2020, González-Bernardo et al. 2021; e.g., Figure 14b). For another, brown bears have been shown to select steeper slopes during times of day when there was greater levels of human activity (Martin et al. 2010; Figure). These behaviors – together with reticence of humans to range farther than 0.5-1 km from roads, less often see wildlife in areas with vegetation cover, and avoid steep slopes – plausibly explain lower risk of mortality for brown and grizzly bears in areas near roads where there is greater screening cover and more rugged terrain.

As a bottom line, these results as well as those summarized in Box 2 suggest that road densities sufficient to provide security for grizzly bears may need to be 1.5 and 2.0-times less in areas with no cover compared to where vegetation provides complete screening. This would apply not only to areas naturally free of forest and shrub cover such as grasslands and tundra, but also areas in which vegetation cover has been removed by human activities such as clearcut harvesting of timber (e.g., Box 1) and removal of trees for agriculture. Managers cannot tenably assume that grizzly bear habitat security is unaffected by lack of cover along roads, even though this assumption is codified in standards for managing grizzly bear habitat security in the contiguous United States (U.S. Fish & Wildlife Service 2007, Greater Yellowstone Ecosystem Grizzly Bear Subcommittee 2016, Northern Continental Divide Ecosystem Grizzly Bear Subcommittee 2019).

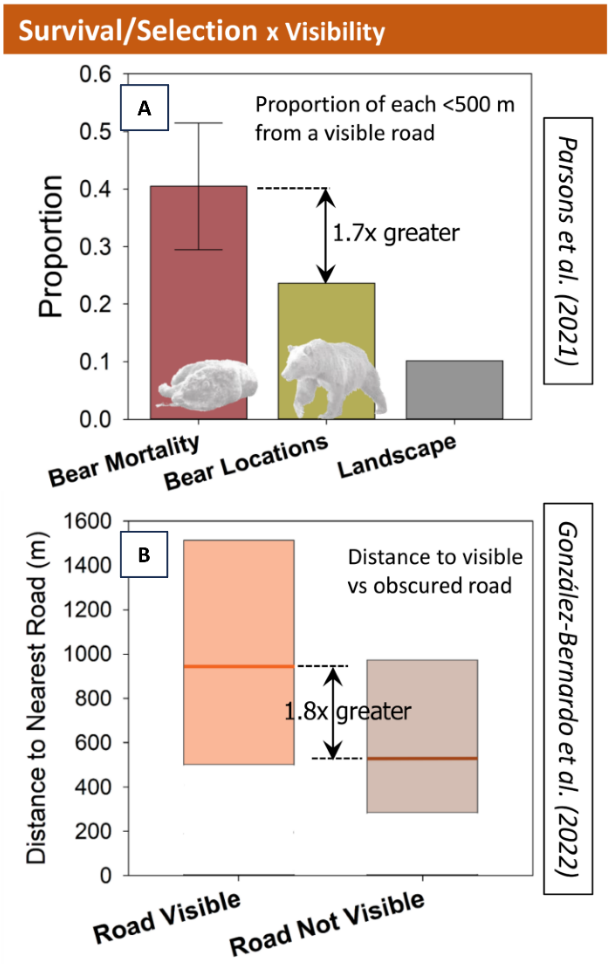
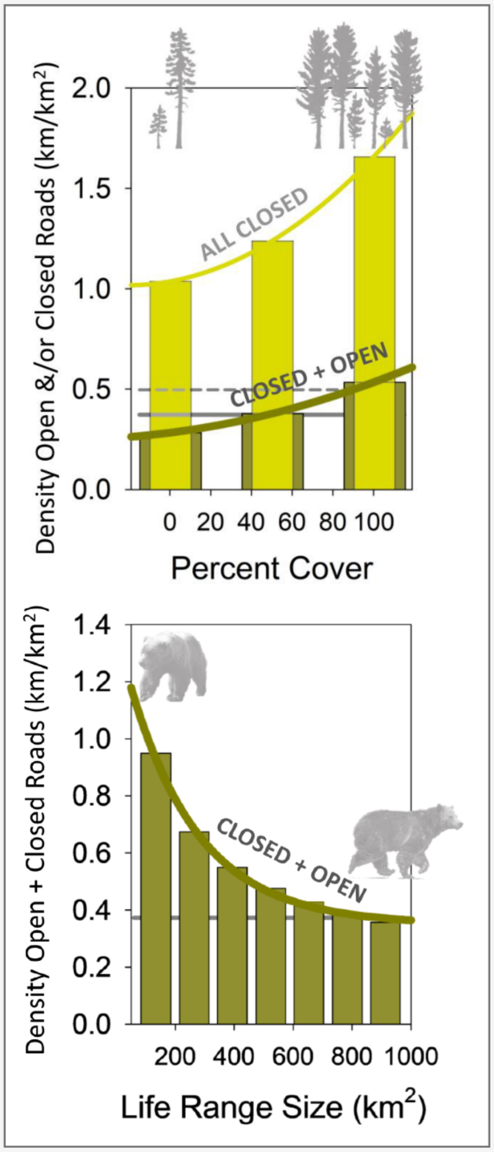


Figure 14. The above figures illustrate the effects of visibility along roads on behavior and survival of grizzly and brown bears. Bar heights in (A) are proportional to the fraction of bear deaths within 500-m of a visible road in southwestern Alberta (burgundy), in contrast to the fraction of telemetry locations from live bears (green) and total fraction of the landscape (gray) within this same zone. Deaths were proportionately 1.7-times more common within 500-m of a visible road compared to locations of live bears. Similarly, bears in a Spanish study area (B) tended to stay 1.8-times farther away from visible roads (orange bar) compared to roads that were visually screened ("obscured"; brown bar).

Box 2: Effects of Roadside Cover & Home Range Size on Road Density Security Standards



The effects of roadside cover and grizzly bear range sizes on prospective standards for managing road densities have not been explicitly studied, although there is ample precedent for taking cover into account as well as a theoretical basis for considering differences in range sizes.

Parsons et al. (2021) found that bears were more likely to die from human causes along roads with greater visibility, which is consistent with evidence that brown bears avoid roadside area with less visual and audio screening (e.g., Archibald et al. 1987, González-Bernardo et al. 2022). These results are lent weight by a codified precedent for increasing the assessed impacts of roads on grizzly bears in areas with no roadside cover in the Greater Yellowstone Ecosystem. The Cumulative Effects Model for this ecosystem made explicit provision for different degrees of impacts with and without roadside cover that varied as a function of different human features and disturbances. The enumerated extent of these impacts was based on a consensus professional judgments (Weaver et al. 1986, Dixon 1997), with the magnitude of non-cover impacts increasing to a maximum at intermediate levels of overall habitat effectiveness (Mattson et al. 2004). These assigned values were the basis for theorizing by Mattson (1993) that densities of open plus closed roads needed to achieve adequate security could increase by nearly two-fold between areas with 0 and 100% cover and that, if all roads were closed, total road densities could be roughly 3-fold greater (A).

Mattson (1993) also postulated that there would be a geometric relationship between road density standards needed to achieve adequate security and sizes of female grizzly bear life ranges. Based on first principles, bears would be more likely to encounter roads at any given road density by approximately twice the square root of home range size (B). This geometric scaling suggests that adequate security could be achieved at road densities roughly 2.6-times greater where life ranges were 130 versus 900-km^2 in size. The lower end of this range in sizes is unlikely to occur anywhere in interior regions of North America, where annual ranges are typically 200-300 km^2 in size (e.g., Blanchard & Knight 1991,Mace & Waller 1997, Wakkinnen & Kasworm 1997, Graham & Stenhouse 2014, Lamb et al. 2020), and where annual ranges are roughly ⅓ the size of cumulative life ranges. Given the geometric scaling of the range size effect, the comparatively small difference in documented sizes of average grizzly bear ranges in interior ecosystems suggests there would be comparatively small differences in road density standards needed to achieve adequate security for bears.

Although these results based largely on professional judgement and theory are not conclusive, they do recommend that bear home range sizes and pervasiveness of visual cover be addressed in management deliberations and future research. Regarding the latter, it is clearly more defensible to assume that range size and cover affect the extent to which a given density of roads provide effective cover for bears that to assume the opposite.

4.3. Grizzly Bear Behaviors & Effects on Demography

Grizzly bears are clearly not automata that respond indifferently to the risks and rewards of their environs. Even so, in common with all sapient animals, bears are prey to perceptual errors arising from the constraints of individual histories, lack of cues, or even misinterpreting the cues that they do perceive (Mattson 2021a). Although most bears astutely navigate the hazards and opportunities of their surroundings most of the time, they can also misread or inadequately anticipate cues regarding the hazards posed not only by humans but also other bears.

Differences in perceptual and interpretive acuity among bears predictably give rise to different vulnerabilities when confronting lethal human environs. Over time, this can lead to the selective removal of naïve individuals or certain behavioral types from a population that manifests in how the remaining composite responds to human infrastructure. Importantly, these sorts of dynamics can become even more complicated when humans and human infrastructure are associated not only with high quality foods, but also safety from threatening conspecifics. Individual bears thus need to not only accurately perceive and interpret the world, but also successfully weigh risks and rewards conveyed by sometimes conflicting cues (Mattson 2021a).

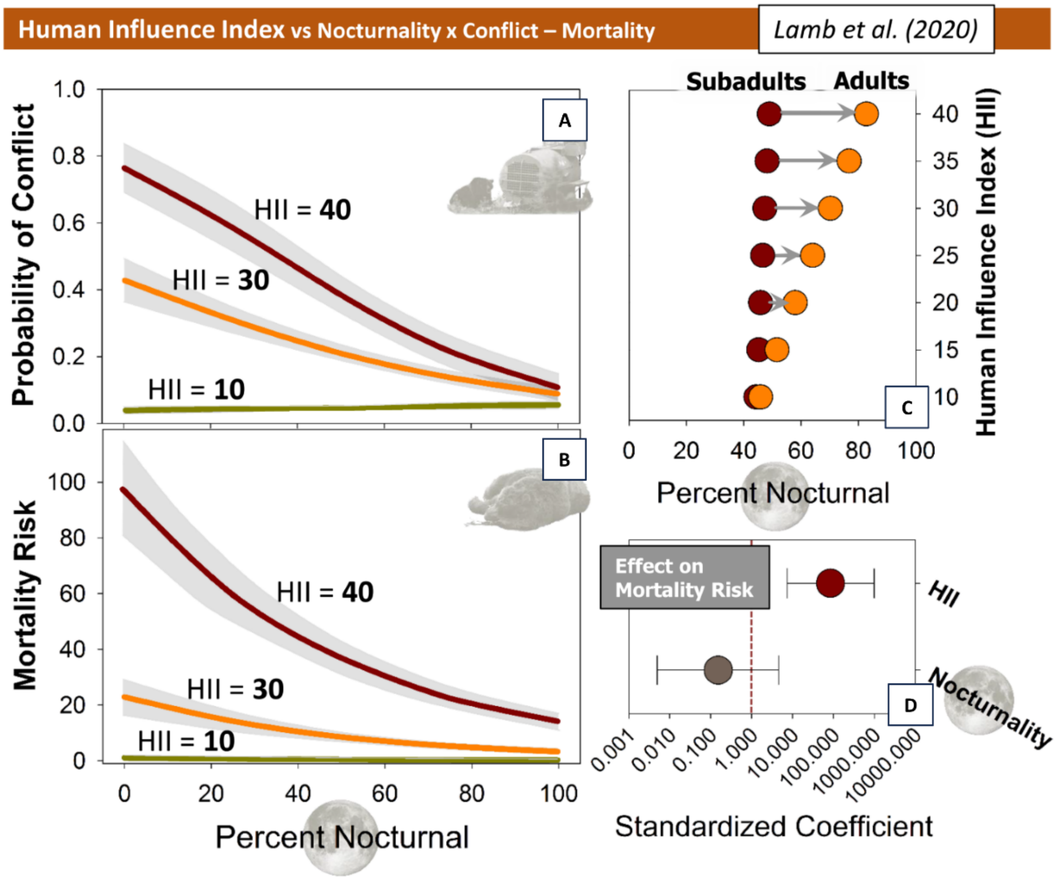


Figure 15. The figures above illustrate how levels of nocturnal activity ("nocturnality") among grizzly bears in southeastern British Columbia interact with levels of human influence (the Human Influence Index, HII; see Figure 13) to affect human-bear conflicts and grizzly bear survival. The trend lines in (A) show decreasing likelihood of human-bear conflict with increasing levels of nocturnality among local bears, conditioned on overall levels of HII (index levels of 10 versus 30 versus 40). The trend lines in (B) render these same relations in terms of grizzly bear survival or mortality risk. The graphic in (C) shows levels of nocturnality among adult (burgundy dots) versus adolescent (orange dots) bears with increasing levels of HII. Adults—i.e., those bears that survived conflicts while adolescents—tended to be more nocturnal than adolescents in areas more heavily impacted by humans. The graphic in (D) shows the comparative effects of HII (burgundy dot) and nocturnality (gray dot) on levels of grizzly bear mortality, expressed in terms of standardized coefficients. A coefficient >1 indicates an effect that increases levels of mortality whereas a coefficient <1 indicates the opposite.

This section is the first of several in which I attempt to interpret how these complexities associated with learning and perception can in turn affect bear behavior and demography near human infrastructure – with resulting variation in observed patterns that can sometimes defy ready explanation.

4.3.1. Grizzly Bear Nocturnality & Demography

Diel avoidance of human infrastructure is a tactic that potentially allows bears to remain more-or-less *in situ* while minimizing exposure to hazards associated with humans. This kind of avoidance, like all others, can arise from association of painful or distressing experiences with certain (temporal) cues or from a lineage of learned behaviors transmitted maternally (Mattson 2021a). There is ample evidence suggesting that grizzly bears – in common with numerous other species worldwide (Gaynor et al. 2018, Procko et al. 2023) – tend to be more nocturnal when near human infrastructure (see Section ; MacHutchon et al. [1998], Olson et al. [1998], Schwartz et al. [2010b], Seryodkin et al. [2013], Wheat & Whilmers [2016], Hertel et al. [2017], Ordiz et al. [2017]), compared to when undisturbed in backcountry areas. Undisturbed bears are more often active during crepuscular periods, but with variation in diel activity potentially tracking daily temperatures and availability of natural foods (Schleyer 1983, Harting 1985, Moe et al. 2007, Ware et al. 2012, McLellan & McLellan 2015).

This well-documented diel response of brown and grizzly bears to human disturbance begs for an explanation of underlying mechanisms, including whether predominantly through learning by individual bears, selective survival of bears with different *de novo* diel behaviors – or both. Lamb et al. (2020) undertook perhaps the most comprehensive investigation of mechanisms driving the emergence of nocturnality among bears in southern Canada using human environs by examining broadscale temporal-spatial patterns as well as life histories of individual bears tracked genetically and with radiotelemetry. They found strong evidence that, compared to night-active bears, day-active bears using human impacted environs were at greater risk of conflict (Figure 15a) and consequently greater risk of being killed by people (Figure 15b and 15d). They also found that adult bears were more nocturnal compared to adolescent bears in these same environs (Figure 15c), suggesting that human-caused mortality potentially selected against diurnal behavior. Even so, it remains unclear from these results whether this dynamic was predominantly through the

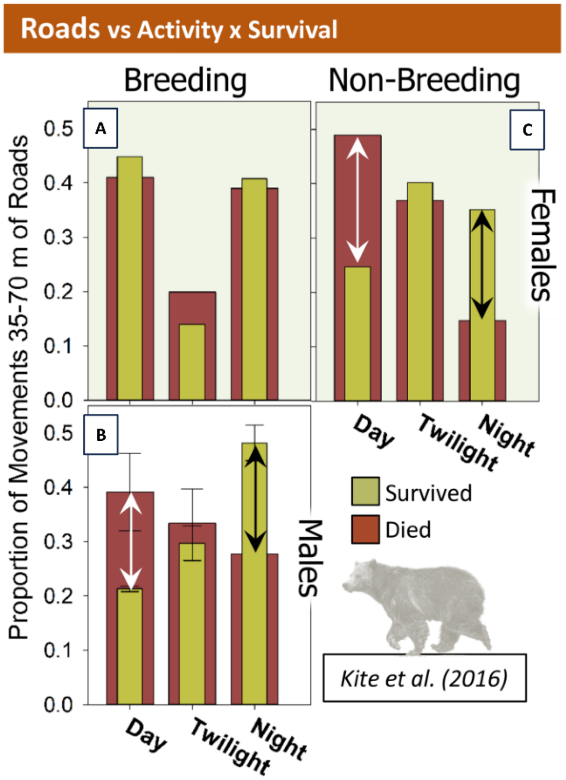


Figure 16. The figures above show the interacting effects of diel period, season, bear sex, and levels of bear activity near roads on survival of grizzly bears in southwestern Alberta. Survival is represented in terms of whether a bear did (green) or did not (burgundy) survive the study period as a function of proportionately how many of the bear's movements were < versus >70-m from a road, broken down by time of day (day, twilight or night). Results are further differentiated by whether the bear was (B) male or (A & C) female and, for females, whether it was the (A) breeding or (C) non-breeding season. Any pairing where the burgundy bar is taller than the green bar indicates a combination of factors where more bears died than survived, typifying individuals that tended to be more active and mobile near roads during daylight hours.

selective removal of individuals or behavioral lineages – or both.

This pattern of differential vulnerability to human-caused mortality between day- and night-active bears has been partly confirmed – as well as disconfirmed – by other researchers. Kite et al. (2017) found that, compared to nocturnal bears, day-active male and female grizzly bears near roads in southwestern Alberta more often ended up dead (Figures 16c and 16b), but with this holding only for females before and after the breeding season. By contrast, Hertel et al. (2017) found that Scandinavian brown bears were equally likely to be killed by bear hunters regardless of diel behavioral patterns. Although any explanation for this last result can only be speculative, it plausibly arises from differences in human lethality that arise from people more passively responding to conflict situations compared to situations where people (i.e., bear hunters) are actively seeking bears out to kill them (Mattson 2019b, 2020).

Taken as a whole, this research not only suggests that nocturnality enhances survival of grizzly bears when near human infrastructure, but also that emergence and persistence of nocturnality arises largely from human-caused mortality selectively removing day-active individuals and behavioral lineages. Even so, a toll may be exacted on surviving night-active bears through reductions in foraging efficiency – although with the proviso that night-time foraging could also allow bears to access anthropogenic foods near human facilities that would otherwise by unavailable.

4.3.1. Grizzly Bear Demography & Tolerance of Humans

Tolerance of people can discernably lessen the reactivity of brown and grizzly bears to the presence of humans or human infrastructure, including during daylight hours (Mattson 2019a). Some researchers have argued that tolerance is the natural ground state for bears absent a history of adverse experiences with people (Stringham & Rogers 2017). Regardless of whether this is true or not, some bears clearly lose their fear of humans either through a process of habituation or because they are raised by human-tolerant mothers (Mattson 2021a). Given that most experiences with people occur near human infrastructure, tolerance is plausibly linked to cues associated with the built environment with resulting associative transference of behaviors by bears to infrastructure such as roads and residences. Resulting temporal-spatial patterns of behavior can thus become explicitly associated with human infrastructure.

Tolerant bears are rewarded for their forgiving behaviors with greater access to resources in human environs. At the same time, increased exposure to people increases the odds that affected bears will die from human causes, especially if anthropogenic foods are involved (Herrero 2018). This potentially lethal outcome is a perverse aspect of benign experiences that foster and preserve tolerance of humans among bears in areas where human-origin foods are freely available (Figures 1b and 1c). Anthropogenic foods can be especially seductive given that they typically occur in environs with less competition or threat from other bears (Mattson 2021a) and can provide a mix of nutrients optimal for accumulating adipose reserves (Coogan et al. 2018). But even in the absence of attractive human foods, the threat posed by increasingly frequent interactions with people can lead wildlife managers to kill tolerant grizzly bears in areas where they are ostensibly protected (Gunther & Wyman 2008).

Assessing whether a bear is tolerant – or habituated – is intrinsically subjective. As a result, various researchers have used whether a bear was trapped by managers because of conflicts with humans as a proxy for tolerance, assuming that behaviors engendered by greater acceptance of people led to the observed conflicts (e.g., Schwartz et al. 2006, Costello et al. 2016). Even so, Pease & Mattson (1999) showed that subjective judgements regarding tolerance or habituation for individual bears were highly correlated with a history of conflict trappings. Regardless of whether assessed directly (i.e., subjectively) or indirectly (i.e., by management-trapping status), tolerant bears using human environs have been consistently shown to die at much higher rates compared to bears that are most active in backcountry areas >4-15 km away from human facilities.

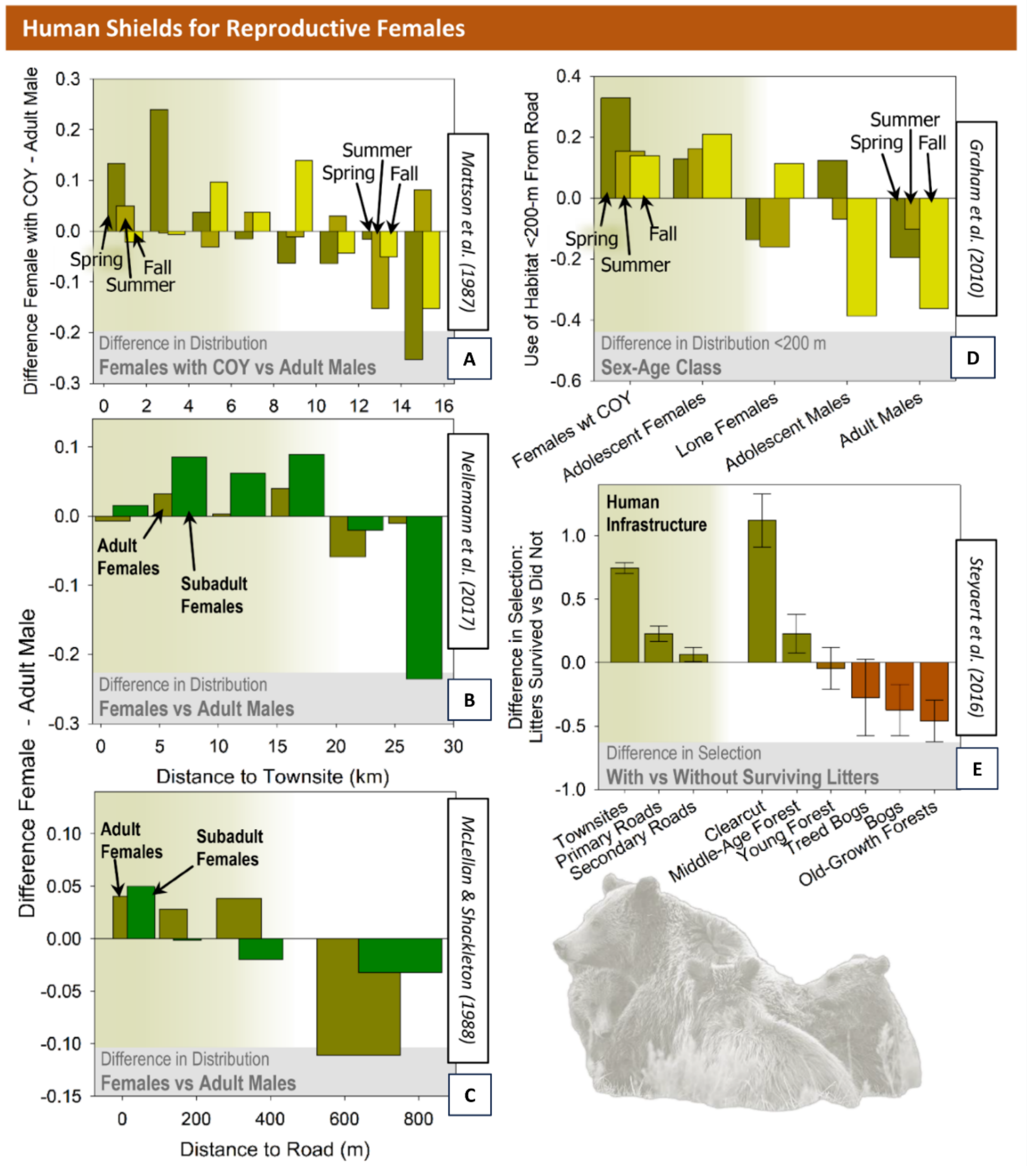
Mattson et al. (1992) were the first to show not only the deadliness of tolerance for humans among grizzly bears, but also the perhaps self-evident fact that tolerant bears tended to concentrate near human facilities. Their study focused on the Greater Yellowstone Ecosystem revealed that, in contrast to wary bears, tolerant (i.e., habituated) bears were not only *ca*. 3-times more likely to use habitats within 4 km (2.5 miles) of recreational developments, but also *ca*. 3-times more likely to die from human causes. Pease & Mattson (1999) subsequently showed that management-trapped bears from the same ecosystem died at roughly twice the annual rate as other bears. Schwartz et al. (2006) and Costello et al. (2016) similarly found that annual survival of bears dropped dramatically the first year after being management trapped, but with survival rates increasing back to population averages within 3-5 years – a consequential period during which most management-trapped bears died. Schwartz et al. (2010), Cristescu et al. (2016), and Shimozuru et al. (2020) presented comparable findings, but in the last study with adolescent bears on Hokkaido experiencing most of the toll from human-caused mortality.

Tolerant bears are clearly afforded greater access to resources concentrated near human infrastructure than would otherwise be available to them, especially during diel periods optimal for foraging (see Section 4.3.1). Although bears with this behavioral trait can survive where they are protected and accepted by involved people (e.g., Gunther et al. 2018), more often they live abbreviated lives. This basic fact cautions against assuming that observations of day-active bears on or near roads translate into demographic benefits for a bear population. More often, the presence of day-active tolerant bears signifies a sink sustained by a nearby source of wary bears (e.g., Pease & Mattson 1999, Lamb et al. 2020).

4.3.2. Compounding Effects of Human Shields

In addition to affording access to underutilized foods, human environs can also offer security-conscious and subordinate bears some degree of safety from aggressive conspecifics, notably adult males (e.g., Elfström et al. 2012). Depending on the region, adult males can pose a dire threat to young bears, especially cubs and yearlings (e.g., Swenson et al. 2001, Bellemain et al. 2006, Allen et al. 2022). Adult males also often dominate food-rich habitats in back-country areas. The resulting dynamics predictably displace adolescent bears and females with dependent young into areas where they not only have freer access to high-quality foods, but also greater safety from threatening adult males.

This dynamic explains an often-observed pattern typified by greater concentrations of females – notably females with cubs – near human infrastructure, especially compared to adult males. Mattson et al. (1987), Reinhart & Mattson (1990), and Graham et al. (2010) all found this pattern, which was particularly pronounced during spring when cubs would have been most vulnerable (Figures 17a and 17d). McLellan & Shackleton (1998) and Nellemann et al. (2017) found a similar spatial sorting of males and females, but without differentiating the reproductive status of involved females (Figures 17b and 17c). Tellingly, Steyaert et al. (2016b) showed that female bears in Scandinavia more often lost litters of cubs when they selected for habitats away from roads and townsites – in habitat more often used by adult males.



Human Shields for Reproductive Females

Figure 17. Numerous studies have documented the phenomenon of female grizzly or brown bears seeking out humans or human facilities to shield themselves and their offspring from potential predation or harassment by adult male bears. Figure (A), above, shows differences in distribution of females with cubs-of-the-year (COY) relative to adult male bears in Yellowstone National Park as a function of distance to the nearest townsite or recreational development. Figures (B) and (C) show this difference for adult and subadult female bears relative to townsites and developments in Scandinavia (B) and secondary and tertiary roads in southeastern British Columbia (C). Figure (D) shows this same basic difference among sex-age classes of grizzly bears in southwestern Alberta represented as comparative concentrations of each class within 200-m of a road. Figure (E) shows habitat selection by female brown bears in Scandinavia, contrasting selection by females with litters of cubs that survived versus those with litters that didn't. In Figures (A)-(D) negative values denote comparatively lower concentrations of telemetry locations for radio-marked bears than might be expected by chance (D), or in contrast to adult male bears (A-C). Negative values in (E) denote selection by successful mothers less than that of those that were unsuccessful.

Shielding offered by human infrastructure to vulnerable bears predictably leads them to spend more time near people, resulting in greater numbers of interactions with people that in turn foster the emergence of tolerance (Mattson 2021a). Dynamics that promote tolerance as a means of accessing under-exploited foods thus get entangled with dynamics that recruit bears to human environs as a means of obtaining safety from conspecifics. Given that the internal workings of an animal's mind can only be a matter of speculation, bears seem to perceive proximal cues signaling benefits of spending time near human facilities more readily than cues signaling mortal threats posed by nearby people (e.g., Johnson et al. 2015, Greggor et al. 2019). These latter cues predictably only emerge shortly before or during a lethal encounter, at which point there is little or no opportunity for bears to learn about the entailed hazards (Mattson 2019a).

Brown and grizzly bears can temporarily find greater security from threatening conspecifics when they are tolerant of people concentrated near human infrastructure where adult males less often venture. This differential distribution provides safety for circumscribed periods of time, but with increased odds of fatal interactions with people. Although conspecific dynamics can dictate short-term choices by bears, interactions with people near human infrastructure typically take a lethal toll (e.g., Section 4.2.1).

4.3.3. Attractive Habitats and Risky Environments: Ecological Traps

Although the concept of ecological traps has been subject to the usual academic debates regarding detection and definition (e.g., Hale & Swearer 2016, Zuniga-Palacios et al. 2021), the notion has relatively straightforward application to bears (Penteriani et al. 2018). Early on, Battin (2004) provided a succinct and somewhat tongue-in-cheek description of the phenomenon as being "when good animals love bad habitats." In common with when humans provide a shield for some bears from threatening conspecifics (Section 4.3.2), an ecological trap emerges when habitat features such as concentrations of high-quality food attract an animal into a situation that is fraught with longer-term risk – for bears typically associated with people concentrated near human infrastructure (Section 2). Resources such as food usually come with compelling proximal cues whereas hazards are often attended by diffuse cues that manifest too late to benefit an affected animal (e.g., Schlaepfer et al. 2002, Gilroy & Sutherland 2007, Robertson et al. 2013).

The mechanisms creating an ecological trap for bears invariably play out at the level of individual choices conditioned on social interactions, but when these choices are compounded over time and space dynamics emerge at the population level, usually manifest in a source-sink structure (Doak 1995). Sinks are typified by conditions so hazardous that local subpopulations cannot be sustained without infusions of immigrants from nearby source areas where survival and reproduction allow for a figurative population surplus (Pulliam 1988).

When the hazards of an area are permuted with comparative productivity or attractiveness, a framework emerges that encompasses ecological traps as one cell in the matrix of possibilities. Apropos, bear biologists have developed frames comprised of primary and secondary sinks (or traps) and habitats (Nielsen et al. 2006, Northrup et al. 2012; Figures 18c and 18d); areas of high and low risk and habitat attractiveness (Boulanger et al. 2018; Figures 18a and 18b); sources and attractive or unattractive sinks (Falucci et al. 2009, Lamb et al. 2017a); source-like and sink-like areas (Braid & Nielsen 2015); and – more complex yet – refuges, sources, sinks, and attractive sinks (Naves et al. 2003).

Lurking behind this hodgepodge of frames, though, is a fundamentally simple notion. Some areas may be unproductive yet safe enough to locally sustain bears. Other areas may be productive as well as safe, allowing for a figurative population surplus. Yet other areas may be both unproductive and hazardous, resulting in a patently unsustainable situation. And, finally, some areas may be productive as well as hazardous, yielding a classic ecological trap.

There is ample evidence of source-sink dynamics in brown and grizzly bear populations organized around ecological traps playing out at multiple scales. At the broadest scale, source-sink dynamics entailing ecological traps are manifest in demographic measures such as population density and annual survival rates.

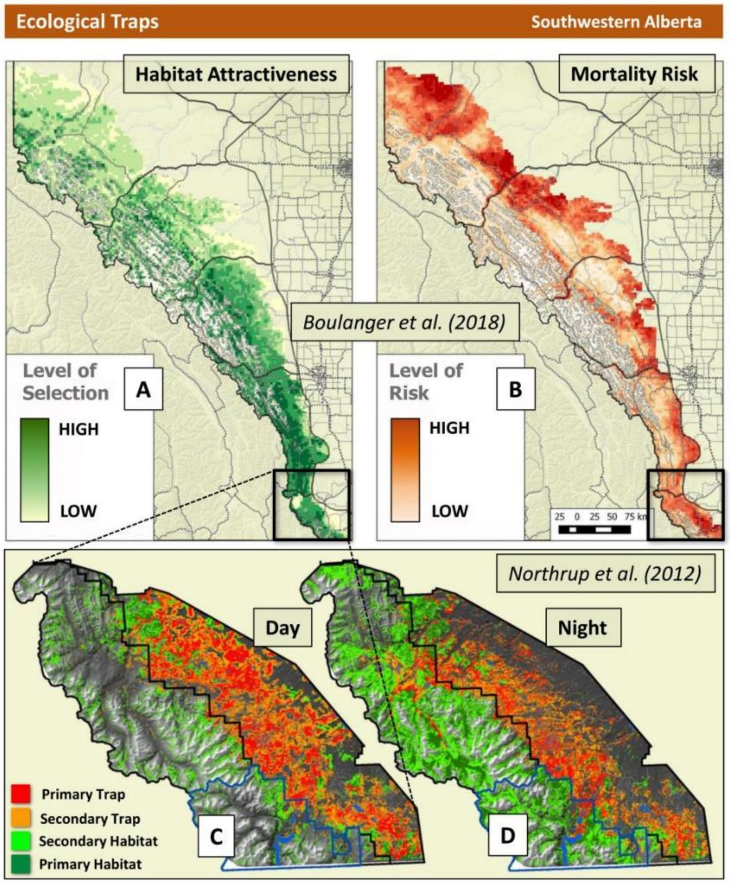


Figure 18. The maps above provide a visual snapshot of how habitat attractiveness interacts with risk of human-caused death ("mortality risk") to create ecological traps for grizzly bears in southwestern Alberta. Maps (A) and (B) show habitat attractiveness and mortality risk throughout southwestern Alberta (Boulanger et al. 2018); maps (C) and (D) show how these patterns configure ecological traps in a small southerly portion of the larger study area, primarily organized around agricultural landscapes (Northrup et al. 2012). These latter two maps highlight not only the geospatial configurations of ecological traps, but also the extent to which these configurations can have transient aspects related to diel changes in human activity and selection of habitats by bears.

Boulanger et al. (2018) showed that grizzly bear densities in Alberta varied substantially at the scale of 3,000-30,000 km^2 largely as a function of interactions between habitat productivity and habitat risk – the latter defined almost wholly by road densities and other human features. Grizzly bear densities were almost 7-times greater in productive secure areas compared to unproductive risky areas (Figure 19a). Compensatory interactions of habitat productivity and risk yielded comparable bear densities elsewhere in Alberta. Source-sink dynamics of a grizzly bear population in southwestern British Columbia not only highlighted the extent to which low annual survival rates in ecological traps configured low bear densities (Figure 19b), but also the extent to which concentrations of fruit-rich habitats played the figurative role of bait (Figure 19c; Lamb et al. 2017a). Notably, human-caused mortality drove lower survival rates in the ecological trap, but with disproportionate impacts on adolescent and younger adult bears (Figure 19c; Lamb et al. 2017a, 2020).

This last result highlights the extent to which adolescent bears – especially males – have often borne the brunt of lethal interactions with people in ecological traps near human infrastructure (e.g., Mattson et al. 1992, Elfström et al. 2012). When propagated through time, the toll taken on young male bears tolerant enough to use areas near people predictably leads to disproportionate recruitment of wary adult males in backcountry areas, with a resulting more balanced sex ratio the farther one goes from human infrastructure (Mattson et al. 1996a, Mattson 2021a). Boulanger et al. (2018) provide evidence of this dynamic in Alberta where comparative densities of males were lower in high-risk environments, including those that could be considered ecological traps (Figure 20; High Risk x High Productivity). By contrast, densities of males and females trended towards parity in low-risk environments, regardless of productivity.

Other research from Alberta provides evidence that likelihood of human-caused mortality is conditioned not only on embedded risks (i.e., vulnerability of bears to lethal interactions with people), but also productivity of habitats used by grizzly bears.