

Roads, Residences, and Grizzly Bears

Effects of Human Infrastructure on Brown and Grizzly Bears

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Recovery Project**

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Roads, Residences and Grizzly Bears

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Summary

Reactions of brown and grizzly bears to and related demographic effects of human infrastructure are complex and highly contingent. There are no invariant universally applicable standards or threshold for managing bear habitat security. Even so, the available research supports reaching generalizable conclusions that are summarized in the following bullets. Bolded text at the end of each point reference sections of this report that provide more details.



Humans have taken and invariably continue to take a consequential, if not catastrophic, toll on brown and grizzly bear populations worldwide (Sections 2 and 5).



Humans kill bears at higher rates near human infrastructure, but with substantial variation in the magnitude of this toll (Section 4).



Brown and grizzly bear populations fare best in the absence of all people and human infrastructure (Sections 4, 5, 6, and 7).



As a corollary, fewer roads are better than more roads if the goal is to conserve bear populations, with no roads being best of all (Box 1; Sections 4.2, 6.1).



Few people are better than more people, especially when in the form of little or no traffic on roads and few if any resident humans (Sections 4.2.4, 6.4.3, and 7.2).



Bears in most populations underuse areas near human infrastructure, but with considerable variation in the extent of this underuse (Section 6).



Bears exposed to humans and human infrastructure invariably fare better when subsidized by immigration from nearby large source areas free of human impacts (Box 2; Sections 4.2.2, 4.2.4, 4.3.5, and 7.3).



All else equal, the extent of areas secure from human impacts needs to be greater where people are armed, intolerant, and likely to violate wildlife protection laws (Box 5; Sections 5.1.2, 5.1.3, 5.2, and 5.3).



Major transportation corridors often constitute fracture zones in what would otherwise be regional meta-populations, with mountainous terrain typically exacerbating this effect (Section 7.4).



Highways are less lethal for bears when there is less traffic, lower speed limits, fewer attractants, and designs that facilitate detection of bears by drivers (Section 7.1 and 7.2).



Human infrastructure located in naturally productive environments or associated with unsecured attractants often lures bears into fatal conflicts with people (Sections 4.3.5, 4.3.6, and 6.4.2).



Bears are more vulnerable to disturbance and human-caused mortality in areas that lack visual and audio screening or protective rugged topography (Box 2; Sections 4.2.5 and 6.4.1).



Most bears in most places mitigate the hazards of human infrastructure by accelerating and directing their movements to minimize the duration of their exposure (Section 6.3.2).



When near humans, nocturnal bears experience less human-caused mortality compared to diurnal bears and are consequently more common among those bears survive interactions with people (Sections 4.3.1 and 6.3.1).



Human-tolerant bears are better able to use human environs, but also die at higher rates compared to less tolerant bears (Sections 4.3.2 and 6.3.3).



The disproportionate killing of human-tolerant male bears by people often leads to security-conscious adolescents and females with dependent young concentrating near human infrastructure, typically with problematic outcomes (Sections 4.3.3 and 6.3).



Bear managers in the United States neglect impacts attributable to locating infrastructure in productive habitats without screening cover (Box 3; Sections 4.3.4).



Most standards employed by bear managers in the United States for managing grizzly bear habitat security lack scientific justification. Some are arbitrary and capricious (Sections 4.2.2 and 4.2.3).



A range of standards or thresholds for managing habitat security can be derived from the available research. One set of standards is “conservative,” appropriate for at risk populations, and the other set is “middle of the road,” appropriate for larger more resilient populations.



Conservative Standards: Road densities $<0.4 \text{ km/km}^2$ (0.6 miles/mile^2) (Sections 4.2.2 and 6.1.2); Buffers for defining patches of secure habitat along roads $>815 \text{ m}$ (0.5 miles) (Section 6.1.2); Buffers for defining patches of secure habitat around townsites $>5,000 \text{ m}$ (3 miles) (Section 6.1.2); Individual patches of secure habitat $>870 \text{ ha}$ ($2,150 \text{ acres}$) in size $>815 \text{ m}$ from the nearest road and $>5,000 \text{ m}$ from the nearest townsite (Section 4.2.4); Secure habitat $>75\%$ of the regional bear distribution (Section 4.2.4); Population source areas $>4,000 \text{ km}^2$ in size ($1,550 \text{ miles}^2$) (Box 2).



Middle of the Road Standards: Road densities $<0.7 \text{ km/km}^2$ (1.1 miles/mile^2) (Sections 4.2.2 and 6.1.2); Buffers for defining patches of secure habitat along roads $>400 \text{ m}$ (0.25 miles) (Section 6.1.2); Buffers for defining patches of secure habitat around townsites $>3,000 \text{ m}$ (2 miles) (Section 6.1.2); Individual patches of secure habitat $>490 \text{ ha}$ ($2,150 \text{ acres}$) in size $>400 \text{ m}$ from the nearest road and $>3,000 \text{ m}$ from the nearest townsite (Section 4.2.4); Secure habitat $>65\%$ of the regional bear distribution (Section 4.2.4); Population source areas $>1,000 \text{ km}^2$ in size (390 miles^2) (Box 2).

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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.

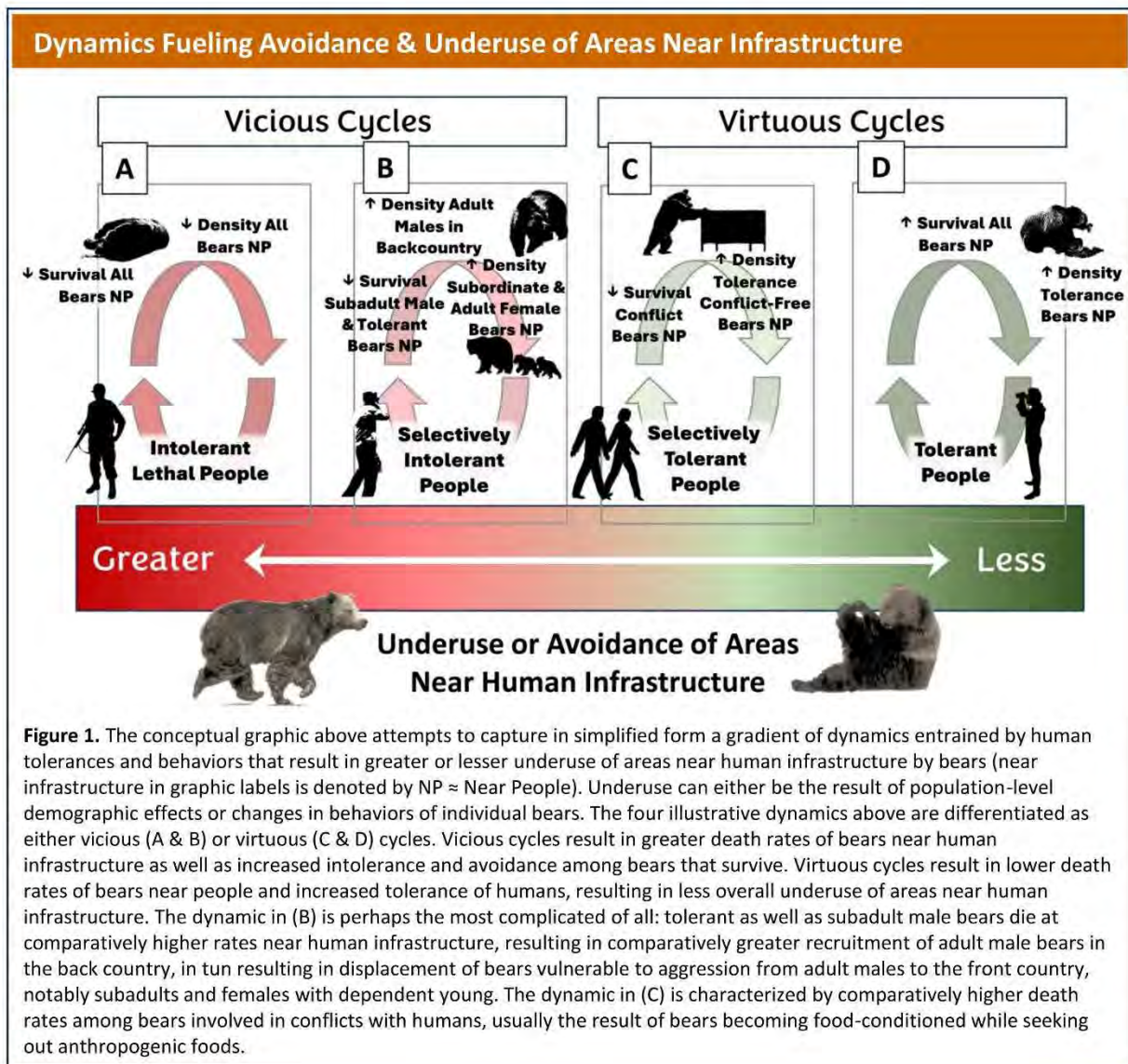
Up front, this complexity debars any credible statements about fixed effects of human infrastructure on bears, with the proviso that certain issues such as impacts of heavily trafficked highways are more amenable to widespread extrapolation. Even so, the effects of traffic on main thoroughfares can be 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 (e.g., Van der Ree et al. 2015). 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 in human environs largely derive 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 conclusions from these reviews to specific situations.

This report attempts to provide a more replete perspective not only regarding 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 otherwise approximated.



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 death 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 (see Section 6.1.1).

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 in these disciplines 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 described in more detail 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” used here 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 road-like linear features or permanent facilities with concentrations of people – the latter much like townsites or recreational developments.

As a corollary, I also do 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 do 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 has 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 attempt 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, different road designs, vehicle speeds, visibility along roads, and diel variation in human activity. Bear behavior is addressed 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 do 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).



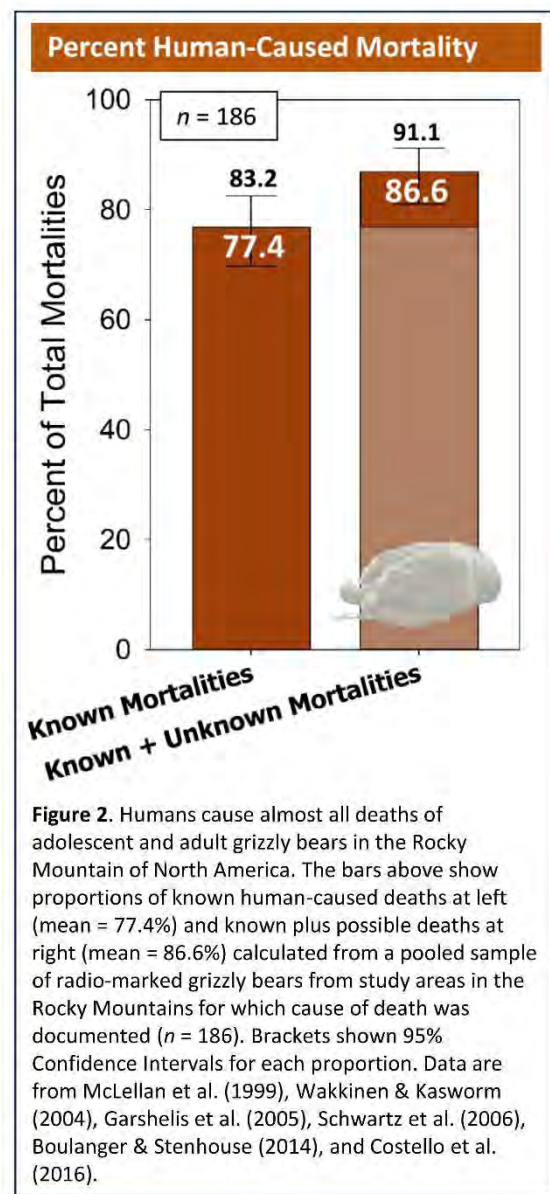
2. The Centrality of Human-Caused Mortality

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 have died 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.

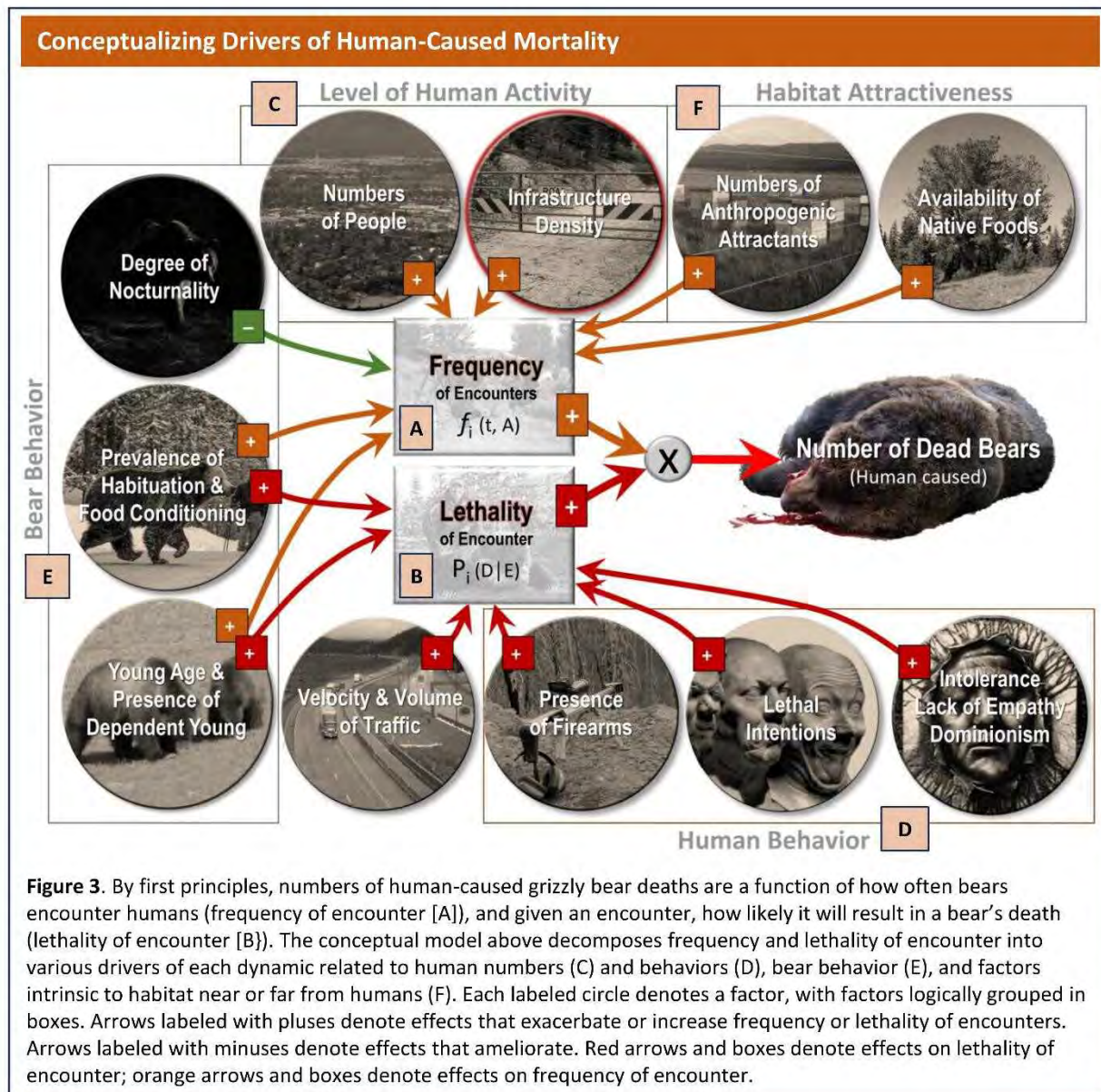
Cast against the background of history (e.g., Mattson & Merrill 2002, Albrecht et al. 2017), the magnitude of contemporary human-caused mortality emphasizes the extent to which humans dictate the fates of brown and grizzly bear populations—a conclusion underscored by several demographic analyses showing 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).



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).



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).

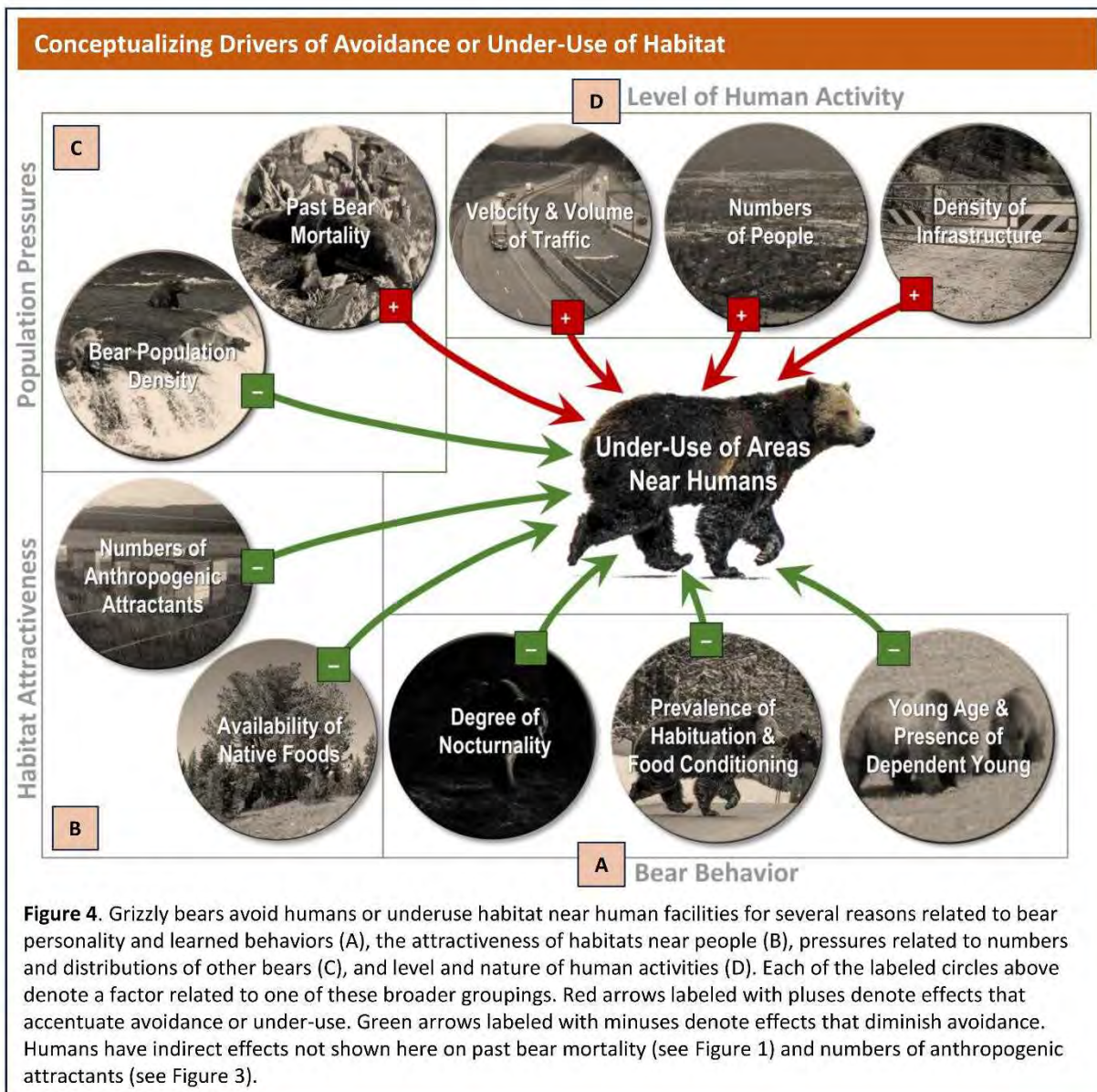
Human lethality is arguably determined largely by human behaviors, most of them directly or indirectly rooted in human attitudes, worldviews, and choices (Figure 3d). Prospectively the deadliest situations for bears arise from when people arm themselves (choice) and go into grizzly bear habitat with 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 so (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

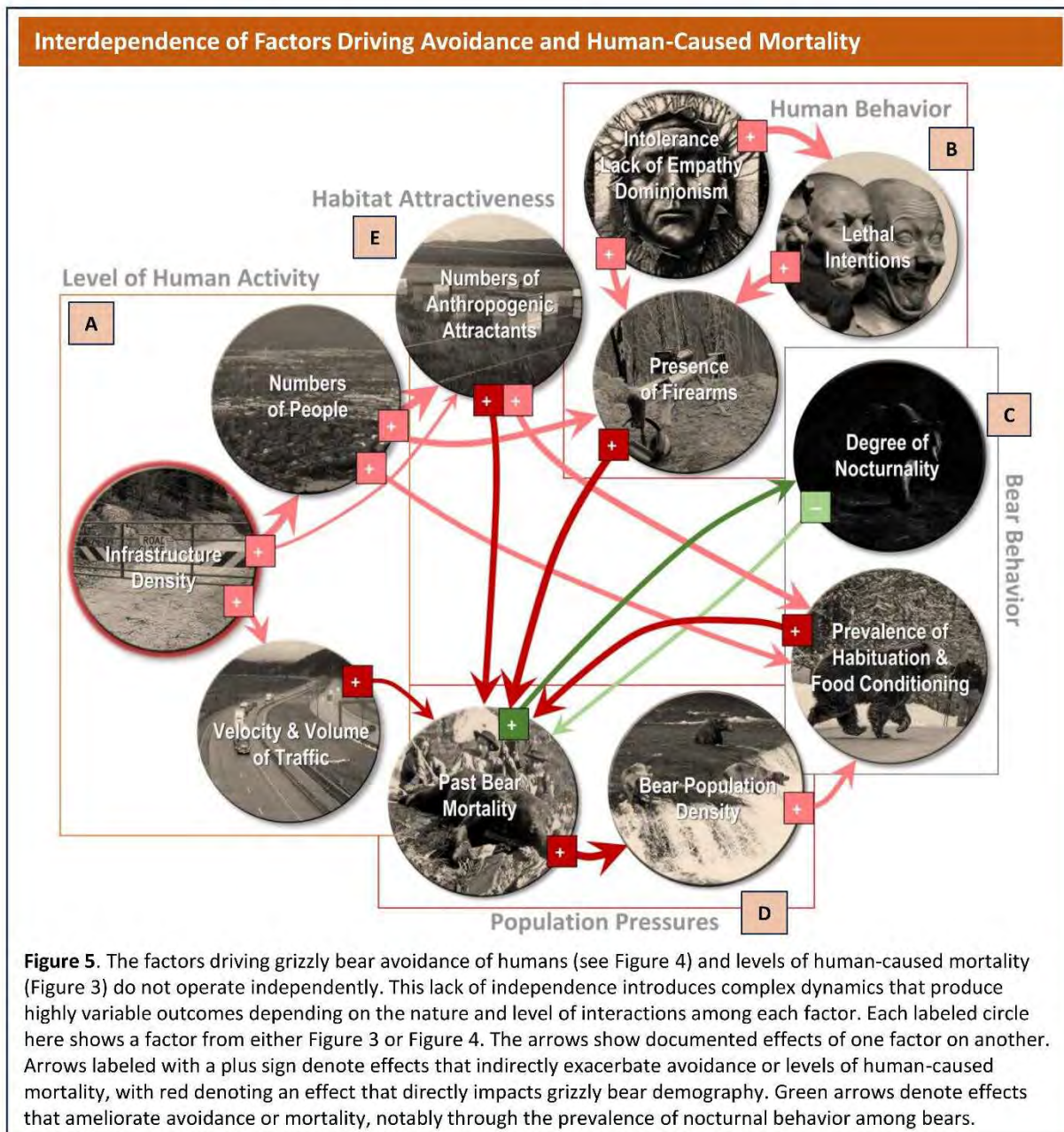
Population-level underuse and individual-specific avoidance of areas near human infrastructure by grizzly bears is the ostensible focus of this report. Yet, as with human-caused mortality, infrastructure *per se* is likely to be only one of several drivers for these phenomena at any given time and place. 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.



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).

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.

Photo Credit: Roger Hayden



3. A Research History

Some of the earliest research focused on grizzly bears 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 few 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 Craigheads 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 Kåre Elgmork in 1978 - the first focused on bears in the Apennine Mountains of Italy 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 for granted the performance of current computers and software 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.

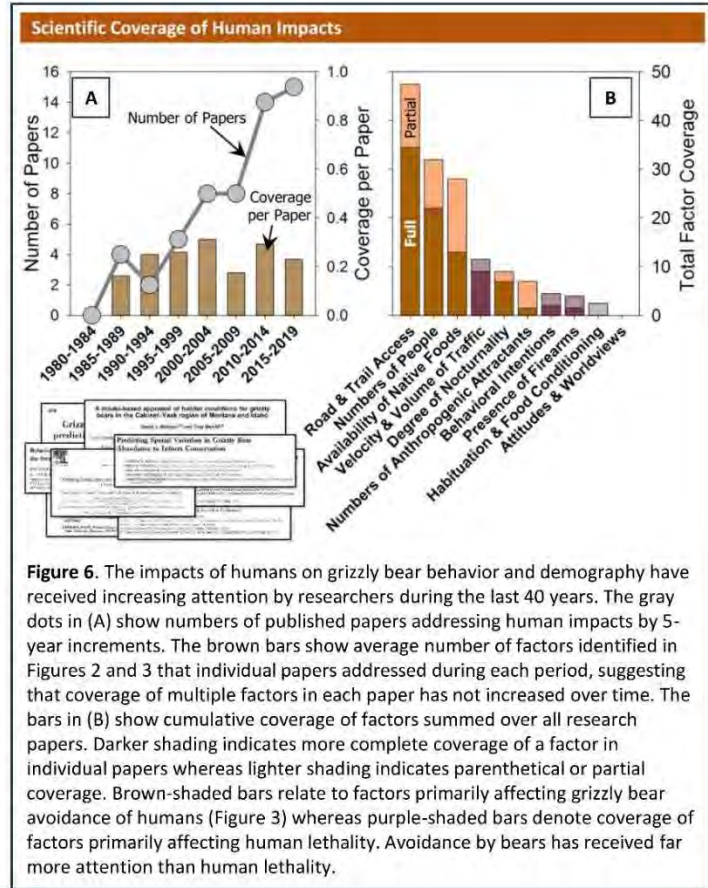
3.2. A Burgeoning of Conceptually Limited Research

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.



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 accidentally 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 7.

4.1. Complexities of Spatial Demographic Analyses

Compared to spatially indeterminate analyses of survival, spatially explicit analyses 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 (Section 3.2). 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 km² 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 grain 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 Bear Demography

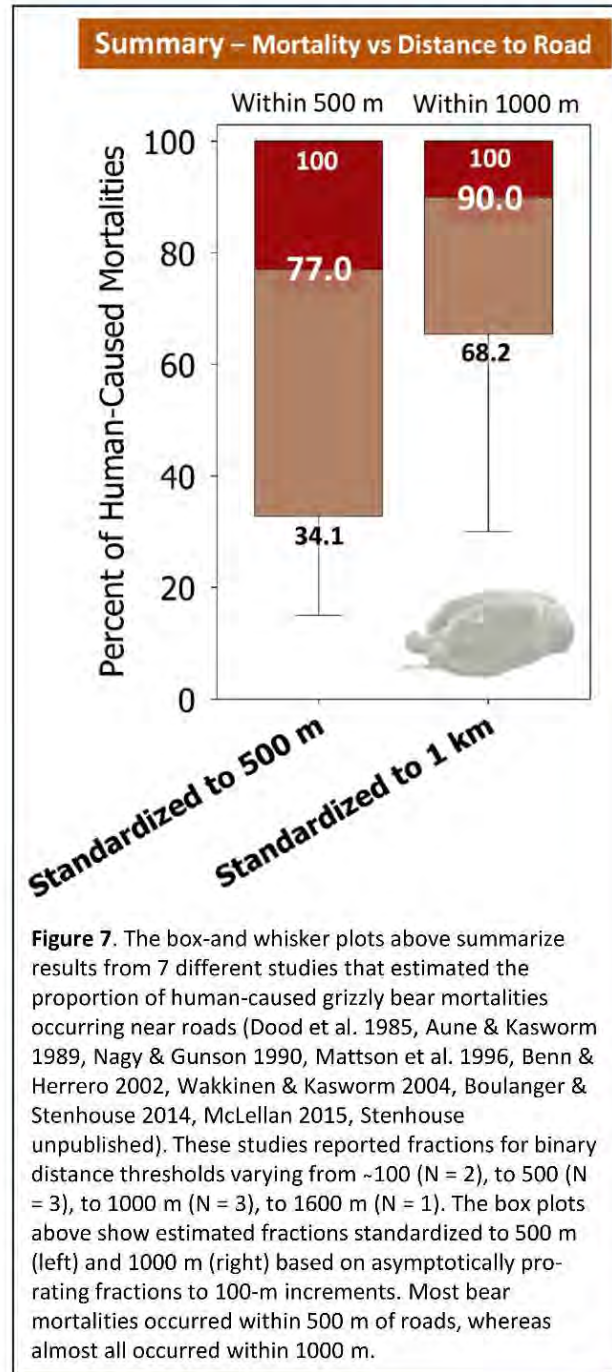
Road densities and the related extent of lands remote from roads have become proxies for almost all human impacts on private and public lands in North America (e.g., Forman et al. 1998, Ceia-Hasse et al. 2017). In an apparent quest for simplicity, federal agencies with authority over grizzly bear management in the contiguous United States have established fixed standards for allowable road densities and derivative calculations of “secure” habitat on public lands. These standards 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 exceeded¹. Various researchers contributed to this logic by publishing conclusions such as: “industrial road management would be a useful tool if...(b) open road densities exceed 0.6 km/km²; (c) less than at least 60% of the unit’s area is >500 m from an open road in patch sizes of ≥10 km² [sic]” (Proctor et al. 2019). Regardless of the nuance or proviso attached by researchers to such statements, managers have historically referenced them to justify an abridged and simplified approach to managing grizzly bear habitat security.

4.2.1. Concentration of 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).



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 are likely to be documented regardless of nearness to roads whereas deaths of the latter are biased towards detection in areas where people are active – near roads and residences (Mattson 1998).

4.2.2. 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, but 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.

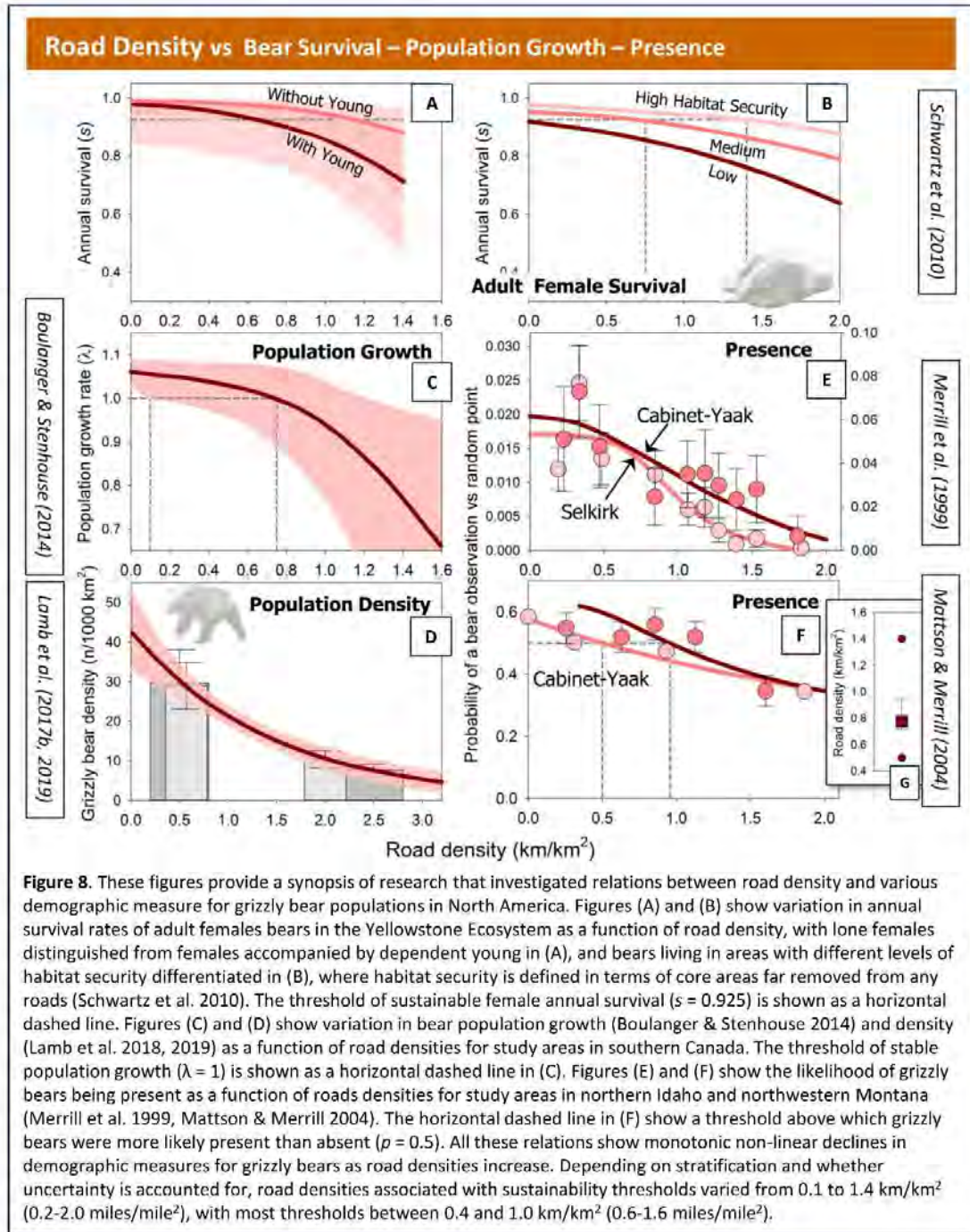
Of relevance to grizzly bear conservation, these monotonic negative responses suggest that any increase in road density will have adverse effects on demographic performance of grizzly bears. There is no intermediate optimum for bears. Instead, the available evidence suggests that the most favorable conditions 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 to inflections where negative responses to increases in road density intensify (Figures 8a, 8b, 8c).

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 (1.6 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/km², with resulting heightened exposure to potentially lethal encounters with humans.

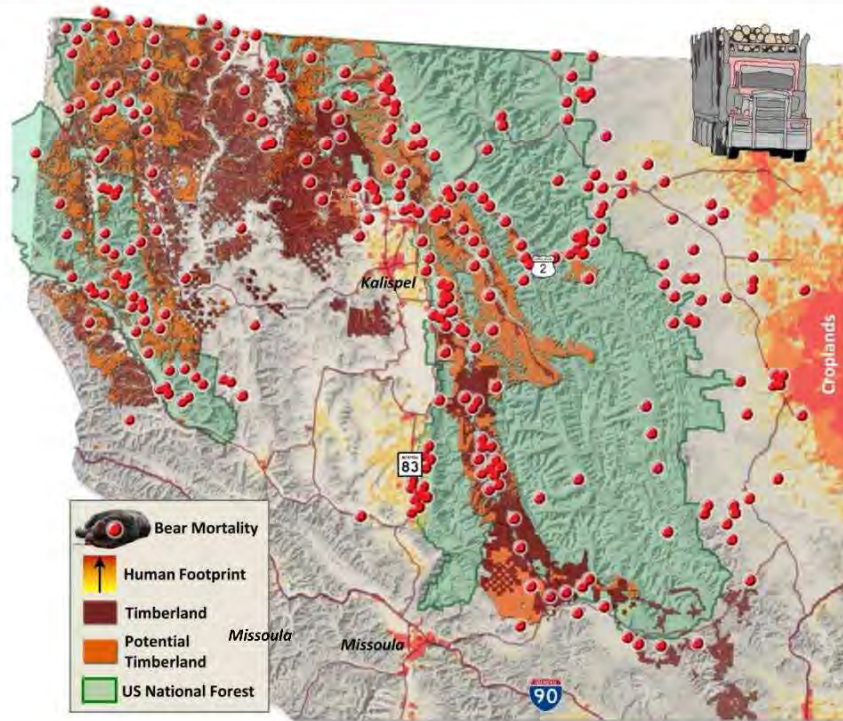


Box 1: Timber, Roads & Grizzly Bear Mortality

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: 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-km² to 1-km²) 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-km² project areas whereas, more conservatively, Mattson (1993) recommended that habitat >2500-m from a road or human development comprise >57% of 28-km² 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/km² 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, researchers in Alberta have shown that bear densities 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-km² (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-km² 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-km² in size, implying a decay of demographic effects that comports with the ca. 200-km² 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-km² 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-km²) nested within larger Bear Management Units (BMUs) approximately the size of cumulative female life ranges (ca. 900-km²; 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 for BMU Subunits in various grizzly bear Recovery Areas of the contiguous United States have evolved 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 due to concurrent levels of habitat security (U.S. Fish & Wildlife Service 2007, Northern Continental Divide Ecosystem Grizzly Bear 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.

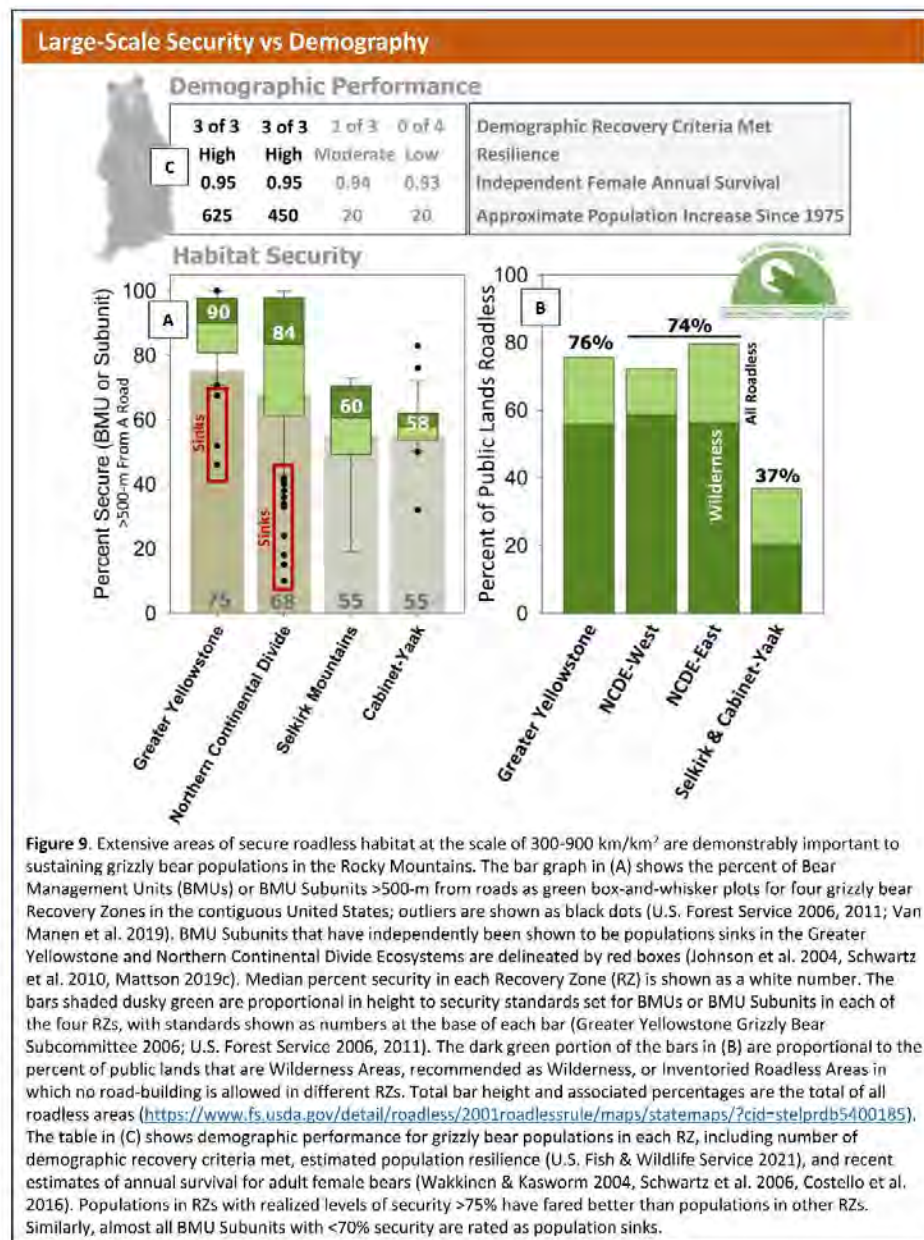


Figure 9 summarizes some key aspects of habitat security, demographic performance, and progress towards recovery for grizzly bear populations in four ecosystems of the contiguous United States. The range of values for all parameters is both substantial and telling. Median levels of core security defined largely in terms of distance to human infrastructure range from >80% in the Greater Yellowstone and Northern Continental Divide Ecosystems (GYE and NCDE, respectively) to 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/km² 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/km²; Schwartz et al. 2010a) versus the CYE (*ca.* 0.8 km/km²; 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 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/km² – at least under conditions that have prevailed in the contiguous United States during the last several decades.

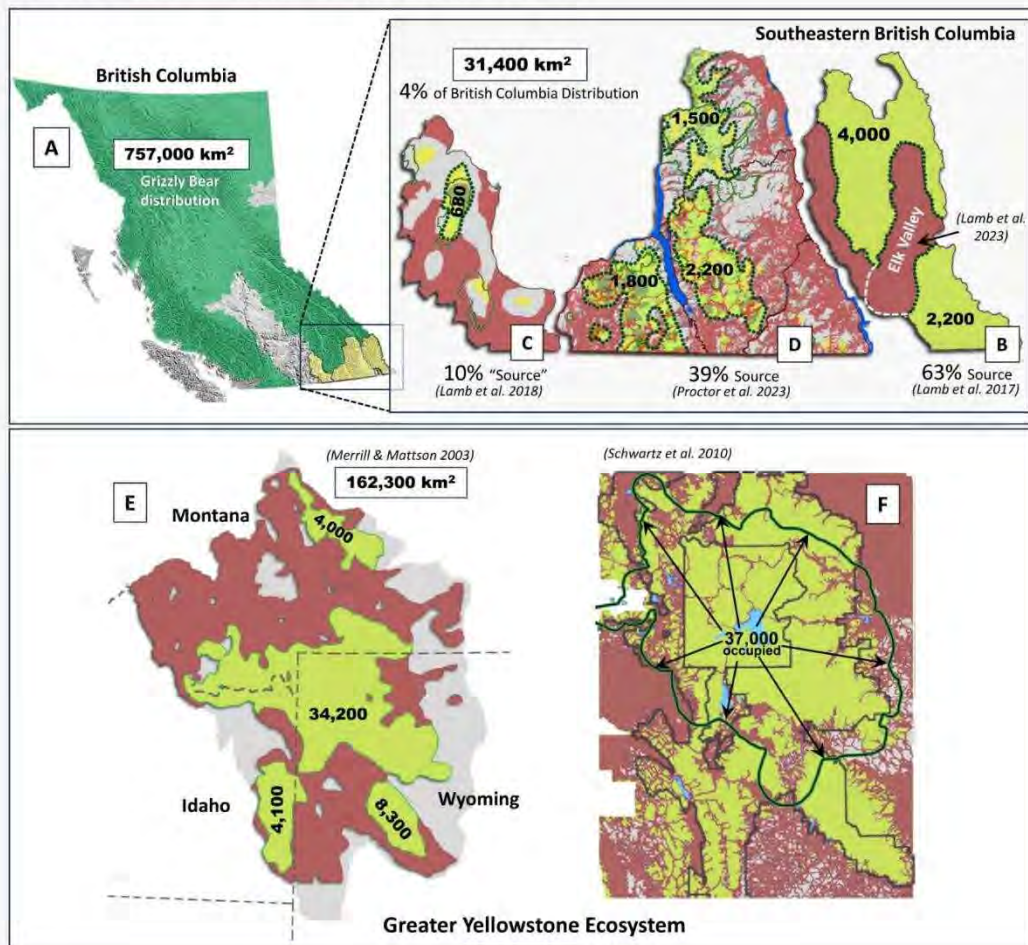
Given this conclusion and observations by others such as Lamb et al. (2017b, 2019, 2020) and Boulanger & Stenhouse (2018), it is paradoxical that the laxest habitat security standards adopted for Recovery Zones in the contiguous United States have been applied to the CYE and SE. Standards in the GYE 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/km² 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/km² 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. More to the point, standards applied to the SE and CYE 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/km², 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 km² in size. As a corollary, there is no evidence to suggest that propagating open road densities of approximately 0.6 km/km² over extensive areas (e.g., >15-20% of life-range-sized areas) is compatible with sustaining grizzly bear populations under conditions that currently prevail in North America.

Box 2: Sources, Sinks & Meaningful Scales

There is little doubt that trajectories of grizzly bear populations are governed by dynamics at the scale of thousands rather than tens or even hundreds of km^2 , with source-sink structures key to sustaining bear populations in areas with widespread human impacts. The figures below show maps from study areas in southeastern British Columbia and the Greater Yellowstone Ecosystem in which population sources (dusky green with sizes in km^2) are differentiated from population sinks (dusky red) reckoned using a spectrum of analytic grains as well as criteria for distinguishing sources from sinks. As important context, the study areas in southeastern British Columbia combined (in B-D) comprise only about 4% of the Province's total grizzly bear distribution (A) and include two populations that are considered threatened. All the featured study areas are approximately 10,000-150,000 km^2 in size – much larger than the area encompassed by deliberations governing uses of most public lands. Criteria for delineating sources and sinks in the figures below include (B) an *a priori* determination premised on a 16-km zone of human impacts (e.g., grain of 200- km^2) associated with a heavily settled valley system; (C) a reckoning of bear densities using a moving window similarly 200- km^2 in size; (D) a synthesis integrating productivity and recruitment at a grain of 29- km^2 with security approximated as areas >5-10 km^2 in size and >500-m from a road; (E) habitat productivity and remoteness averaged at the scale of female life ranges (900- km^2); and (F) areas secure enough for annual survival of adult females to exceed 0.91, reckoned primarily as any area >500-m from an open road.

Regardless of the grain or reckoning of source-sink structure, almost all areas prospectively functioning as sources at the scale of a grizzly bear population are >1,000- km^2 in size and largely free of impacts associated with human infrastructure. Most are associated with Provincial and National Parks or road-free wilderness areas. None are associated with extensive areas with appreciable road systems, and none where road densities average near 0.6 km/km^2 . The important take-away from all this is that grizzly bear populations have only survived and grown where there are large (>1,000 km^2) source areas with little human infrastructure that subsidize nearby human-impacted population sinks.

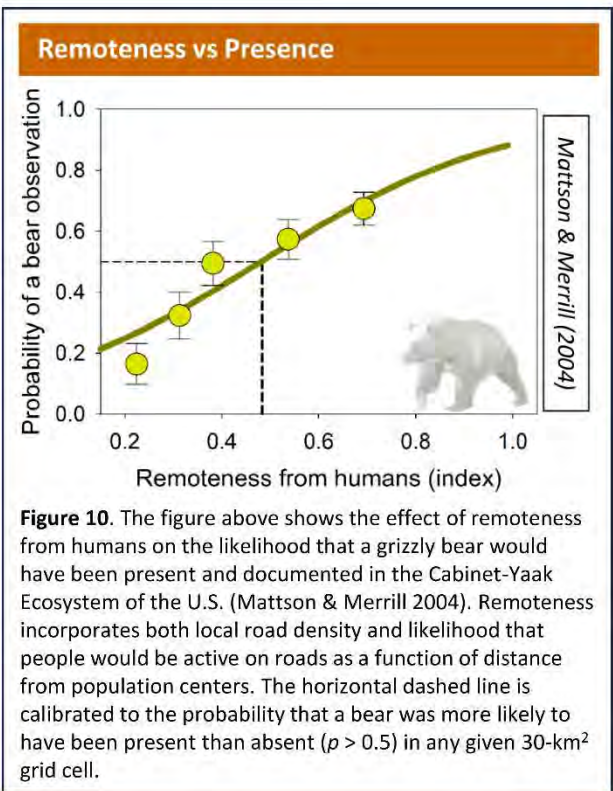


However, even this conclusion comes with several important caveats. First, almost all the results reviewed here have been obtained from data gathered largely on multiple-use public lands, some under long-term tenure of private companies, with most access devoted to industrialized extraction of resources – less often to recreational traffic. Private lands typically comprise a small portion of the studied landscapes. Strictly protected areas also 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 (Sections 2.1 and 5; Mattson 1996b).

4.2.4. Demography versus Human Populations and Activity on Roads

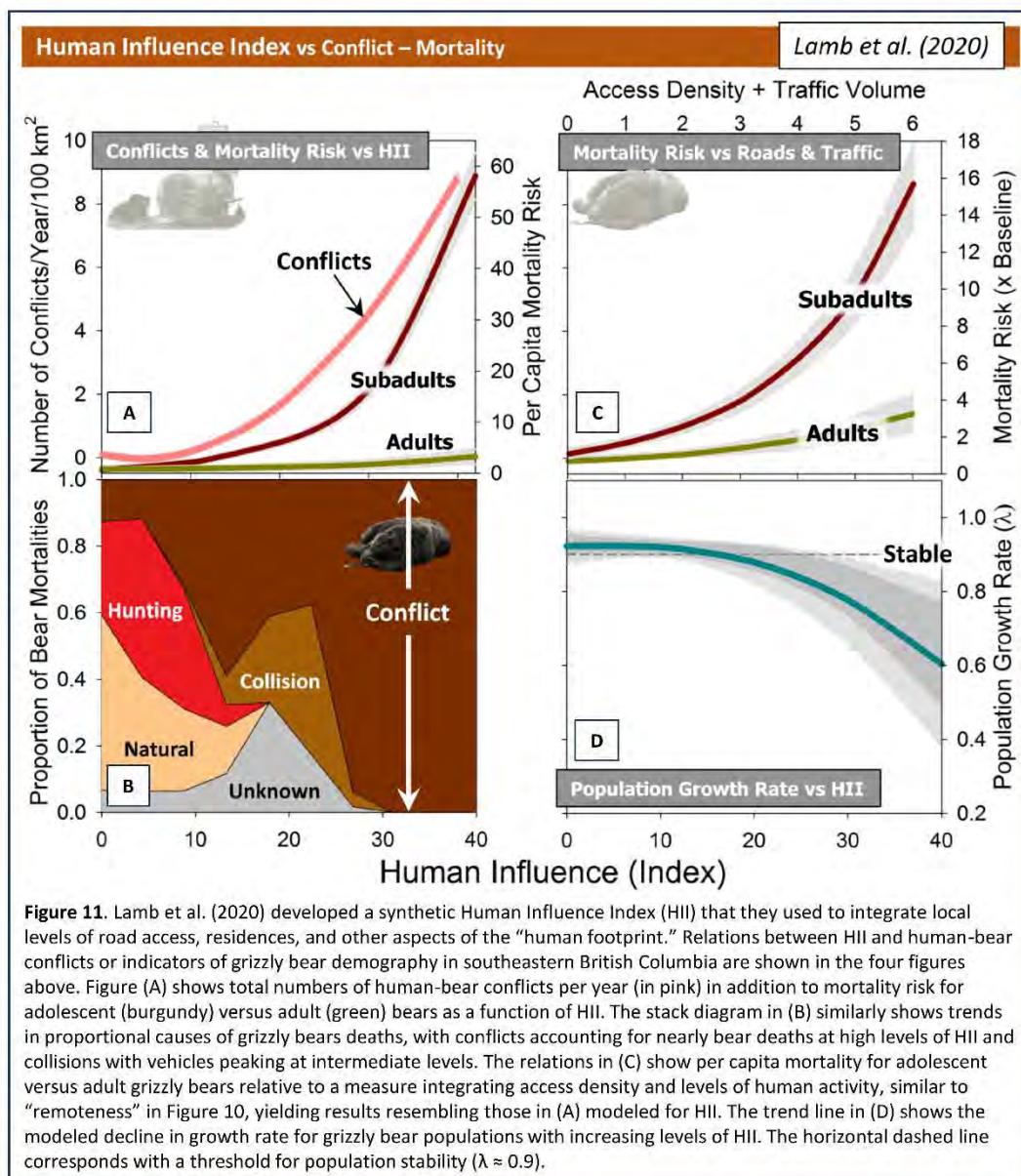
Given that physical infrastructure such as roads doesn't by itself kill grizzly bears, a key factor in judging effects on bear demography is the extent to which this infrastructure correlates with or expedites the activities of people who directly or indirectly cause bear deaths (Section 2.1, Figure 3). As a case in point, McLellan (2015) postulated that high densities of grizzly bears were sustained in his 2,800-km² study area despite an average open road density of 0.74 km/km² 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 (Section 5).

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 or 'built up' areas, and human land use at a 1-km² resolution (WCS & CIESIN 2005).

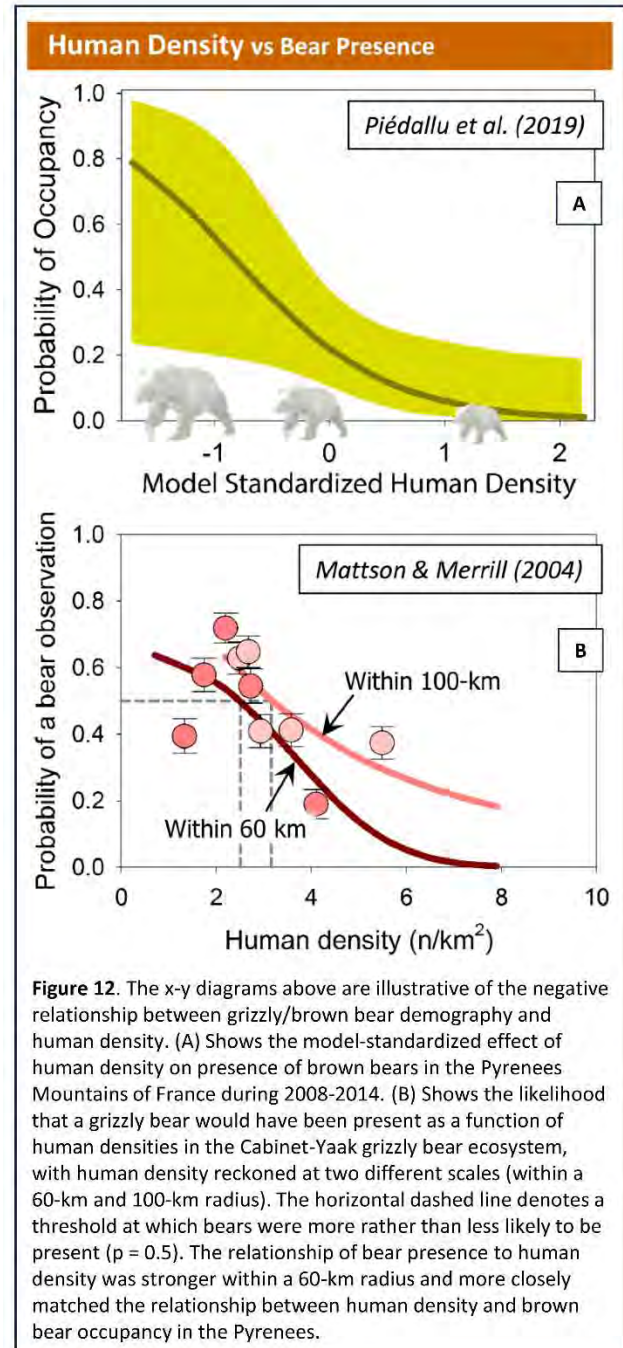
All these synthetic measures exhibited strong relations with some aspect of grizzly bear demography, including presence versus absence of bears (Merrill et al. 1999, Merrill & Mattson 2003, Mattson & Merrill 2004; Figure 10). But the strongest and most comprehensive relations with demography were demonstrated 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 11 total 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. 2010a, Peters et al. 2015, Steyaert et al. 2016, Piédallu et al. 2019). Of the



ten that considered some measure of road access, eight likewise showed a negative effect – and none 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 about 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 4.2.2) – 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-monotonic 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, the best situation for bears is unequivocally when there is no human infrastructure or local human population.

4.2.5. Demography versus Structural Configurations of Habitats

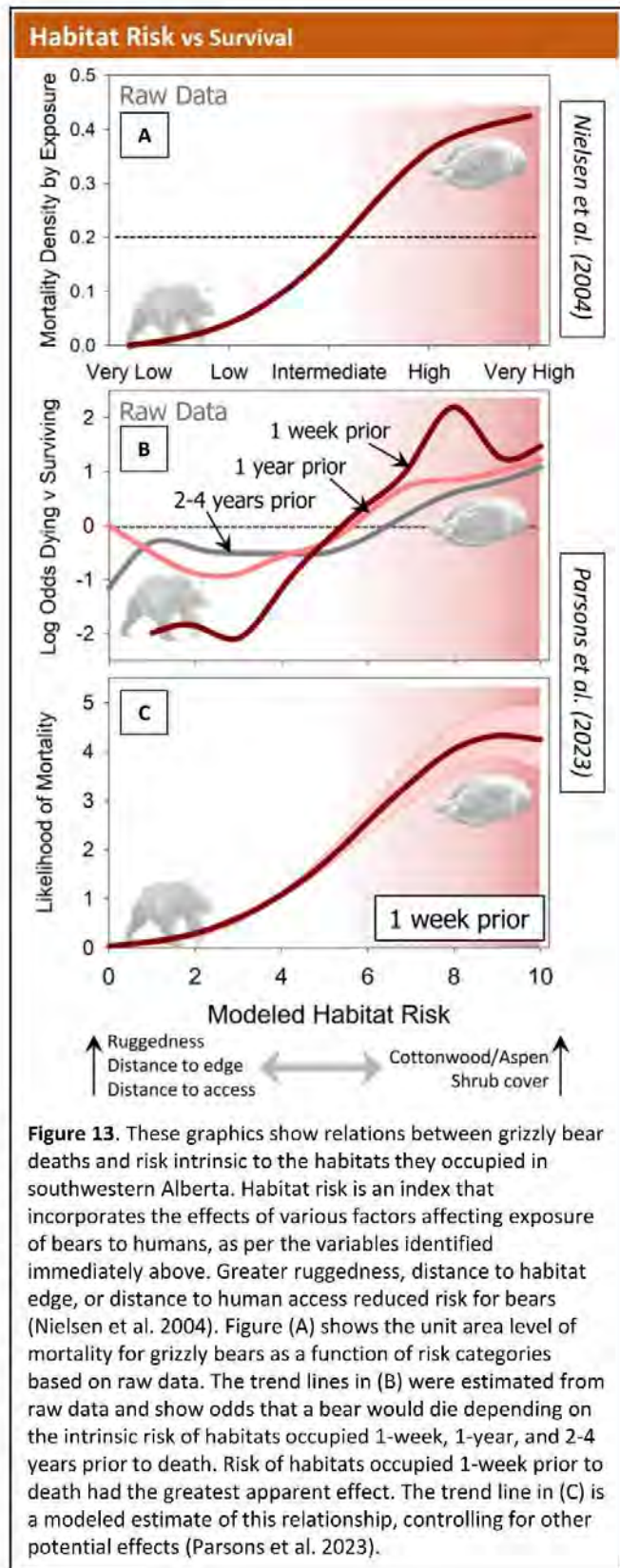
Any natural feature that either directly or indirectly reduces exposure of grizzly bears to people concentrated at or near human infrastructure also plausibly reduces associated levels of human-caused bear mortality (Section 2.1). The mechanisms behind this could include (1) decreased likelihood that 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 that have 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 potentially explaining these patterns, there is evidence supporting all three, including behaviors of bears when near roads as well as behaviors of people – especially hunters –

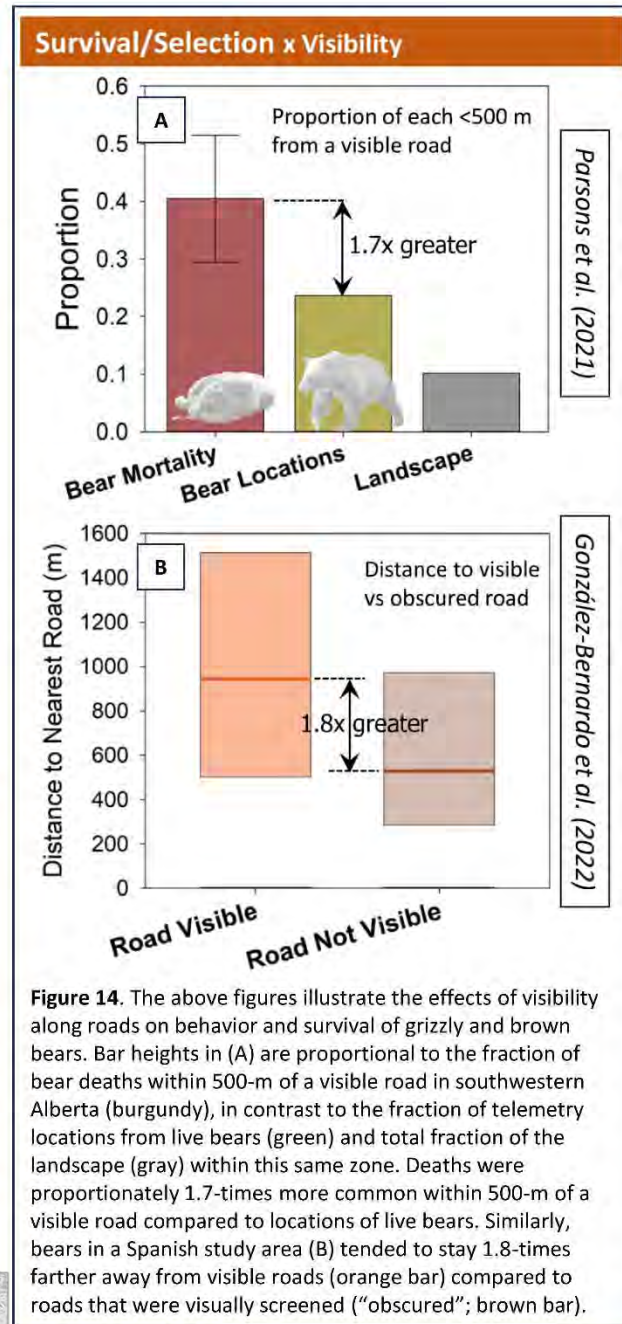
in the backcountry at large. Hunters are an especially useful focus because they are plausibly more motivated than other people to observe wildlife and pursue animals away from roads. Even so, hunters have almost universally been shown to distribute themselves nearer roads or other access, with maximum distances traveled from points of departure ranging from around 500 to 850 m (e.g., Thomas et al. 1976, Gratson & Whitman 2000, Stedman et al. 2004, Diefenbach et al. 2005, Lebel et al. 2012, Jones et al. 2015, White et al. 2017, 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]).

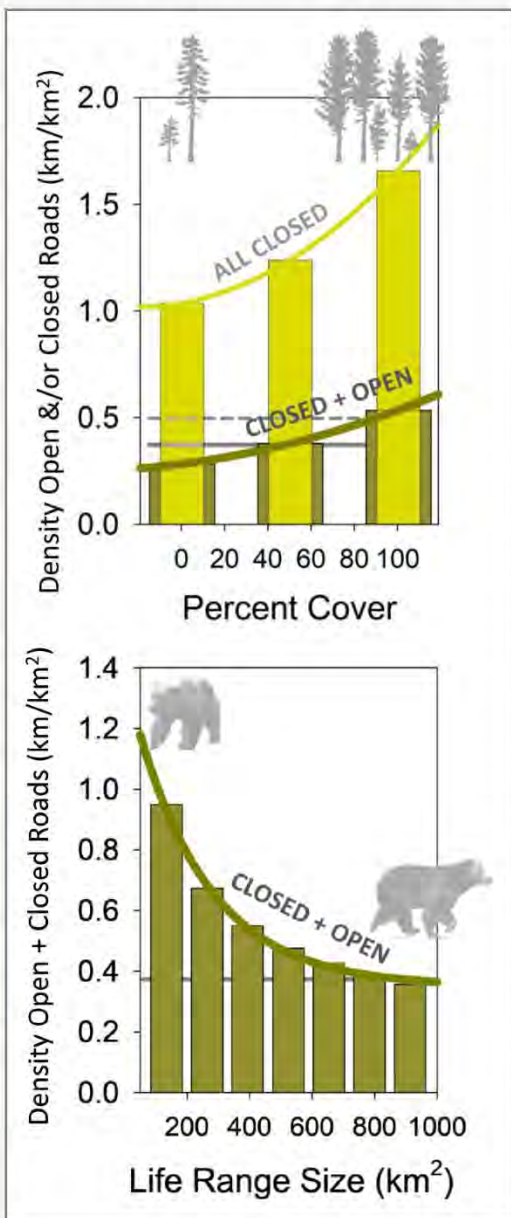
Documented bear behaviors predictably tended to magnify the screening effects of topography and vegetation within 500-1000 meters of motorized access (see Section 6.4.1). Although the body of research addressing the effects of vegetation and topography on behaviors of brown and grizzly bears near roads 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 41). 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).



Box 3: 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).

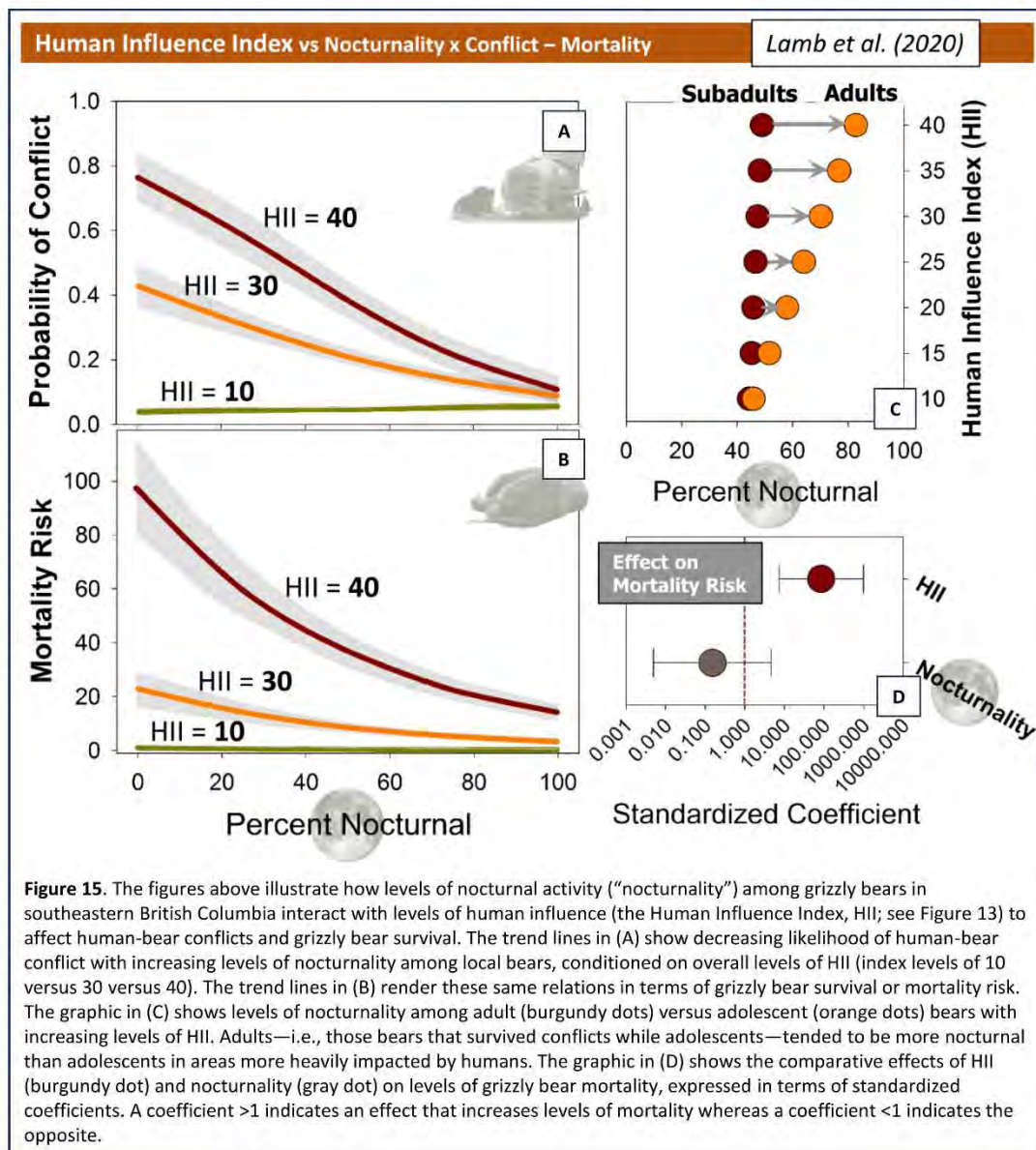
Mattson (1993) also postulated that there would be a geometric relationship between road density standards needed to achieve adequate security and sizes of female grizzly bear life ranges. Based on first principles, bears would be more likely to encounter roads at any given road density by approximately 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-km² in size. The low end of these sizes is unlikely to occur anywhere in interior regions of North America, where annual ranges are typically 200-300 km² in size (e.g., Blanchard & Knight 1991, Mace & Waller 1997, Wakkinnen & Kasworm 1997, Graham & Stenhouse 2014, Lamb et al. 2020) – roughly ½-⅔ the size of cumulative life ranges. This distribution suggests that road density thresholds sufficient to provide security for grizzly bears would be higher in more productive regions such as southeastern British Columbia compared to less productive regions such as western Alberta (Proctor et al. 2023).

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 than to assume the opposite.

4.3. Effects of Bear Behaviors on Risk

Grizzly bears are 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 (Figure 1). Importantly, these sorts of dynamics can



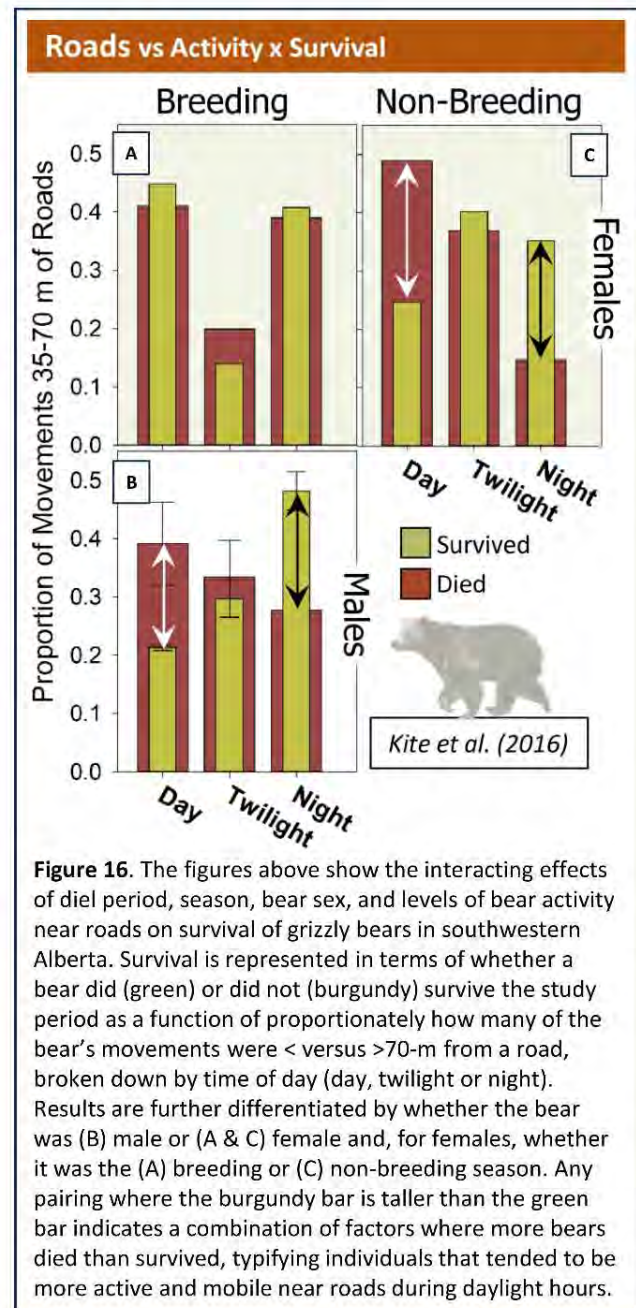
become even more complicated when humans and human infrastructure are associated not only with high quality foods, but also safety from threatening conspecifics. Individual bears thus need to not only accurately perceive and interpret the world, but also successfully weigh risks and rewards conveyed by sometimes conflicting cues (Mattson 2021a).

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. Nocturnality & Demographic Outcomes

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 compared to when undisturbed in backcountry areas (see Section 6.3.1; 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]). 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 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 be unavailable.

4.3.2. Tolerance of Humans & Demographic Consequences

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).

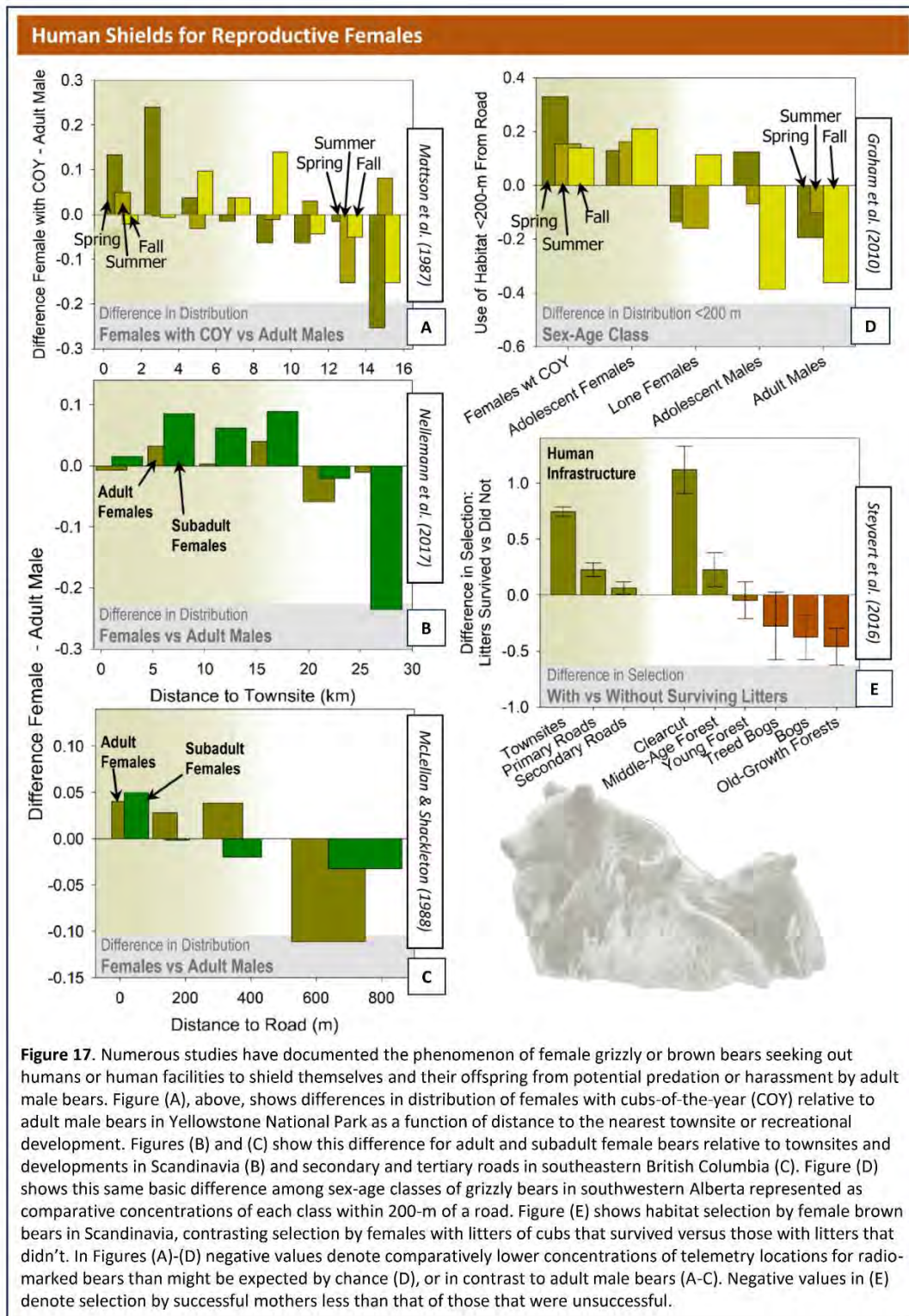
Assessing whether a bear is tolerant – or habituated – is intrinsically subjective. As a result, various researchers have used whether a bear was trapped by managers because of conflicts with humans as a proxy for tolerance, assuming that behaviors engendered by greater acceptance of people led to the 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 more 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 then increased back to population averages within 3-5 years among surviving bears – 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 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).

4.3.3. 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.

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).

4.3.4. 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 4.3.3), 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. However, when these choices are compounded over time and space dynamics emerge at the population level that 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 a matrix of possibilities. Apropos, bear

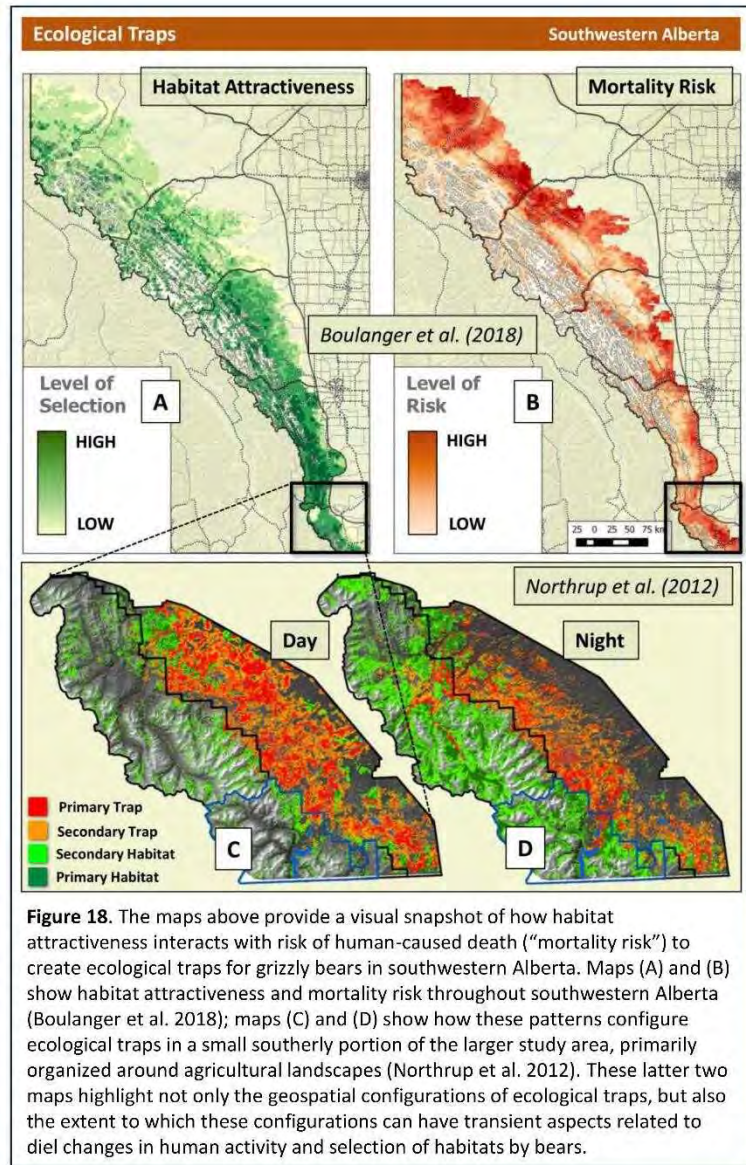
biologists have developed conceptual frames comprised of primary and secondary sinks (or traps) and habitats (Nielsen et al. 2006, Northrup et al. 2012; Figures 18c and 18d); areas of high and low risk and habitat attractiveness (Boulanger et al. 2018; Figures 18a and 18b); sources and attractive or 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 that source-sink dynamics are common place in brown and grizzly bear populations, often feeding ecological traps at multiple scales. At the broadest scale, source-sink dynamics that include ecological traps are manifest in substantial differences in population density and annual survival rates.

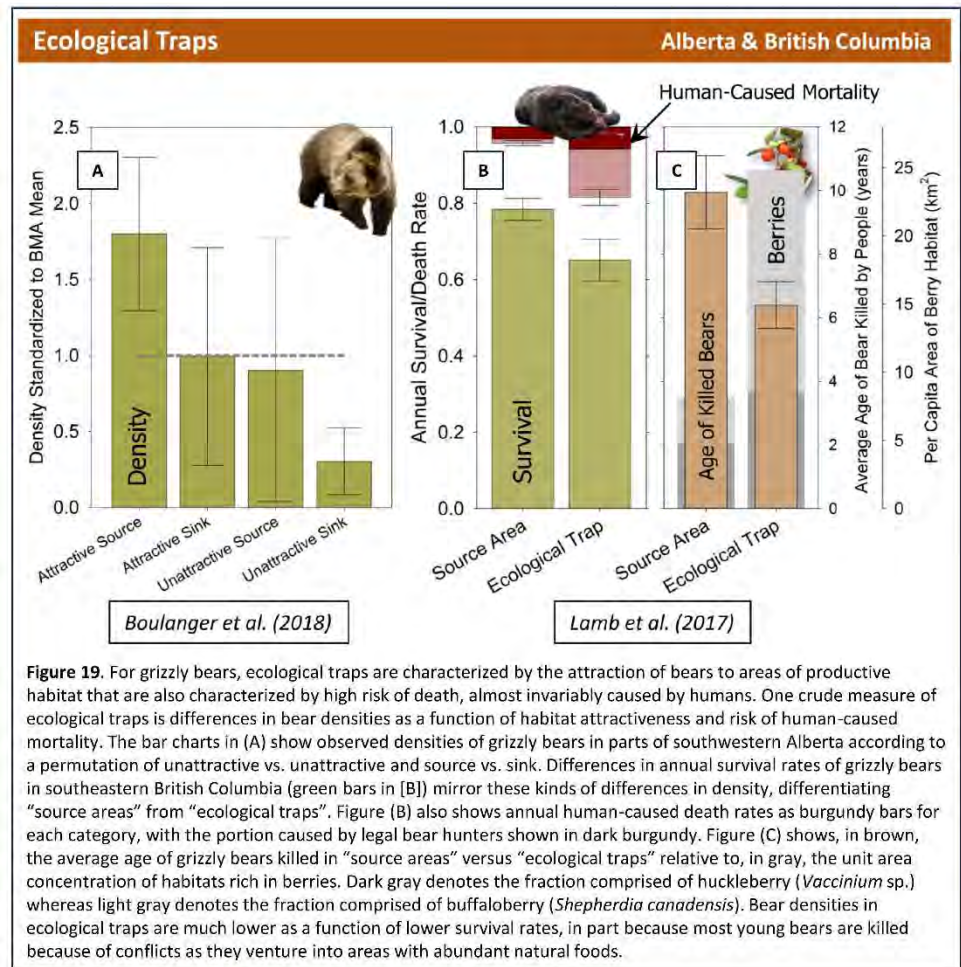
Boulanger et al. (2018) showed that grizzly bear densities in Alberta varied by nearly an order of magnitude at the scale of 3,000-30,000 km², largely as a function of interactions between habitat productivity and habitat risk, with the latter defined almost wholly in terms of road densities and other 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 neighboring southeastern 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).

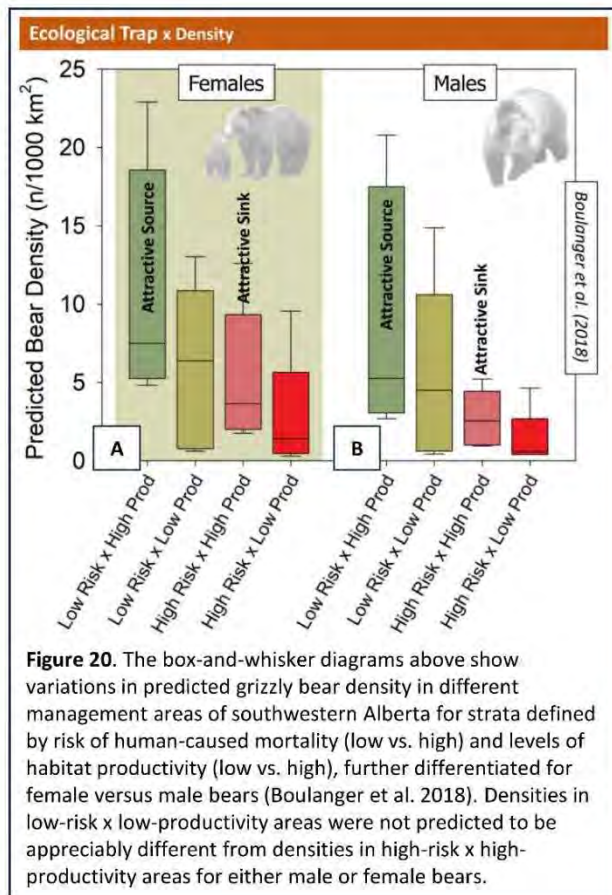
This last result highlights the extent to which adolescent bears – especially males – have often borne the brunt of lethal interactions with people in ecological traps near human infrastructure (e.g., Mattson et al. 1992, Elfström et al. 2012). When propagated through time, the toll taken on young male 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) – a type of vicious cycle (Figure 1b).



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.

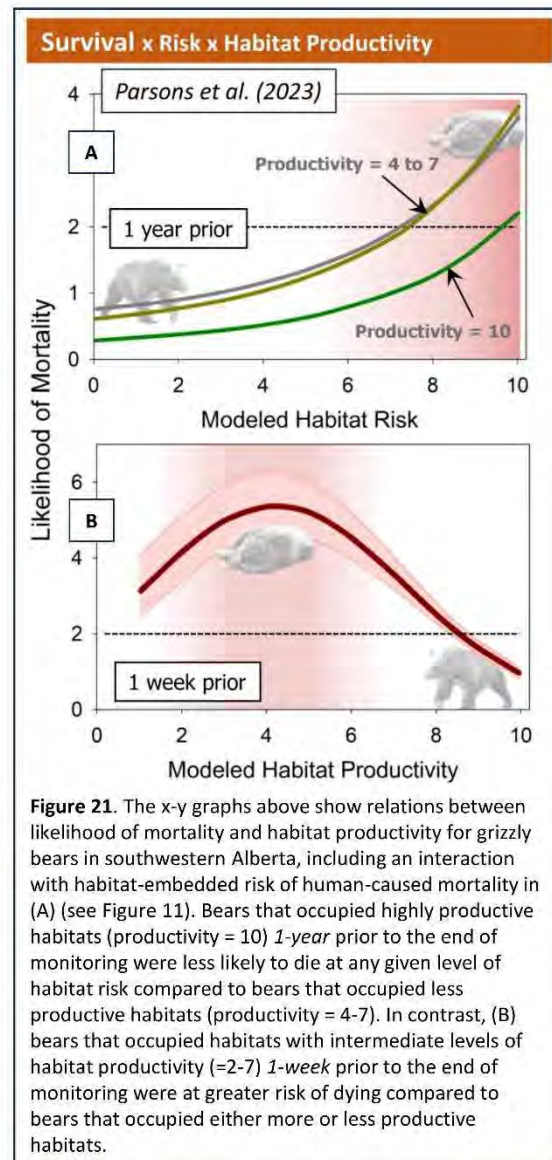
Other research from Alberta provides evidence that rates of human-caused mortality are conditioned not only on embedded risks (i.e., vulnerability of bears to lethal interactions with people), but also on whether bears have access to a mosaic of productive habitats (Parson et al. 2023). This research found that bears using highly productive habitats were much more likely to survive compared to bears using less productive habitats in areas with comparable hazards, with this difference most pronounced one year prior to when monitoring of individuals ended either because of death or radio-collar failure (Figure 21a). Somewhat more nuanced, bears that used habitat of intermediate quality 1-week prior to the end of monitoring were far more likely to die compared to bears that used highly productive habitat (Figure 21b).

These patterns suggest that bears exploiting productive habitats were able to reduce daytime exposure to roads and people (see Section 4.3.1) in contrast to bears relegated to using less profitable habitats, whether because none were available or because of competitive exclusion by other bears. Regardless of the reason, bears struggling to find high-quality foods in productive habitat patches were presumably more likely to expose themselves to human-related hazards, whether because they undertook more numerous long-range movements (Box 2), were more day active (Section 4.3.1), or became more tolerant of people and roads (Section 4.3.2).



class to roads during the time they were monitored (Boulanger et al. 2013). Basically, these researchers asked whether body condition was correlated with likelihood of death when bears were exposed to the same density of roads; and, as an obtuse corollary, whether bears in the best condition tended to exploit environments that were more rather than less hazardous. Perhaps counterintuitively – as well as in contrast to what might be expected from the results of Parson et al. (2023) – bears in good condition tended to die at a higher rate than bears in poor condition at any given road density (figure

However, this seemingly straight-forward explanation is confounded by yet more research undertaken in Alberta that not only contrasted the fates of bears in poor, intermediate, and good condition exposed to comparable road densities, but also the cumulative exposure of bears in each



22a). Similarly, bears in good condition tended to spend comparatively more time in areas with high vs low road densities.

This seeming paradox can be explained by the singular conditions of southwestern Alberta where most data analyzed by Boulanger et al. (2013) were collected, i.e., industrial timberlands typified by habitats that produce few bear foods absent disturbance leading to opening of forest canopies (e.g., Hamer & Herrero 1987a; Hamer 1996, 1999). These kinds of disturbances were historically caused in this study area by both wildfire and timber harvest (e.g., Nielsen et al. 2004c; Souliere et al. 2020), with the latter pervasive during the past 50 years.

Insofar as the results of Boulanger et al. (2013) are concerned, the association of increased habitat productivity with timber harvest logically translated into bears benefiting from greater access to food

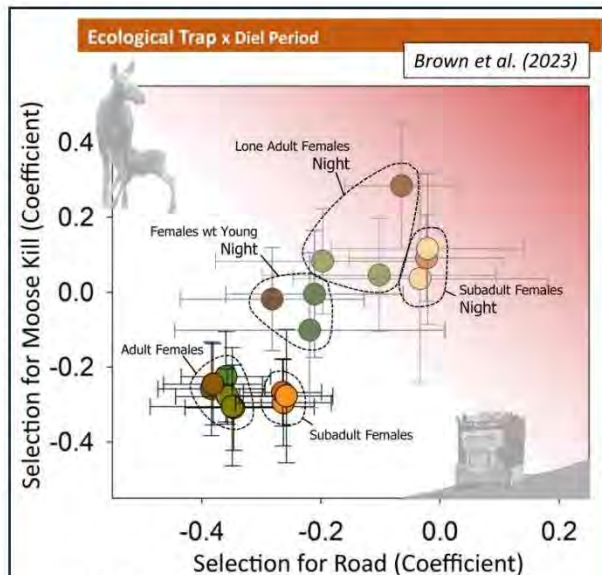


Figure 23. This x-y diagram based on research from Sweden shows the degree to which female brown bears jointly selected for moose (*Alces alces*) kills by human hunters and areas near roads. Selection is further differentiated by night versus day, season, and age-class and reproductive status of involved bears. Negative values denote selection against a moose kill or roadside habitat, whereas positive values denote selection for kills or roadsides. Adolescent and lone adult females selected for moose kills near roads (upper right quadrant) at night during all three seasons. All bears during all seasons tended to select against roads and moose kills (lower left quadrant) during daylight hours.

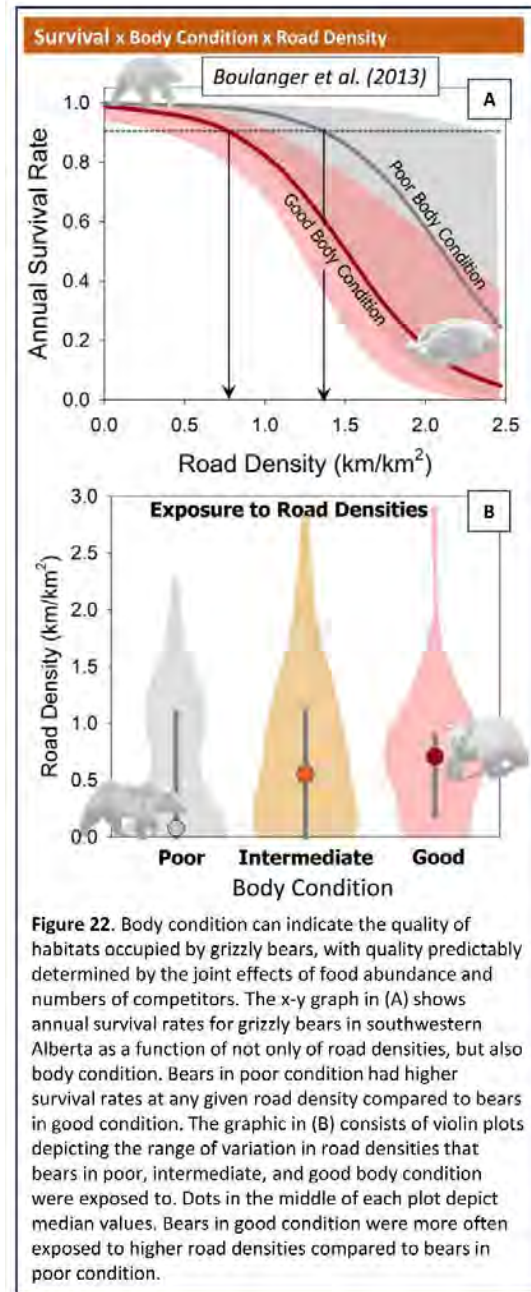


Figure 22. Body condition can indicate the quality of habitats occupied by grizzly bears, with quality predictably determined by the joint effects of food abundance and numbers of competitors. The x-y graph in (A) shows annual survival rates for grizzly bears in southwestern Alberta as a function of not only of road densities, but also body condition. Bears in poor condition had higher survival rates at any given road density compared to bears in good condition. The graphic in (B) consists of violin plots depicting the range of variation in road densities that bears in poor, intermediate, and good body condition were exposed to. Dots in the middle of each plot depict median values. Bears in good condition were more often exposed to higher road densities compared to bears in poor condition.

being exposed to high-density road systems, especially when natural disturbances were locally uncommon (Nielsen et al. 2004b; Roever et al. 2008a, 2008b; Kearney et al. 2019). More to the point, individual bears that benefited from access to more abundant high-quality foods were at the same time penalized by greater odds of death – the classic signature of an ecological trap (Nielsen et al. 2008).

This still begs the question why bears in better condition would have more often died compared to bears in poor condition when exposed to the same densities of industrial roads. Without detailed information on behaviors of individual bears any explanation can only be speculative, but the most likely invokes different tolerances that would have affected the amount of time bears chose to spend in the immediate vicinity of roads during daylight hours – under conditions that amplified hazards at a temporal-spatial grain finer than that of the Boulanger et al. (2013) analysis. According to this explanation, bears attracted to and exploiting productive habitats near roads and in clearcuts would have become increasingly tolerant of people, leading to diminished avoidance and a culminating lethal outcome (Mattson 2021a; see Sections 4.3.1 and 4.3.2). Regardless of whether this explanation is true or not, the results of Boulanger et al. (2013) point to potentially complex dynamics catalyzed by road infrastructure associated with vegetation modifications that create attractive habitat conditions entraining changes in bear tolerance for humans, ultimately leading to increased odds of death for involved bears – all independent of road density, as such (Figures 3-5).

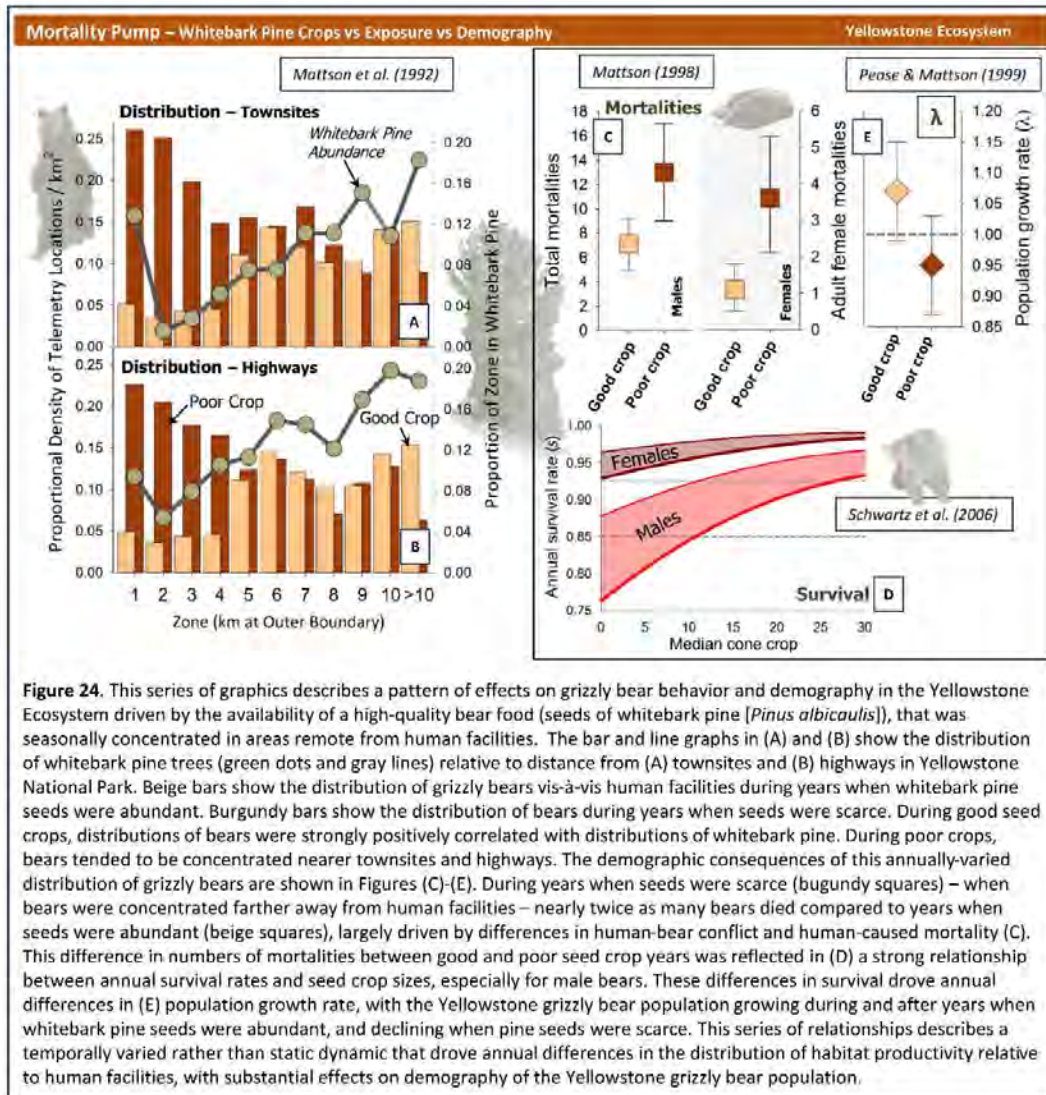
Lending weight to this speculative explanation for results of Boulanger et al. (2013) – and returning to the theme of Section 4.3.1 – research from Scandinavia highlights the important tempering effect of nocturnality on risks to bears exploiting human-associated foods near secondary road systems. Brown et al. (2023) investigated the joint effects of roads and availability of moose carcasses (*Alces alces*) produced by big game hunters on habitat selection by female brown bears, differentiated by time of day and reproductive status. Not surprisingly, bears preferentially selected areas with carrion near roads during night-time hours (Figure 23), but with this pattern most pronounced for adolescent and adult females without dependent young. Even at night, females accompanied by cubs or yearlings tended to forego habitats with the most abundant carrion as a means of avoiding roads and hunters.

The substantial body of research summarized in this section emphasizes the extent to which distributions of foods and productive habitats govern exposure of grizzly bears to human infrastructure at multiple scales – with potentially orders of magnitude effects on lethal interactions of bears with people. The potential extent of these effects puts the lie to widespread assumptions among bear managers that habitat security can be assessed solely in terms of road densities or other measures of physical human infrastructure, independent of how infrastructure is juxtaposed with attractive habitats. This basic idea was codified over 35 years ago in early conceptualizations of models for managing the cumulative effects of human activities on grizzly bear habitat (Weaver et al. 1986, Mattson et al. 1986, Mattson et al. 2004) and is further substantiated by ample research published since then.

4.3.5. A Multiplex Ecological Trap: Whitebark Pine and Infrastructure

A culminating level of complexity for the phenomenon of ecological traps arises when geo-temporal variation in availability of high-quality foods triggers adaptive changes in bear distributions and behaviors relative to comparatively static spatial configurations of human features. This kind of complexity has only rarely been described, and when so, largely as the fruits of legacy research dating to the 1970s-1990s. Perhaps the best example comes from a corpus of research undertaken in the Greater Yellowstone Ecosystem documenting the effects of variation in whitebark pine (*Pinus albicaulis*) seed crops on distributions and behaviors of grizzly bears vis-à-vis human infrastructure, ultimately with

interannual effects not only on bear survival, but also growth of the grizzly bear population (e.g., Mattson et al. 1996a).



Whitebark pine seeds were a critically important food for especially female grizzly bears in this ecosystem (e.g., Mattson 2000) prior to near functional extirpation of whitebark pine as a bear food by an outbreak of mountain pine beetles (*Dendroctonus ponderosae*) unleashed during 2000–2009 by unusually warm winter temperatures (Macfarlane et al. 2013). Whitebark pine grows exclusively at higher elevations, well above the distribution of most human facilities, evident in progressively greater numbers of whitebark pine trees with increasing distance from roads and recreational developments (Mattson et al. 1992; Figures 24a and 24b). Of relevance here, whitebark pine seeds crops were highly variable from one year to the next (e.g., Mattson et al. 1994), with resulting effects on the distributions of grizzly bears. During years with good seed crops, bears tended to concentrate in the remote haunts of whitebark pine. During years of seed scarcity, bears concentrated in habitats nearer roads and developments where they exploited anthropogenic as well as alternative natural foods (Figures 24a and 24b).

This contrasting distribution of bears arising from interannual variation in abundance of foods with niches differentiated by remoteness from or nearness to human facilities regulated exposure of grizzly bears to potentially lethal interactions with people in this ecosystem. Grizzly bears consequently died at roughly twice the rate during and after years when pine seeds were scarce compared to years when pine seeds were abundant (Mattson et al. 1992, Mattson 1998, Pease & Mattson 1999, Schwartz et al. 2006; Figures 24c and 24d), with effects dramatic enough to cause detectable declines or increases in the population (Pease & Mattson 1999; Figure 24e).

On a broad scale, variability of whitebark pine seed crops regulated interannual exposure of grizzly bears to ecological refuges and traps in a landscape of static human features, functioning as a figurative “mortality pump”. However this coarser-grain dynamic linked to geospatial-temporal availability of an important food was accentuated by the extent to which human environs served as a place of refuge – a shield – for adolescent males and females with dependent young (Mattson et al. 1992; Section 4.3.3); changes in tolerance for humans entrained by increased exposure of bears to roads and residences during years of pine seed scarcity (Mattson 2021a; Section 4.3.2); and the extent to which these increases in tolerance heightened longer-term odds of death at the hands of people (Mattson et al. 1992, Pease & Mattson 1999; Section 4.3.2). All else equal, bears seeking refuge from threats posed by adult males were more likely to end up near human facilities during poor seed crop years, become more human-tolerant, and incur greater risk of mortality – with this dynamic most pronounced for adolescent males (Mattson et al. 1992). Longer-term, the differential recruitment of human-intolerant adult males into backcountry areas – sometimes to the exclusion of other bears during times of food scarcity – further accentuated this vicious cycle (Figure 1b).

This case history featuring the effects of whitebark pine seed crops on Yellowstone grizzly bears highlights the extent to which impacts of human infrastructure on bear demography are potentially governed by complex and synergistic interactions involving bear distributions, reactions to conspecifics, and tolerances of humans ultimately driven by annual variation in abundance of key foods and configurations of food-rich habitats relative to human facilities. These sorts of dynamics further emphasize the importance of considering not only the juxtapose of human infrastructure with productive habitats, but also the prospective short- and long-term dynamics specific to a given ecosystem that can synergistically amplify or abate the effects of people on bears.



Box 4: Proctor et al. (2023) – Preconceptions and Limits of Inference

MONOGRAPH

WILDLIFE
NO COUNTRY IS STRANGE

THE WILDLIFE SOCIETY

Berries and bullets: influence of food and mortality risk on grizzly bears in British Columbia

Michael F. Proctor¹ | Clayton. T. Lamb² | John Boulanger³ |
A. Grant MacHutchon⁴ | Wayne F. Kasworm⁵ | David Paetkau⁶ |
Cori L. Lausen⁷ | Eric C. Palm⁸ | Mark S. Boyce⁹ |
Christopher Servheen¹⁰

Proctor et al. (2023) undertook an in-depth analyses of how geospatial arrangements of *a priori* secure habitat and high-quality habitats affected grizzly bear habitat selection and demography, the latter indicated by bear densities and recruitment of offspring into the population (i.e., ‘fitness’). The analysis focused on southeastern British Columbia, an area typified by heavy precipitation, dense forests, rugged terrain, industrialized logging, confinement of residences to narrow steep-sided valleys, and dominance of huckleberries (*Vaccinium membranaceum*) in bear diets. High-quality huckleberry patches were first identified based on known bear use and then modeled in relation to environmental variables. Habitat security was defined in terms of road densities and extent of ‘secure’ habitat >500-m from a road and >5-10-km² in size.

The authors found that availability of huckleberry patches had comparative effects that were progressively greater in models explaining bear densities, female fitness, and female habitat selection, with berry patches dominating the latter phenomenon typified by choices of individual bears. Habitat security had greatest effects on bear densities at broad scales (200-km²) – manifesting the longer-term population-level reproduction and survival – and least effect on proximal decisions entailed by habitat selection. Road density thresholds that correlated with all these phenomena ranged from 0.3 to 1.2 km/km² depending on the scale, response variable, particulars of analysis, and model uncertainties, but with an *a priori* ‘road target’ of 0.6 km/km² selected for use by the researchers in several analyses. The extent of ‘secure’ habitat associated with road density thresholds based on demographic parameters ranged from 73% to 89% at 200-km² and 28-km² grains, respectively. Parenthetically, it was not surprising that habitat selection was so strongly related to presence of huckleberry patches given that initial definition of patches was framed by examination of sites where grizzly bears were known to consume berries, and that habitat security had a comparatively weaker effect given that comparable *a priori* attention was not given to defining this variable either in terms of observed bear behavior or modeled environmental relations.

Despite considerable complexity of methods and associated variation in results, Proctor et al. (2023) distilled a surprisingly simplistic management recommendation from their work, i.e., that “backcountry road densities be maintained, on average, below approximately 0.6 km/km² and secure habitat of >60% [sic].” This recommendation was at variance with a close reading of their results and was, moreover, represented by the authors as having blanket application to a wide range of conditions. Politically, simplistic statements such as this one aligned with pre-existing management guidelines are predictably seized upon by managers to justify *status quo* arrangements.

Even more problematic, the results and derivative management recommendations featured by the authors under-stated a broad-scale source-sink structure evident not only in this study area, but also featured in the adjacent and encompassing study areas of Lamb et al. (2017, 2018, 2020, 2023; see Box 2). The extent and spatial arrangement of source-like and sink-like habitats in all three study areas – ranging in size from 600 to 3,000 plus-km² – revealed a situation where populations in extensive areas with habitat both secure and productive enough for female bears to produce a figurative surplus of emigrants sustained grizzly bears in nearby large-scale areas dominated by human impacts – including some ecological traps. This self-evident pattern featured in adjacent study areas was inconsistent with the extent to which Proctor et al. (2023) implied that dynamics at the scale of 28 to 200-km² dominated demographic processes.

Aside from problems related to a selective emphasis of results, scope of inference for this study was limited, as well as discrepant from what the authors often implied. The combined productivity, topography, level and nature of human activities, and comparative simplicity of bear diets in the Proctor et al. (2023) study area are singular. There are few places where bear diets are dominated by a single high-quality food, or where the landscape is as verdant, rugged, and heavily forested, barring openings created by timber harvest. Although the authors make brief reference to unaddressed effects associated with levels of human activity on roads, comparative lethality of access users, and home range sizes of study area bears, none of these unaddressed effects are highlighted in a description of study limitations (see Section 4 and Box 5), nor do the authors address contrasts between the simplified conditions and analyses of their study and the interannual variation in availability and distribution of food typifying many areas occupied by grizzly bears (see Section 3).

5. Human Lethality

Section 2.1 introduces the axiom that numbers of human-caused grizzly bear deaths are a function of how often bears encounter people and whether those encounters turn out fatal for the involved bears, i.e., frequency of encounter and probability of a lethal outcome from encounters. Encounter frequency is directly or indirectly dictated by the spatial configuration of infrastructure used by people to travel, work, or live; numbers of people using this infrastructure (Sections 4.2.2-4.2.3); behavioral as well as distributional responses of bears to infrastructure-associated disturbances (Section 6); superimpositions of productive habitats (Sections 4.2.4, 4.3.4, and 4.3.5); and cumulative effects of real-time learning, transmitted learning, and differential demographic recruitment among bears (Sections 4.3.1-4.3.3). By contrast, encounter lethality is dictated largely by the attitudes, intentions, and armaments that people bring to interactions with bears (Section 2.1; Figure 3d).

It is hard to overstate the importance of human lethality to the outcomes of encounters between people and grizzly bears. This proposition is perhaps self-evident. Even with an equivalent physical human footprint, encounters will predictably be orders-of-magnitude less lethal for bears when encountering people who are unarmed and tolerant compared to when encountering people who are armed, intolerant, and intent on doing harm – as in the stark contrast between outcomes of human-bear encounters in National Parks vs encounters with poachers sustained by community narratives of victimhood (e.g., Gunther et al. 2018, Mattson 2020: Section E).

Although the lethality of humans to grizzly bears can theoretically be measured, logistical pragmatics render this possibility moot. Measurement would require not only closely monitoring the movements and behaviors of a representative sample of people occupying the same space as bears, but also attributing the involved people with covariates that allow for the specification of generalizable models. Absent well-conceived covariates, sampled people end up being drawn from a population without any known relationship to people in different times and places. Hunters in pursuit of bears perhaps pose the only exception to this proposition, largely because of their demonstrably lethal intentions (to kill a bear), preparations (arming themselves with a lethal weapon), and behaviors (killing bears they encounter). Otherwise, the demographic, cultural, intentional, and behavioral profiles of people encountering bears are relegated to speculation and proxy measures.

Even so, human lethality can be crudely approximated by examining patterns residual to exposure of bears to people in analyses of demographic phenomena potentially ranging from historical extirpations; to contemporary distributions; to population-averaged odds of bear survival. The dictum that human-caused grizzly bear deaths are a function of frequency and lethality of encounters allows for the prospective isolation of lethality effects if encounter frequencies can somehow be conceptually or statistically controlled whether through landscape-level approximations of human density or time- and jurisdiction-specific measures of human activity levels.

This section summarizes evidence for the paramount effect of human lethality on fates of brown and grizzly bears at multiple temporal and spatial scales ranging from regional extirpations spanning many decades; to more recent differences in fates of bear populations; to source-sink population structures driven by policy prescriptions and associated configurations of human behaviors in different management jurisdictions.

5.1. The Role of Human Lethality in Extirpations

The idea that grizzly or brown bears fare worse in areas with more people is perhaps commonsensical. However, the histories of bear populations on different continents provide a striking commentary on the added importance of human lethality, especially when contrasting periods or places with roughly equivalent human population densities. These contrasts serve to highlight not only the role of formal legal protections for bears, but also the cultural norms, material resources, and social structures of sympatric people, most prominently when differentiating occupants of Europe, eastern China, and the colonized United States.

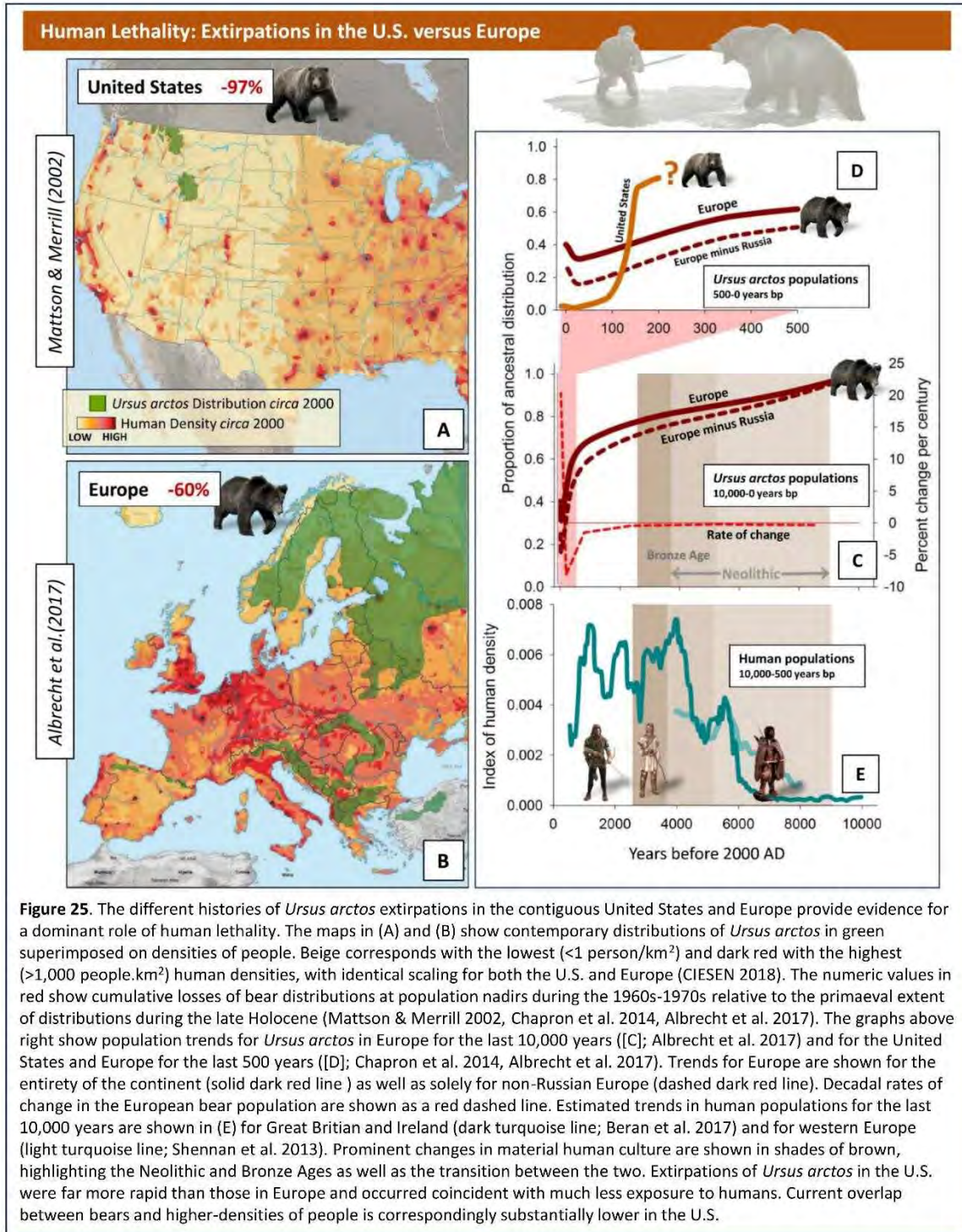
5.1.1. Human Densities and Extirpations on Different Continents

The timing and pace of brown and grizzly extirpations in these three geographic areas were starkly different, with extirpations of grizzly bears in the United States distinguished as being by far the most rapid. Mattson and Merrill (2002), Albrecht et al. (2017), Turvey et al. (2017), and Teng et al. (2020) document these extinctions for the United States, Europe, and China, respectively. Extirpations of grizzly bears from roughly 97% of pre-European distributions in the United States occurred within a startlingly brief 70-year span (Figure 25a and 25d), perpetrated almost entirely by European colonists and adventurers (Brown 1996, Storer & Tevis 1996, Mattson 2022b, Mychajliw et al. 2024). Lord Gore, an Irish aristocrat, was an exemplar who killed more than 100 bears during a single expedition through the northern Great Plains in the mid-1850s (Roberts 1977). By contrast, extirpations of brown bears in Europe itself were gradual and largely concentrated between 1550 and 1970 CE – a 400-year period. Even when contrasted with bear distributions *circa* 12,000 years ago, total declines in Europe amounted to little more than 60% (Figures 25b, 25c, and 25d). A similar situation existed in China. Extirpations of brown bears during the past 2,000 years occurred almost exclusively in densely populated eastern portions of the country between 1880 and 1950 CE, amounting to total distributional losses of only around 30-40% for the species (Turvey et al. 2017, Teng et al. 2020).

Human population densities could be unreflexively invoked to explain these differences, yet even superficial knowledge of human demography in colonial-era North America and in Europe and China during the past two millennia is grounds for dismissing this explanation out of hand. Although very gradual declines in distributions of brown bears did occur in Europe between 6,000 and 2,000 years ago and in China between 2,000 and 500 years coincident with increases in human populations (e.g., Figures 25c and 25e, Teng et al. 2020), these trends did not correlate closely; nor can they explain acceleration of bear losses in these regions starting 600-700 years ago in Europe and 150 years ago in China.

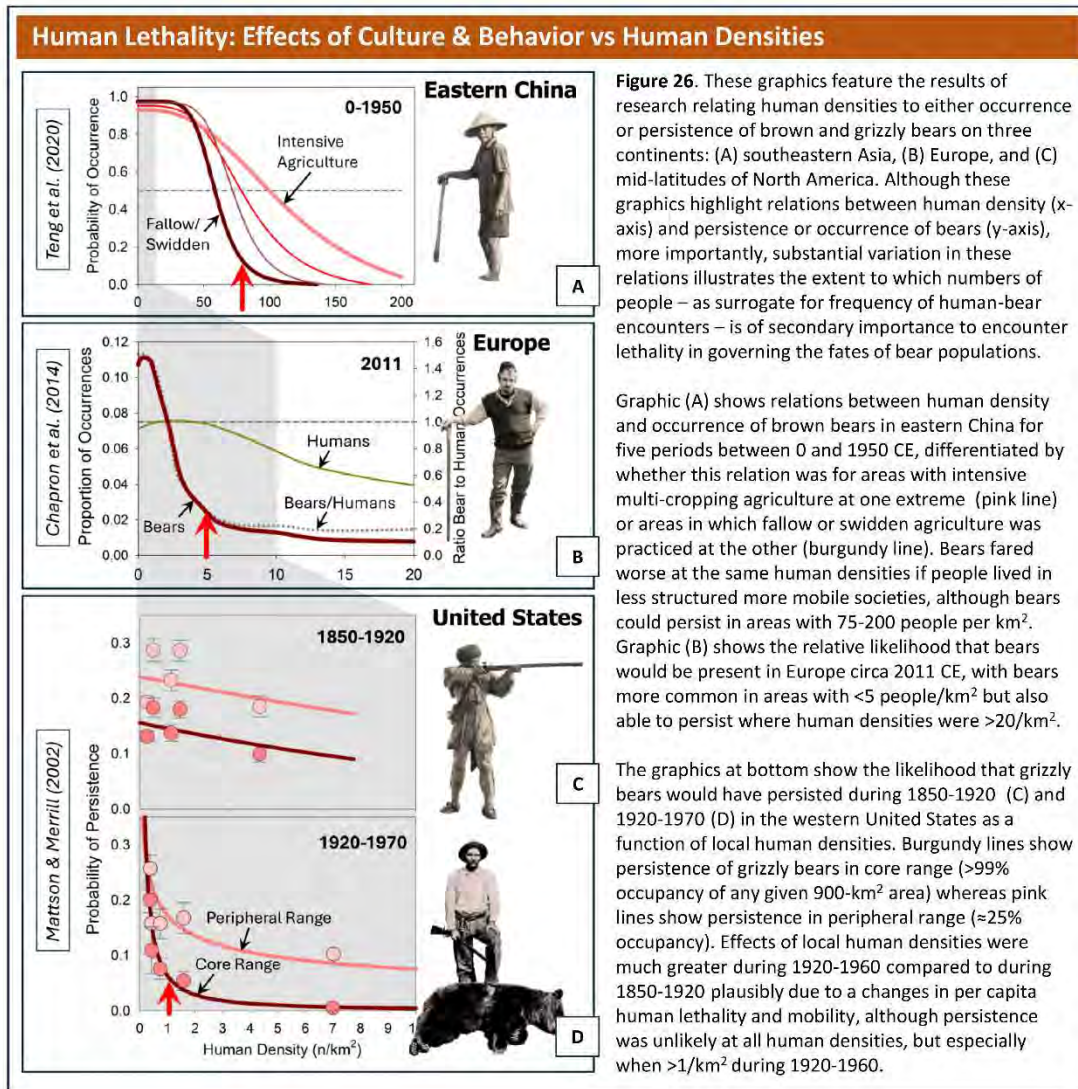
Explicit relations between human densities and persistence of brown and grizzly bear populations provide additional grounds for relegating human densities, as such, to the role of a secondary explanation for extirpation patterns. The maps in Figures 25a and 25b provide a visual impression of the marked discrepancy between human densities in the United States and Europe and current distributions of brown and grizzly bears. All else equal, bears in Europe have fared comparatively much better in areas where they have been exposed to high densities of people, especially in the Balkans and Carpathian and Apennine Mountains.

The graphs in Figure 26 not only render relations between human densities and persistence of brown and grizzly bear in more explicit form, but also highlight stark contrasts in these relations between continents and time periods. Brown bears had a >50% chance of persisting in eastern China between 0



and 1950 CE even where human densities were as high as 50-100 people/km² – although, paradoxically, odds were greatest in areas with more intensive agricultural systems and associated stringent social controls (Teng et al. 2020, Figure 26a). Brown bears in Europe were more likely to be present circa 2011 CE in areas with <2 people/km², although they could also be present where local human densities exceeded 5-20/km² (Chapron et al. 2014, Figure 26b). By contrast, grizzly bears in the United States had a <30% chance of surviving between 1850 and 1970 CE even in areas where human densities

approached 0/km², but with those odds close to nil (<5%) between 1920-1950 CE wherever human densities exceeded 1-2 people/km² (Mattson & Merrill 2002, Figure 26c). Notably, odds of persistence at any given human density declined substantially between 1850-1920 and 1920-1970. These discrepancies amount to orders-of-magnitude differences in likelihood that brown or grizzly bears would have persisted at any given human density depending on region and time period.



5.1.2. Culture and Extirpations on Different Continents

These heterogeneous effects of human density highlight a potentially paramount role for human lethality in brown and grizzly bear extirpations, which still begs the question of what might have driven such substantial disparities between responses of people to bears in the United States, Europe, and China, as well as differences in human lethality within the United States between 1850-1920 and 1920-1970. In theory, fewer lethal responses by people to bears at any given level of exposure (e.g., human density) could arise from greater reciprocal tolerances among people and bears, people who are

comparatively sedentary or poorly armed, greater centralized political control, human practices that minimize likelihood of conflict with bears, abundant natural foods in remote areas, and lack of organized government programs targeting predators (e.g., Sections 2.1, 2.3, and 4.3). All these factors could alone or in some combination explain differences in fates of brown and grizzly bear populations exposed to similar numbers of people at different times in different places.

The scope of this review does not include developing a nuanced view of how the cultures and societies of people in China, Europe, and the United States might have shaped human-bear relations and related persistence of bear populations. Nonetheless, several major themes are clear. Government officials clearly exercised considerable control over peoples' lives during millennia of Imperial rule in China (e.g., Mote 2003, Wang 2022), in stark contrast to the amorphous social contract that accompanied westward expansion of European colonists in North America (e.g., Murtazashvili 2013) – all with plausible effects not only on how people interacted with each other, but also animals such as bears. There is also little doubt that firearms have long been more common in the United States compared to in China or Europe – currently 30x, 9-10x, and 4x more common on a pro-rated basis in the US compared to China, central and southern Europe, and Scandinavia, respectively (Small Arms Survey). The mythologization of guns and violence in American history would have predictably amplified the lethal effects of these numerous firearms (see the epic trilogy by Slotkin [1998a, 1998b, 2000]). More speculatively, European colonists in North America likely parted cultural company with their Europeans counterparts through invigorated adherence to an evolving baggage of Christian-era myths that demonized bears (e.g., Shepard & Sanders 1996, Brunner 2007, Pastoureau 2011).

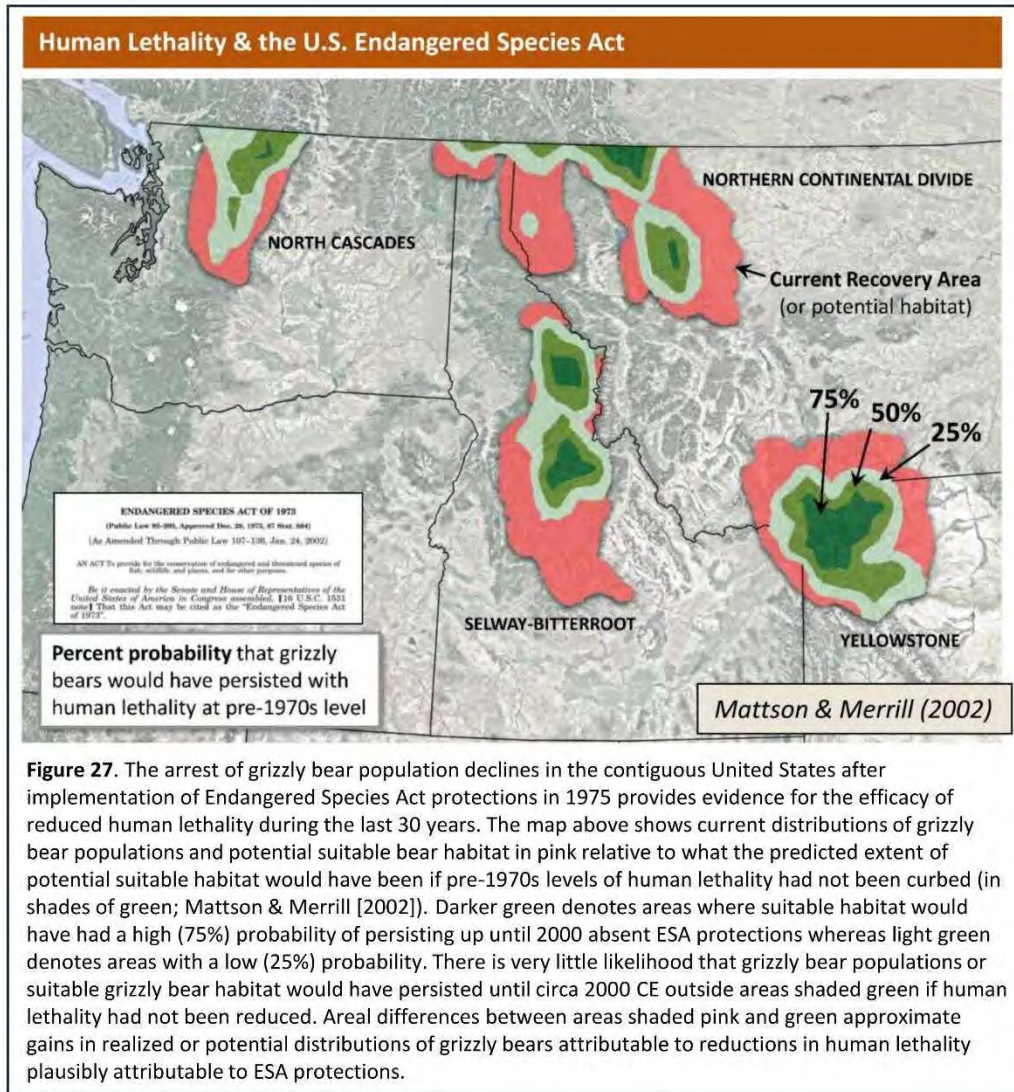
5.1.3. Intra-Regional Effects of Culture and Policy on Extirpations

Intra-regional variation in relations between human densities and bear persistence in the United States and China further highlight the extent to which material culture and formal policies have likely dictated the fates of bear populations largely through effects on human lethality. In the case of China, brown bears were more likely to be present at a given human density in areas that practiced intensive multi-cropping agriculture compared to areas where croplands were only periodically cultivated (i.e., left fallow), regardless of historical period (Figure 26a). Teng et al. (2020) speculated that this difference arose primarily from the greater control exercised by centralized authorities over peoples' behavior and movements in intensively cultivated areas – with plausible unintended benefits for local bear populations.

In the case of the United States, the dramatically lessened odds of grizzly bear persistence during 1920-1970 compared to 1850-1920 were plausibly driven by government-funded predator eradication programs that had peak impacts during 1910-1940 (Robinson 2005, Wise 2016), coincident with extirpation of grizzly bears from most of the West (Brown 1996; Peterson 2014; Mattson 2021c, 2022b). A dominant role for government policy in the United States is further implicated by the persistence of grizzly bears in areas roughly three-times the size otherwise predicted by human densities after federal Endangered Species Act protections were instituted in 1975 (Mattson & Merrill 2002, Figure 27).

All of this having been said, differences in behaviors of brown bears in Eurasia and grizzly bears in the United States – both *Ursus arctos* – could have played a role in the persistence of bear populations. Brown and grizzly bears exhibit remarkable behavioral plasticity entailing an equally remarkable range of tolerance for humans resulting from lived experiences, matrilineally transmitted behaviors, as well as

transference of conspecific accommodation to people (Smith et al. 2005, Mattson 2021a). Increased tolerance could have had potentially complex effects on human-bear relations. Tolerant bears are more likely to use areas near human infrastructure and incur risks associated with more frequently encountering people (see Section 4.3.2), while at the same time mitigating those risks by being less aggressive during encounters, thus lessening real or subjective threat to involved people (Mattson 2019b, 2021a). Adding yet more complexity, bears in various regions could have collectively transmitted behaviors that simultaneously entailed avoiding human infrastructure as well as tolerating people, possibly including a genetic component (e.g., Benazzo et al. 2017).



Regardless of causal mechanisms, brown and grizzly bears living in more remote areas where there are fewer people are apparently more likely to respond aggressively to encounters, albeit contingent on triggering behaviors of involved people (Penteriani et al. 2016; Bombieri et al. 2019, 2023; Mattson 2019b: Section 1b; Kudrenko et al. 2020). If transmission of less aggression and/or greater tolerance through genetic or behavioral lineages plays a role, this still begs the question of why results could be so geographically variable. Axiomatically, trait selection through genetic or any other mechanisms can only happen if some bears sympatric with humans survive long enough to transmit adaptive behaviors. In the

case of European and Chinese brown bears, this could have plausibly happened in sublethal environments typified by sustained culling of more aggressive or less fearful bears – prospectively over a period of centuries or even millennia (cf., Berger et al. 2001, Åbjörnsson et al. 2004, Chevin et al. 2010). By contrast, in the United States a lethal onslaught of well-armed Europeans intent on killing every grizzly bear they encountered would not have allowed for selective transmission of any adaptive traits (e.g., Brown 1996; Storer & Tevis 1996; Mattson 2021c, 2022b).

5.2. Effects of Local Culture on Malicious Killing

By first principles, people who set out well-armed and intent on killing a bear are the most lethal humans a bear will likely encounter (Sections 2.1 and 2.3). In developed countries with well-codified wildlife management regimes, these sorts of people can be categorized by those who pursue bears under legal versus illegal auspices – the former categorized as hunters and the latter loosely categorized as poachers, of which a subset could be considered malicious killers. Licensed bear hunting is, by definition, legally sanctioned and almost invariably done in a regulated way. Illegal killing is not. This distinction does not cleanly align with the motivations of involved people, but it does crudely differentiate those who could be considered law-abiding – at least in the pursuit of bears – from those who are willingly engage in a criminal activity, at least from the perspective of formal jurisprudence (e.g., Muth & Bowe 1998). The unprovoked killing of bears in putative defense of life or property (DLP) occupies an ill-defined middle ground. Regardless of legalistic definitions, a portion of bear killings claimed to be DLP are likely attributable to predisposed people taking advantage of an encounter to manifest prior lethal intent. On a related note, humans will axiomatically be more lethal to bears wherever local cultures and communities condone intolerance and related extra-legal killing of bears.

5.2.1. Local Culture, Tolerance, and Illegal Killing

There is ample evidence that local culture has a powerful configurative effect on not only intolerance but also illegal killing of carnivores. Much of this effect arises from strong relations between peoples' attitudes towards large carnivores and generalized views of proper relations between humans and the natural world (e.g., Kaltenborn et al. 1998, Bjerke & Kaltenborn 1999, Kaltenborn & Bjerke 2002, Mattson & Ruther 2012, Schroeder et al. 2022). Not surprisingly, these baseline attitudes are additionally affected by the extent to which people fear large carnivores (e.g., Johansson & Karlsson 2011, Johansson et al. 2012, Slagle et al. 2012), perceive costs arising from their presence (e.g., Naughton-Treves et al. 2003, Zajac et al. 2012, Kaltenborn et al. 2013, Schroeder et al. 2018), and distrust government authorities (Højberg et al. 2017). All these proclivities tend to be consolidated and sustained by shared narratives (e.g., Byrd 2002, Mattson et al. 2006, Lute & Gore 2014, Lute et al. 2014), further amplified by community norms and resentments (Lüchtrath & Schraml 2015, Von Essen et al. 2018, Peterson et al. 2019).

Much of the anger, conflict, and distrust surrounding management of large carnivores—including grizzly bears—furthermore arises from people feeling victimized by decision-making arrangements that marginalize them. People who feel they are being treated unjustly often act out of a place of resentment that can easily translate into illegally killing animals identified with perceived injustices, notably brown and grizzly bears (e.g., Pohja-Mykrä & Kurki 2014, Lüchtrath & Schraml 2015, Jacobsen & Linnell 2016, Højberg et al. 2017, Pohja-Mykrä 2016, Von Essen et al. 2018) – often in the context rural communities with strong hunting traditions that condone poaching (Eliason 1999, Gangass et al. 2013). As Primm

(2000) observed, much of the resentment arising from unequitable power arrangements gets symbolically displaced onto both the involved animals (e.g., brown and grizzly bears) as well as people with values hostile to rural hunting traditions – many of whom live in urban areas.

5.2.2. Evidence from the U.S. Northern Rockies

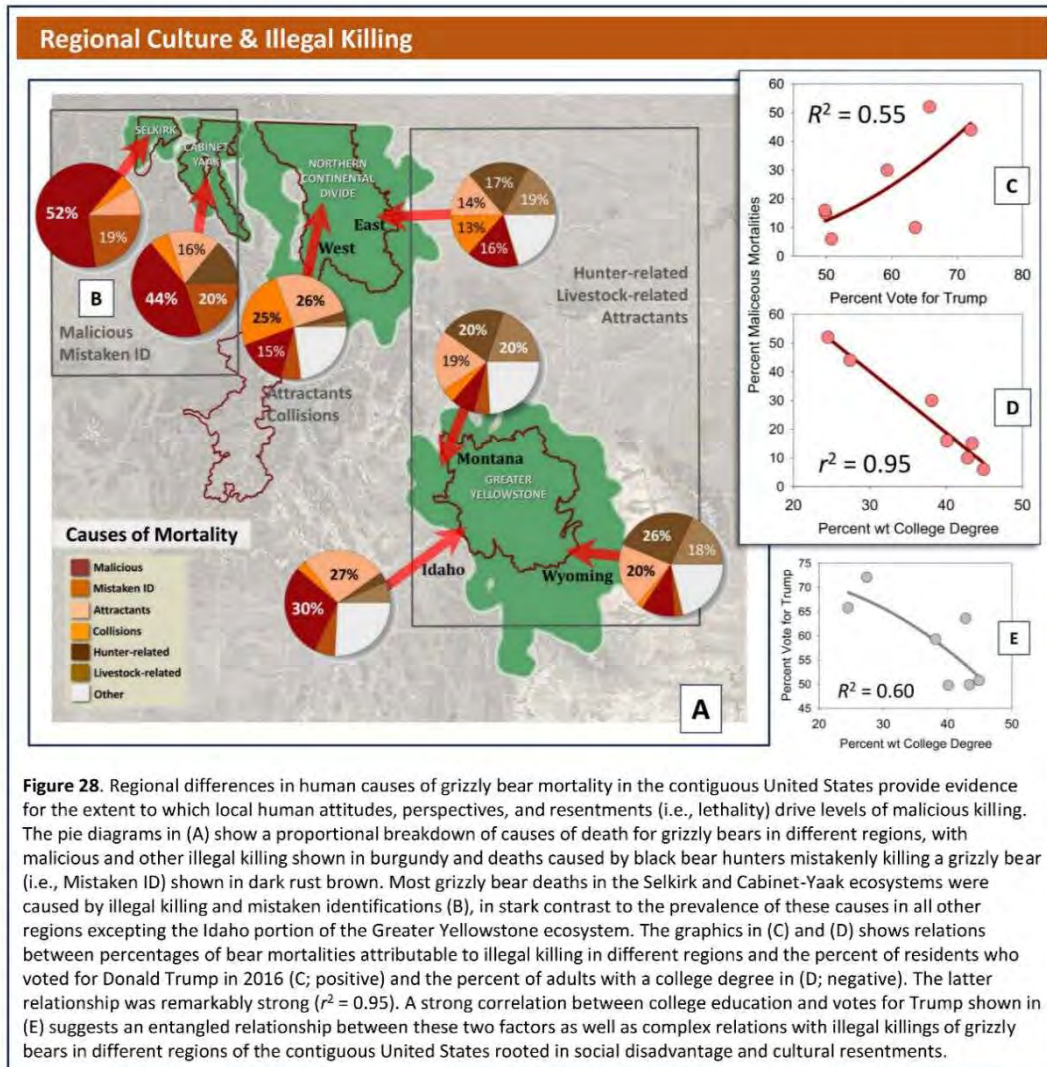


Figure 28. Regional differences in human causes of grizzly bear mortality in the contiguous United States provide evidence for the extent to which local human attitudes, perspectives, and resentments (i.e., lethality) drive levels of malicious killing. The pie diagrams in (A) show a proportional breakdown of causes of death for grizzly bears in different regions, with malicious and other illegal killing shown in burgundy and deaths caused by black bear hunters mistakenly killing a grizzly bear (i.e., Mistaken ID) shown in dark rust brown. Most grizzly bear deaths in the Selkirk and Cabinet-Yaak ecosystems were caused by illegal killing and mistaken identifications (B), in stark contrast to the prevalence of these causes in all other regions excepting the Idaho portion of the Greater Yellowstone ecosystem. The graphics in (C) and (D) shows relations between percentages of bear mortalities attributable to illegal killing in different regions and the percent of residents who voted for Donald Trump in 2016 (C; positive) and the percent of adults with a college degree in (D; negative). The latter relationship was remarkably strong ($r^2 = 0.95$). A strong correlation between college education and votes for Trump shown in (E) suggests an entangled relationship between these two factors as well as complex relations with illegal killings of grizzly bears in different regions of the contiguous United States rooted in social disadvantage and cultural resentments.

Given the well-established link between local culture and illegal killing, it is reasonable to expect that this connection would manifest as regional variation in the reasons why grizzly bears are killed by people, especially where legal bear hunting does not swamp all other causes. More specifically, cultures configured by poverty, resentment of central authority, rurality, and a hunting tradition are likely to spawn more illegal killing (Section 5.2.1; also, e.g., Forsyth et al. 1998, Rytterstedt 2016, Serenari & Peterson 2016, Skogan & Krange 2020). Notably, rural resentments in the United States have often focused on management of threatened species such as the grizzly bear under auspices of the federal Endangered Species Act (e.g., Nie 2003, Diamond 2021, Dunn 2023).

Of relevance to culturally informed human lethality, the pie diagrams in Figure 28a show the proportional break-down for causes for grizzly bear deaths in various ecosystems of the contiguous

United States. The burgundy and rust-brown shaded fractions are of particular interest. The latter accounts for instances where hunters in pursuit of black bears (*Ursus americanus*) claim to have mistakenly killed a grizzly bear; the former accounts for instances where there was not only a formal determination of poaching or malicious killing, but also enough circumstantial evidence to suspect some degree of malicious intent (see the introduction to Section 5.2 above).

The historical dominance of poaching, malicious killing, and mistaken identifications in the Selkirk and Cabinet-Yaak ecosystems of northwestern Montana and northern Idaho (71% and 64%, respectively; Figure 28b) differentiate these regions from all others in the contiguous U.S. where most bear deaths have been attributable to encounters with ungulate (e.g., elk and deer) hunters, conflicts over human refuse, conflicts over depredations on livestock, and collisions with vehicles. Not surprisingly, grizzly bear populations in the Selkirk and Cabinet-Yaak ecosystems have fared poorly compared to other bear populations in the contiguous U.S., partly because of inadequate habitat security (see Section 4.2.3 and Figure 9), but also plausibly because of greater intolerance among local human residents manifest in an epidemic of poaching and malicious killing – and despite the fact that human densities in the Cabinet-Yaak ecosystem, in particular, are roughly half those in other ecosystems (1.8 humans/km² versus a median 3.7/km² elsewhere).

There is, in fact, evidence supporting the proposition that the prevalence of poaching and malicious killing in the Selkirk and Cabinet-Yaak ecosystems has been rooted in local cultural norms and resentments. The x-y diagrams in Figures 28c and 28d show relations between levels of malicious (i.e., illegal) killing of grizzly bears in the various regions identified in Figure 28a and percent of the almost wholly white voting populace that chose Donald Trump during the 2016 presidential elections (Figure 28c; a positive relation) and percent of adults with a college degree (Figure 28d; a negative relation). Donald Trump very prominently distilled the grievances of predominantly white middle class voters who felt increasingly disenfranchised by social and cultural trends (e.g., Hooghe & Dassonneville 2018, Morgan & Lee 2018, Smith & Hanley 2018). Levels of education have similarly been shown to affect economic performance and social status, both of which can also fuel generalized resentments and resulting displacement onto political processes (e.g., Kinder & Kiewiet 1979, Hout 2012, Fording & Schram 2017). Remarkably, prevalence of college degrees explained almost all variation in regional variation of illegal bear killings and was also strongly related to levels of support for Trump (Figure 28e).

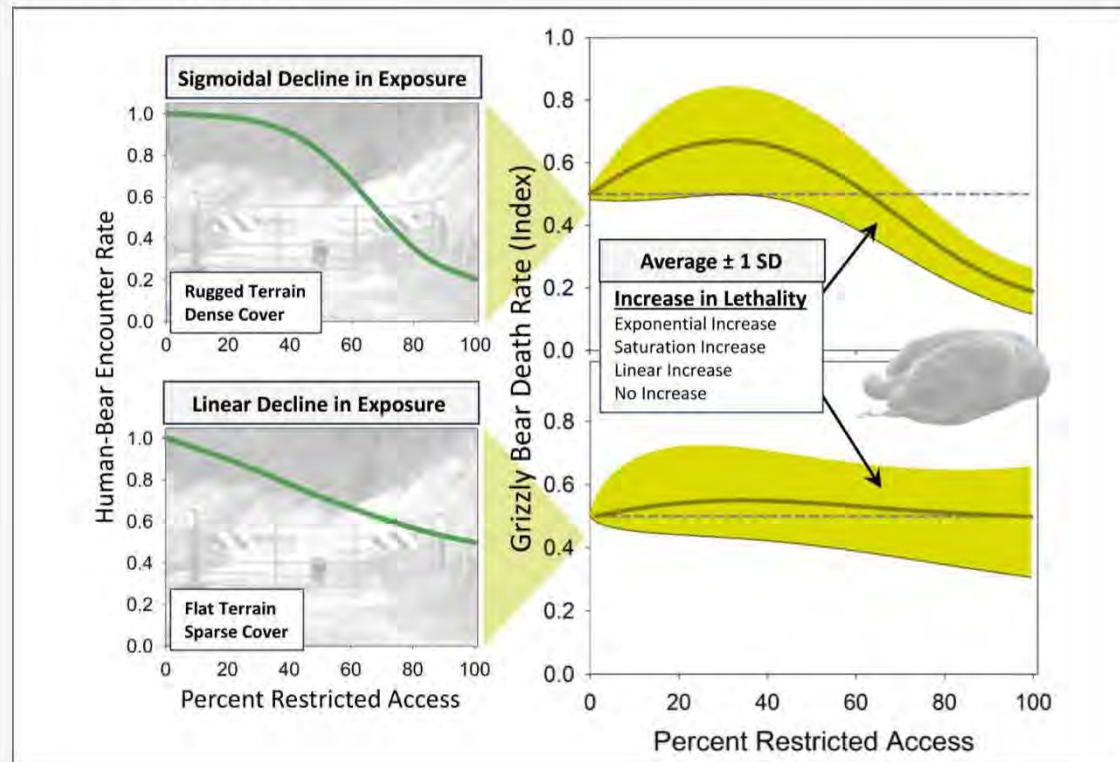
This kind of evidence provides support for the hypothesis that poaching and other illegal killing of large carnivores – including brown and grizzly bears – is often driven by displacement of anxieties and resentments onto animals that symbolize those perpetrating perceived injustices (Section 5.2.1). Of specific relevance to the featured Selkirk and Cabinet-Yaak ecosystems, these areas have comparatively little bear habitat sequestered from roads and other human facilities compared to other areas occupied by grizzly bears in the contiguous United States (Figure 9). This lack of remote habitat combined with a highly lethal local human populace has predictably contributed to the precarious plight of grizzly bears in the Selkirk and Cabinet-Yaak ecosystems (Section 4.2.3). Ideally, standards for managing habitat security would be stringent in these ecosystems – yet are laxer than in other ecosystems. Even so, imposing more restrictions on human access and activities could plausibly fuel even greater resentment among regional residents along with more frequent poaching of grizzly bears – creating a conundrum for bear managers (see Box 5 for a more in-depth exploration of this issue).

Box 5: Access Restrictions vs Human Lethality vs Reduced Exposure of Bears to People

Enhancing grizzly bear habitat security by closing roads could have unintended adverse consequences if access restrictions cause increased intolerance of bears among local human residents (Mattson et al. 1996b). Under this scenario, increased resentment would translate into greater human lethality either through malicious killing (Figure 28) or interest in lethally resolving human-bear conflicts (Figure 3). This proposition has not been empirically tested simply because the needed data on human behavior have never been collected. Even so, changes in human lethality in response to access restrictions would likely vary with local cultures, societies, and economies (Section 5). Regardless, any change in levels of human-caused mortality caused by increased human lethality could logically be offset to some extent by closure of roads that reduced numbers of encounters between people and bears (Section 2.1).

The figures below integrate several plausible scenarios of exposure decline and human lethality increase as a function of access restrictions ranging from 0% to 100% of an area *ca.* 300-km² in size. Exposure is postulated to decrease either (A) sigmoidally to low levels or (B) linearly to moderate levels largely as a function of terrain ruggedness and vegetation cover (Naves et al. 2003, Nielsen et al. 2004, Parsons et al. 2021). Increases in human lethality could range from linear, to exponential, to saturation, to none at all. The average of these possible increases in lethality are shown in the figures below right relative to offsets introduced by (C) sigmoidal and (D) linear decreases in exposure integrated in an index of human-caused bear mortality set to equal 0.5 with baseline human lethality and 0% restricted access.

These simulations suggest that, barring a scenario with no increase in human lethality, levels of human-caused mortality would likely increase with modest restrictions on access but drop well below initial levels under circumstances where access is functionally limited on >60% of a home-range-sized area and off-road human mobility is impaired by rugged terrain and dense vegetation cover (C). Conversely, if off-road human mobility is facilitated by flat terrain and sparse cover, access restrictions may offer few benefits, again barring a scenario where human lethality remained constant (D). The main conclusion to be drawn from these simulations is that the nature and extent of human responses to road closures, either through exacerbations of resentments or functional decreases in access, will largely determine the efficacy of policies designed to enhance grizzly bear habitat security through closure of roads, but with closures needing to be more extensive in areas such as the Cabinet-Yaak Recovery Zone where local residents are more likely to react negatively to access restrictions (Mattson et al. 1996b; Figure 28).



5.3. Effects of Jurisdiction on Human Lethality

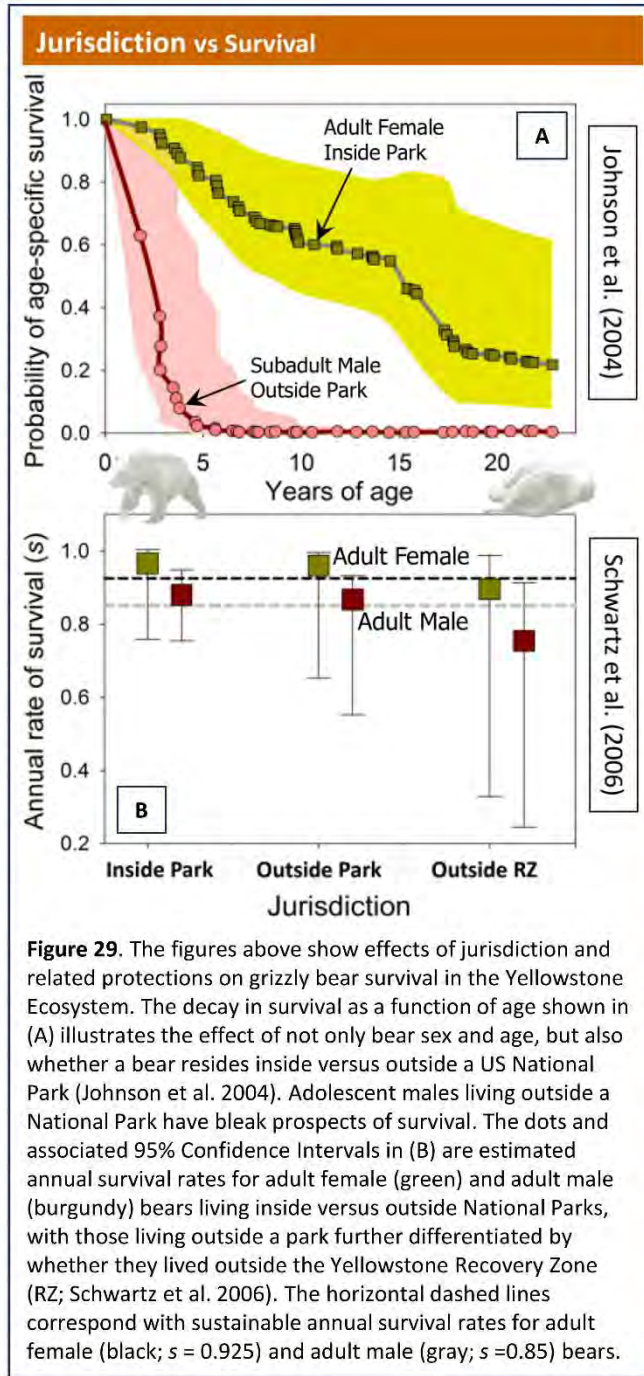
Governments have an almost universal prerogative to impose restrictions on peoples' behavior, often in the form of policies that govern different jurisdictions. Of relevance to brown and grizzly bear populations, the greatest differences in authoritative policy and protections arise from delineations of strictly protected areas such as National Parks or zones in which protection is otherwise prioritized, as with Recovery Areas for grizzly bear populations created under auspices of the U.S. Endangered Species Act. Protections geospatially often take the form of restrictions on possession and use of weapons, protection of habitat, and exclusion of conflict-engendering activities – typically accompanied by enhanced authorities that allows government officials to rigorously enforce these sorts of restrictions.

In the contiguous United States, jurisdictional delineations of greatest consequence for grizzly bear survival are National Parks, Recovery Areas, Wilderness Areas, and private versus public lands. Hunting of any sort is prohibited in National Parks, along with free disposition of firearms. Wilderness Areas exclude roads and associated motorized access. Recovery Areas come with restrictions on human activities judged harmful to grizzly bears as well as motorized access routes that potentially displace bears or exacerbate risk of human-caused mortality (U.S. Fish & Wildlife Service 2021; see Section 6). Very few restrictions intended to benefit grizzly bears apply to private lands.

Differences in policies governing disparate jurisdictions occupied by grizzly bears in the United States have obvious implications for bear survival. By first principles, people will be predictably much less lethal to bears in National Parks compared to in areas where big game hunting is allowed and firearms not regulated (e.g., Gunther et al. 2004, Haroldson et al. 2004, Mattson 2020). Similarly, encounters with people will likely be less lethal for grizzly bears where there are well-enforced restrictions on disposition of human foods that attract bears and engender conflicts, again, as in National Parks or on public lands where there are official policies mandating the secure storage of foods (e.g., Northern Continental Divide Ecosystem Flathead, Lewis & Clark, and Helena National Forests 2000, Kootenai National Forest 2011, and Custer-Gallatin National Forest 2014). For the same reason, encounters with people will likely end up more lethal for involved grizzly bears in areas where livestock are vulnerable to depredation (e.g., Gunther et al. 2004; Wilson et al. 2005, 2006; Northrup et al. 2012b; Well et al. 2019).

5.3.1. Jurisdictional Effects on Bear Survival in Greater Yellowstone

There is compelling evidence primarily from the Greater Yellowstone ecosystem of the contiguous United States confirming all these expectations. Figure 29 summarizes survival of grizzly bears in the Yellowstone ecosystem differentiated by sex and age class as well as time spent in different jurisdictions. Importantly, the age-specific survival curves in Figure 29a from Johnson et al. (2004) not only illustrate the comparatively bleak prospects of survival for adolescent male bears, but also the greater odds of survival for bears residing inside versus outside of Yellowstone National Park – all this controlling for exposure to roads and residences. Although the estimated annual survival rates for adult male and female grizzly bears in Figure 29b don't explicitly control for exposure of bears to human infrastructure (Schwartz et al. 2006), they do show a similar deterioration in survival rates with occupancy of jurisdictions where protections are less stringent, to the point of becoming unsustainable outside of the Greater Yellowstone Recovery Zone (or 'Area').



Schwartz et al. (2006, 2010) explicitly attribute reduced survival of grizzly bears outside of National Parks to the toll taken by conflicts with big game hunters pursuing elk (*Cervus canadensis*). Figure 30 lends weight to this speculative conclusion. Numbers of licensed elk hunters and tourists visiting Yellowstone Park are shown as grey lines in panels (B) and (A), respectively. Each prospectively serves as a crude proxy for levels of exposure by bears to these two human subpopulations. Total numbers of human-caused grizzly bear deaths in Yellowstone Park attributable to all human causes are shown as a burgundy line in panel (A); deaths attributable to conflicts with hunters are shown in burgundy in panel (B). The scale for numbers of bear deaths is the same in both panels, whereas the scale for numbers of tourists is more than an order of magnitude greater than the scale for numbers of licensed hunters.

Panel (C) more explicitly contrasts trends in Yellowstone Park with trends on public lands open to big game hunting. The ratio of hunters to National Park visitors is shown in gray, with an annual range of 0.004 to 0.016 (i.e., 0.4 to 1.6%). The ratio of hunter-caused to total human-caused deaths in the Park is shown in red, with an annual range of 3.0 to 30.0 (i.e., 300 to 3,000%). In other words, despite numbers of hunters afield being <1-2% numbers of park visitors, numbers of bears killed by hunters are 300-3,000% greater than the toll from all human causes in Yellowstone Park.

There are several phenomena evident not only in the contrasts but also the trends of Figure 30. For one, human-caused mortalities in Yellowstone Park stayed relatively constant despite a substantial increase in numbers of visitors, in stark contrast to the dramatic increase in hunter-caused bear deaths concurrent with an approximate halving in numbers of hunters – the former consistent with a substantially improved management regime in the park (Gunther et al. 2018), the latter evincing the effects of increased meat consumption by bears in response to environmental change (Mattson 2023). Perhaps even more consequential, bears killed by hunters as a proportion of hunter numbers have consistently

been several orders-of-magnitude greater than bears dying from all human causes as a proportion of visitors to Yellowstone Park. Park visitors are clearly much less lethal than big game hunters to grizzly bears. Although tourists are largely confined to human infrastructure in Yellowstone Park, they have 100s of well-documented yet benign encounters each year with grizzly bears that are also often tolerant of humans (Gunther & Wyman 2008, Gunther et al. 2018). By contrast, any explanation that invokes differences in the extent and nature of movements by elk hunters vis-à-vis human infrastructure cannot plausibly account for their approximately 150-3,000-fold greater comparative lethality to grizzly bears. Much of this difference almost certainly arises from the fact that hunters are armed, intent on using their weapons, inclined to be intolerant, and active in areas where there are attractants in the form of elk carrion (Mattson et al. 2020, 2022a; see Section 4.3.2).

5.3.2. Effects of Areas Designated for Grazing on Bear Survival

Finally, there is convincing evidence that the milieu of circumstances typifying areas grazed by livestock are also comparatively lethal to grizzly bears. Grazed areas in the United States consist not only of private lands, but also allotments on

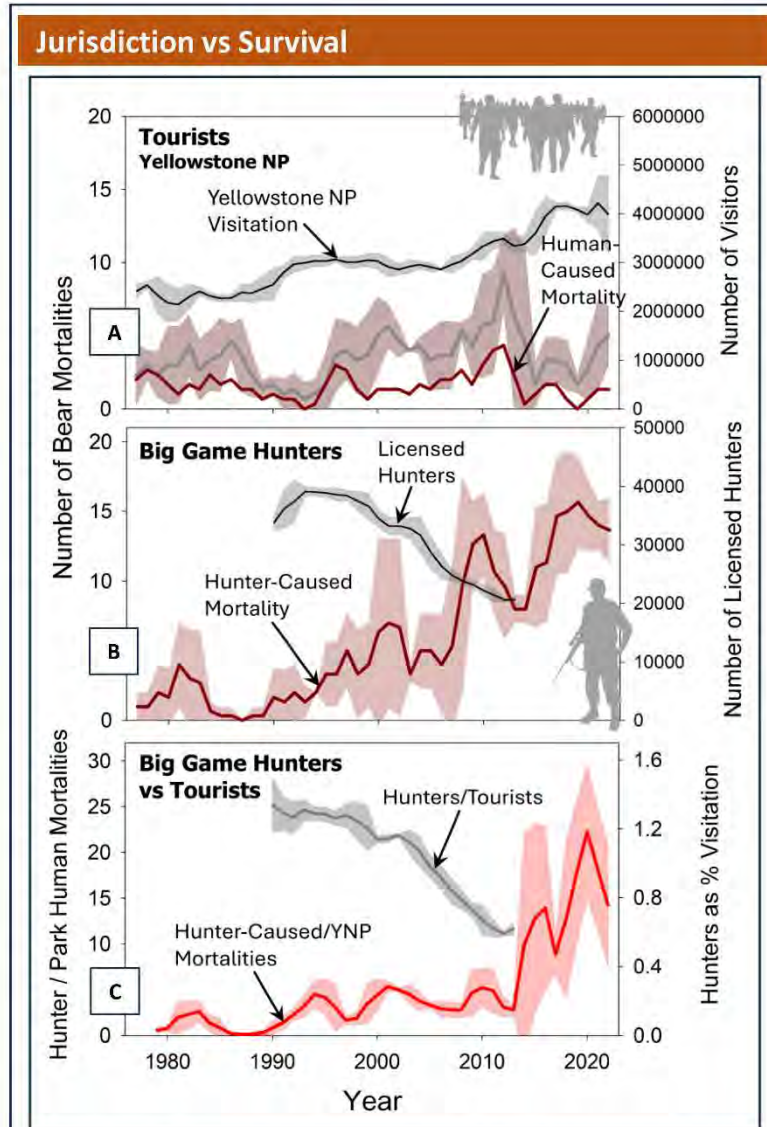


Figure 30. The figures above show numbers of grizzly bears annually dying in the Greater Yellowstone Ecosystem from human causes relative to comparative exposure to people, differentiating Yellowstone National Park (A) from areas open to big game hunting (B). In (A) total bear mortalities, including from natural causes, are shown in light burgundy whereas those solely from human causes are shown in dark red. Annual visitation to the Park is shown in gray. In (B), total numbers of bears killed during encounters with big game hunters are shown in burgundy. Total numbers of licensed hunters in the ecosystem during 1990-2013 are shown in gray. Figures (C) shows contrasts between Yellowstone Park and areas open to hunting, with the ratio of hunter-caused bears deaths to human-caused deaths in the Park shown as a red line and licensed hunters as a percent of park visitors shown in gray. Human-caused mortality in the Park remained constant despite increasing visitation, whereas hunter-caused mortality increased dramatically despite declining numbers of licensed hunters. Even more telling, hunter numbers have been only 0.5-1.5% the numbers of park visitors, whereas hunter-killed bears have escalated from 5-times to 25-times the number of bears dying from human causes in the Park.

public lands where livestock owners are permitted to graze their animals. In the Greater Yellowstone ecosystem, most allotments occupied by grizzly bears are grazed by cattle (Wells et al. 2019).

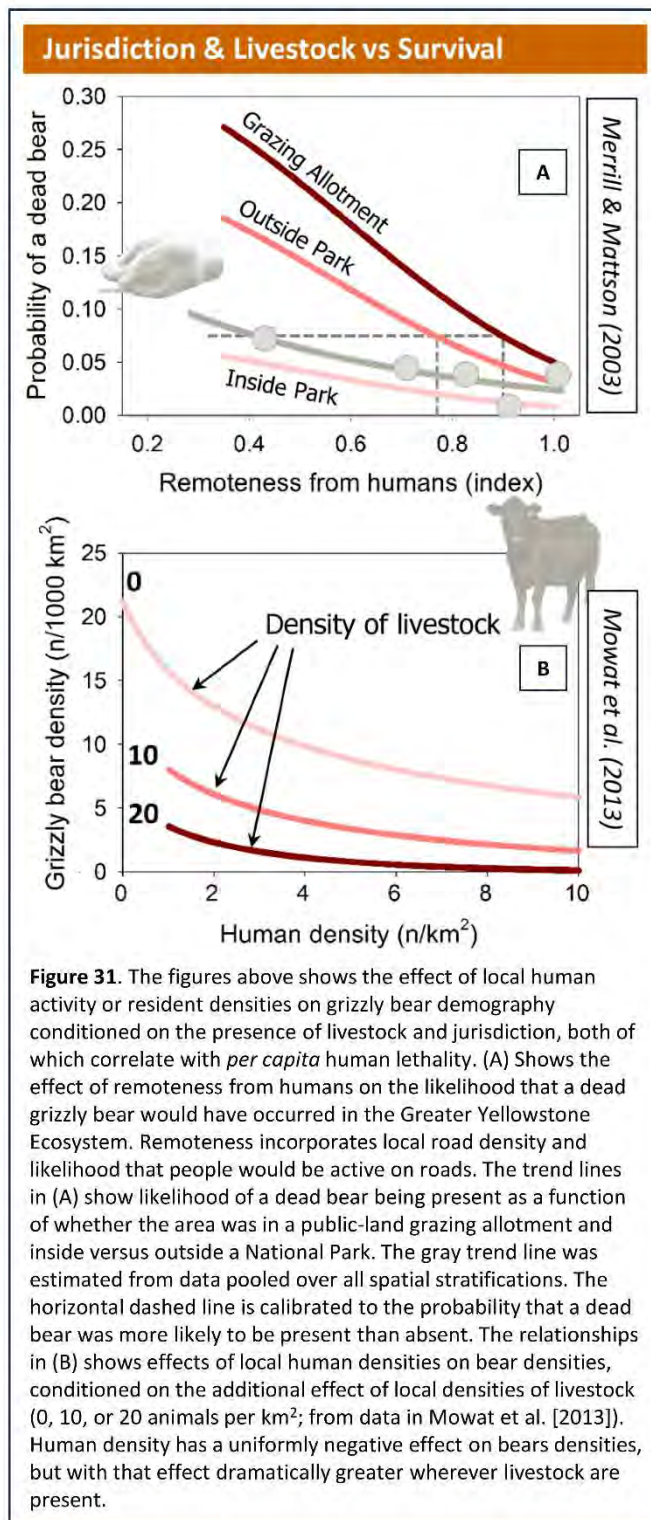


Figure 31 provides evidence of the deleterious effects of areas stocked with livestock at two different scales. In (A), the likelihood that a dead grizzly bears would have been present in an area is shown not only relative to remoteness from humans (see Section 4.2.3), but also as a function of whether the site was inside a National Park and, if outside, whether it occurred on a public land grazing allotment (Merrill & Mattson 2003). In (B), grizzly bear density is shown relative to livestock density controlling for the effects of human numbers (Mowat et al. 2013). In both relationships, the effects of livestock presence on grizzly bears are isolated by controlling for other factors, including proxies for exposure to people (i.e., remoteness and local human density).

The available evidence clearly suggests that areas designated for grazing livestock are hazardous for grizzly bears in the contiguous United States, regardless of whether these designations are attached to property rights or arise from policies governing management of public lands. There is also ample confirmatory evidence from other regions that the presence of livestock engenders conflict between humans and brown or grizzly bears, along with reprisals or preventative measures that are not only often lethal to involved bears but also to unimplicated conspecifics (e.g., Sagør et al. 1997, Kaczensky 1999, Ambarlı & Bilgin 2008, Can et al. 2014, Dai et al. 2020, Hipólito et al. 2020, Gervasi et al. 2021). Of more importance, the evidence presented in this section isolates the lethal effects of people involved in raising livestock from effects potentially associated with levels of exposure to humans or human infrastructure.

5.4. Human Lethality in Context

My intent here has not been to plumb the depths of how human lethality affects bears or all the factors that configure intolerance, lethal intent, and deadly behavior of people. Nor do I intend to diminish the effects of human infrastructure – the primary theme – on grizzly and brown bear demography and behavior. Rather, my emphasis is on the major role played by human attitudes, perspectives, and behaviors in arbitrating the effects of infrastructure and related exposure of bears to people. The evidence presented in this section makes clear that bears could survive numerous encounters with people if those involved were tolerant, unarmed, and otherwise benign – or, if not, curbed by substantial authoritative penalties such as those accompanying U.S. Endangered Species Act protections. By contrast, only a handful of encounters with intolerant well-armed people intent on meting out death could be the death knell for a local bear population, as evidenced by the history of grizzly bear extirpations in the United State during the late 1800s and early 1900s (Mattson & Merrill 2002).

There are substantial implications arising from the dual effects of encounter frequency and lethality. For one, if encounters with people are rarely deadly for involved bears, then not only will conservation of bear populations be compatible with numerous human-bear interactions, but also more extensive infrastructure that facilitates human access to bear habitat. By contrast, if encounters are deadly, survival of bear populations will depend on minimizing human-bear interactions along with any features that facilitate access to areas occupied by bears – potentially amounting to 10s of thousands of square kilometers (Section 4.2.3, Box 2).

However, even in best case scenarios, the basic life-history of brown and grizzly bears necessitates that conservation of bear populations will depend on preserving extensive areas comparatively free of humans and human impacts (Mattson 1997, Hendee & Mattson 2009). Brown and grizzly bears are, along with megaherbivores, classic examples of species that have irreducible impacts on people they share space with, including hazards to domestic animals, damage to crops, and threats to human safety. Access to bear habitat provided by roads, trails, and other human infrastructure will thus always need to be limited to some extent. The question is, how by much (Mattson et al. 1996a)?

The evidence presented in this section makes clear that the answer to this question will be dictated by local human culture, traditions, and material resources. Of relevance to the United States, our cultural identification with guns and violence (Slotkin [1998a], [1998b], [2000]; but see Haag [2016]), the domination of management by hunters who instrumentalize animals (Mattson 2022a), and the displacement of grievances among conservative less-well-educated residents onto management of carnivores (Section 5.2.2) unfortunately conspire to dictate an enduring need to preserve extensive *de facto* wilderness conditions as a prerequisite for conservation of viable grizzly bear populations.

This consideration is a critically important contingency for extrapolating research regarding the effects of human infrastructure on bear demography and behavior from any given study area to other areas typified by different environmental conditions and human cultural norms. More to the point, if humans in areas subject to extrapolation are more lethal to grizzly or brown bears than humans in source study areas, interpretation and application would need to err on the side of conservatism if intended protections are to be achieved. Of relevance, this important contingency has been neglected altogether or given short shrift in previous summaries of how human infrastructure affects bears (e.g., Penteriani et al. 2018, Proctor et al. 2019, Morales-González et al. 2020).

6. Effects on Bear Behavior

Section 4 features the effects of human infrastructure – roads and residences – on brown and grizzly bear demography. These effects on the fates of bears and bear populations cannot be divorced from levels of human activity (Section 4.2.3), adjacent habitat features (Sections 4.2.4, 4.3.4, and 4.3.5), bear behaviors (4.3), and attitudes and behaviors of people (Section 5). As important, the extent to which individual bears respond to human features – or bear populations under-utilize areas impacted by human infrastructure – is entangled with the differential survival and recruitment of bears exhibiting different tolerances for people (Section 1.1, Figure 1), with shorter-term effects playing out during an individual bear’s lifetime (Mattson 2021a) and longer-term effects playing out over decades or even millennia (Sections 5.1 and 5.2.1; Mattson et al. 1996a).

The phenomena encompassed by bear behavior can logically be differentiated by those that typify individual bears and those arising from cumulative spatial patterns manifest at the scale of bear populations. Individuals exhibit attraction, repulsion, or indifference to people and the built environment (Mattson 2021a). Populations exhibit geospatial differences in distribution vis-à-vis human infrastructure ranging from comparative underuse to comparative overuse. This distinction between individual responses and aggregate population patterns is critical to interpreting varied and sometimes conflicting research results because individuals can exhibit behavioral responses at variance with patterns exhibited by populations. Changes in diel behavior can also mask aggregate human impacts if bears are incurring costs by becoming more nocturnal while still using areas near people (Section 4.3.1).

Notably, these sorts of contradictions can arise when people provide a security shield (Section 4.3.3) or are spatially associated with abundant natural and anthropogenic foods that attract human-tolerant bears (Section 4.3.4) simultaneous with bears at an aggregate population level underusing human-impacted environs. If human-tolerant bears outnumber human-intolerant bears there may be no apparent underuse of areas near human infrastructure, especially if recruitment of human-tolerant bears exceeds that of intolerant bears, exemplifying the distinction between reactions of individuals and patterns generated over multiple lifetimes by demographic processes. Situations can become yet more complicated if changes in the environment (e.g., spatially explicit losses of productive habitat), human lethality (e.g., the institution of a bear hunt), or bear behavior (e.g., increased tolerance of humans) are driving transient demographic dynamics.

Finally, all these distinctions are intrinsically fuzzy because of the extent to which individual bear behaviors drive demography and finer-scale aggregate distributions, and finer-scale distributions vis-à-vis human infrastructure grade into demographic proxies such as regional presence or absence that serve as a basis for reckoning the distributions of populations or processes such as extirpation. The practical upshot of these fuzzy boundaries is that specific research results can prospectively be covered as part of the behavioral focus of this Section or the demographic focus of Sections 4 and 5 without betraying any sanctified classification.

The following subsections synthesize literature that addresses various dimensions of this complexity, confounded by the fact that different researchers and different study areas have focused on different combinations of factors, with none comprehensively addressing them all. Section 6.1 summarizes documented population level responses of brown and grizzly bears to human infrastructure without distinguishing sex or age class, season, bear-specific behaviors, time of day, or nature of adjacent habitat.

Section 6.2 also focuses on population level patterns, but with the added distinction of seasonal differences and effects of sex-age class, habitat productivity, and whether the infrastructure is a road or townsite. Section 6.3 introduces potentially mitigating behavioral responses of bears reckoned in terms of activity levels or movements, further parsed by time of day, and nearness or density of roads and townsites. Section 6.4 addresses effects of the physical environment, including the presence of physical obstructions and distributions of productive habitat. Section 6.5 summarizes the effects of road designs, roadside environments, and levels of human activity on the rates at which brown and grizzly bears cross roads and highways, absent a comprehensive infrastructure built to facilitate passage. All this allows for a concluding summary in Section 6.6 that not only reconciles the diversity of summarized patterns, but also emphasizes the derivative highly contingent application and extrapolation of research results to different management situations and the related burden placed on managers to give these contingencies due consideration.

6.1. Population-Level Responses to Roads and Townsites

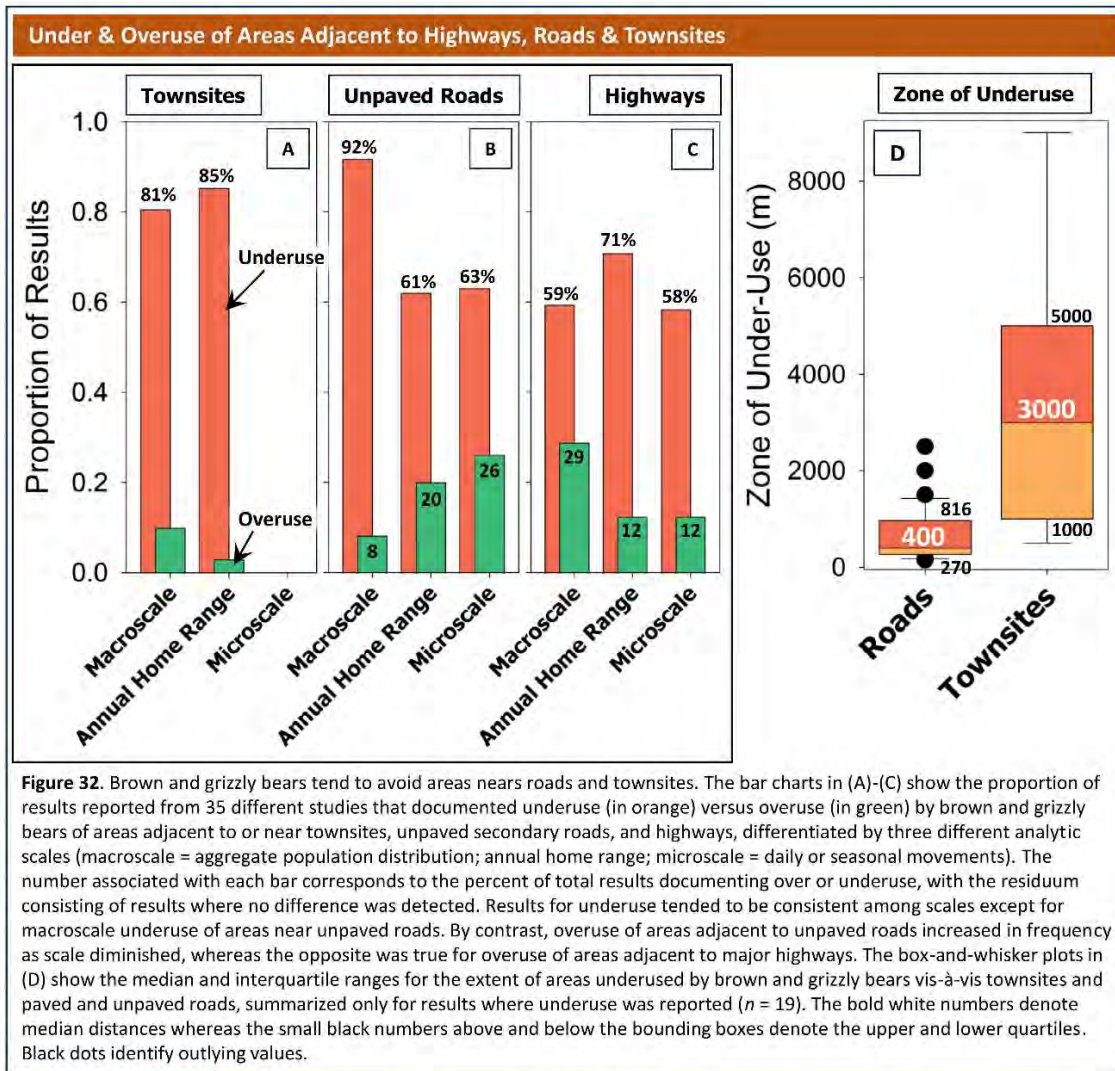
As might be expected by the numerous contingencies described in the introduction above, researchers in different study areas have documented a wide range of aggregate responses by grizzly and brown bears to areas near highways, roads, and townsites, including overuse, underuse, and no apparent response. Some of these differences conceivably arise from the fact that researchers have investigated aggregate responses of bears at different scales (e.g., Curveira-Santos et al. [2024] for black bears), including seasonal and daily movements (i.e., microscale), annual home ranges, and total population distributions (i.e., macroscale), but most differences are likely attributable to variation among individual bears and differences in study area characteristics that are previewed in the following subsections and more thoroughly examined in Sections 6.2-6.5.

6.1.1. Extent of Underuse Near Roads and Townsites

Regardless of the scale or human feature, brown and grizzly bears have more often been found to under rather than overuse areas adjacent to roads and townsites (Figure 32a-32c). Perhaps most definitively, researchers documented grizzly and brown bears underusing areas near townsites 8- to 30-time more often than they found bears overusing these areas, with roughly 80-85% of all results showing underuse ($n = 11$ study areas). Less dramatically, bears underused areas near highways 4.7-5.7-times more often (58-71% of all results; $n = 10$ study areas)² than they overused these areas, and similarly underused

² Several individual studies reported patterns of under and overuse vis-à-vis human facilities for different seasons, diel periods, bear sex-age-reproductive classes, individual bears, and scales. For analysis purposes, I first differentiated within-study results by whether they registered underuse, overuse, or neutral use of areas adjacent to human infrastructure, differentiating scales (macro, home range, and micro) and types of human structures (highways, secondary roads, and townsites). As a means of giving equal leverage to individual studies, I then weighted multiple study-specific results to sum to one for each reported scale and infrastructure type. I summed these weighted results for each scale and structure type to calculate support for underuse, overuse, or neutral use aggregated across all studies. Studies used for this analysis included Tracy (1977), Elgmork (1978), Harding & Nagy (1980), Mysterud (1983), Zager et al. (1983), Singer & Beattie (1986), Mattson et al. (1987), McLellan & Shackleton (1988), Aune & Kasworm (1989), Kasworm & Manley (1990), Reinhart & Mattson (1990), Mace et al. (1996, 1999), Clevenger et al. (1997), Green et al. (1997), Mattson & Reinhart (1997), Wakkinen & Kasworm (1997), Gibeau (2000), Kobler & Adamic (2000), Yost & Wright (2001), Gibeau et al. (2002), Wielgus et al. (2002), Chruszcz et al. (2003), Mueller et al. (2004), Waller & Servheen (2005), Suring et al. (2006), Ciarniello et al. (2007), Roever et al. (2008a, 2010), Chetkiewicz & Boyce (2009), Graham et al. (2010), Martin et al. (2010), Graves et al. (2011),

areas adjacent to secondary or industrial roads 2.4-3-times more often (62-63% of all results; $n = 20$ study areas) – all at the scale of annual home range and seasonal or daily movements. At the scale of populations (i.e., macroscale), grizzly and brown bears were comparatively less likely to underuse areas near highways and primary roads (by only 2-fold; 59% of total results), while at the same time far more likely to underuse areas near secondary roads (by 11-fold; 92% of all results), suggesting a powerful adverse role of people using secondary roads on demographic processes affecting geospatial distributions of bear populations (see Section 4.2).



This explanation comports with the increasing comparative frequency of results showing overuse of areas near secondary or unpaved roads at progressively finer scales, opposite the trend for overuse of areas near more heavily trafficked high-speed highways (Figure 32b and 32c). These scale-dependent trends can plausibly be interpreted as evidence of differences in comparative lethality of people using

Northrup et al. (2012), Frackowiak et al. (2014), McKay et al. (2014), Cristescu et al. (2016), Ziołkowska et al. (2016), Ladle et al. (2018), Oberosler et al. (2020), Ahmadipari et al. (2021), Hernando et al. (2021), Clarke (2022), Gonzalez-Bernardo et al. (2022), Sells et al. (2022), Whittington et al. (2022), and Proctor et al. (2023).

highways versus secondary unpaved roads. People traveling at higher speeds and intent on reaching a destination – as on a highway – likely pay little attention to surrounding wildlife and landscapes. The opposite is plausibly true of people traveling more slowly and with different intentions on backroads, of which a higher proportion are likely to be armed hunters and poachers motivated to kill bears (see Section 5.3.1). All else equal, differences in lethality between people on highways and secondary roads conceivably lead to less recruitment of tolerant bears to the vicinity of backroads versus highways, with resulting underuse of the former more often evident than underuse of the latter, especially at the scale of population distributions (Section 1.1., Figure 1).

The greater propensity of brown and grizzly bear populations to underuse areas near or adjacent to human facilities does not address the spatial extent of these effects, although the greater prevalence of documented underuse around townsites and secondary roads at broader (i.e., population and home range) scales suggests that impacted areas would encompass a larger fraction of any given landscape around these features compared to impacted areas along highways – an expectation that is broadly consistent with the extent of underused areas (i.e., zones of impact; ZOI) around undifferentiated roads and townsites reported for 19 study areas where underuse had been documented (i.e., excluding results with no apparent underuse).

As might be expected by study area-specific variation in whether bears underused areas adjacent to infrastructure, the spatial extent of impacts varied widely among study areas, with underuse concentrated in buffers typically 400-m wide adjacent to roads and highways, with the interquartile range of this impacted area ranging from 270 to 816 m (Figure 32d). These figures for ZOIs associated with

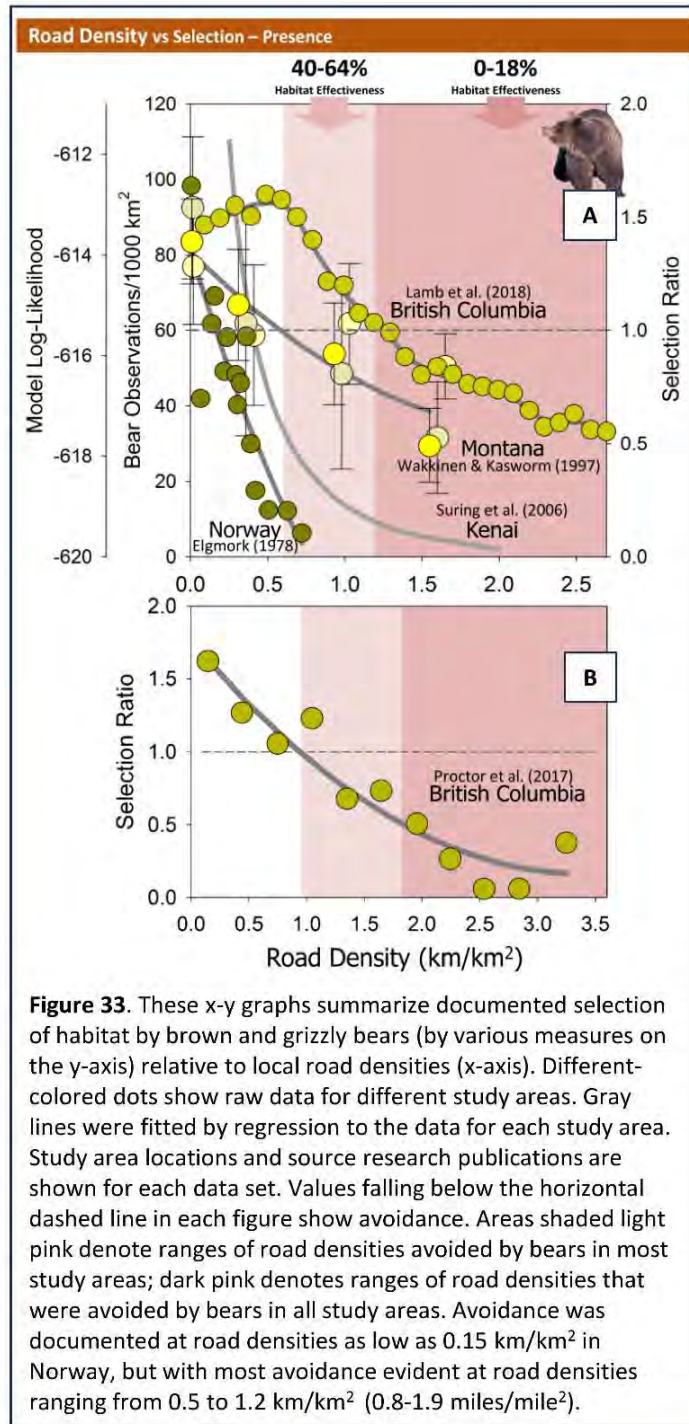


Figure 33. These x-y graphs summarize documented selection of habitat by brown and grizzly bears (by various measures on the y-axis) relative to local road densities (x-axis). Different-colored dots show raw data for different study areas. Gray lines were fitted by regression to the data for each study area. Study area locations and source research publications are shown for each data set. Values falling below the horizontal dashed line in each figure show avoidance. Areas shaded light pink denote ranges of road densities avoided by bears in most study areas; dark pink denotes ranges of road densities that were avoided by bears in all study areas. Avoidance was documented at road densities as low as 0.15 km/km^2 in Norway, but with most avoidance evident at road densities ranging from 0.5 to 1.2 km/km^2 (0.8-1.9 miles/mile²).

townsites were a heftier median 3,000 m and interquartile range 1,000-5,000 m, consistent with the near universal underuse of areas near townsites by brown and grizzly bears wherever this effect was studied (Figure 32a).

6.1.2. Underuse Relative to Road Density

The extent to which bears underuse areas adjacent to roads is useful for judging the adequacy of security at various distance intervals. However, this distance-based approach does not explicitly address how patterns of underuse relate to *densities* of secondary roads, which is often a focus of attention for land managers (Sections 4.2.2 and 4.2.3) and prospectively at variance with calculations of putatively secure habitat based on categorical distance thresholds alone (Proctor et al. 2019).

The research results summarized in Sections 6.1.1 and 6.1.2 clearly show that distance-based reckonings of spatial use by brown and grizzly bears vis-à-vis roads and townsites vary substantially from one study area to another. Not surprisingly, this also holds true for results focused on effects of road density, but with the important proviso that levels of bear activity more consistently show a negative monotonic trend. Unfortunately, interpretation of this variability in responses to road density is confounded by inter-study differences in how geospatial use was measured, including univariate selection ratios, observations of bear sign along transects, and parsimony of competing models.

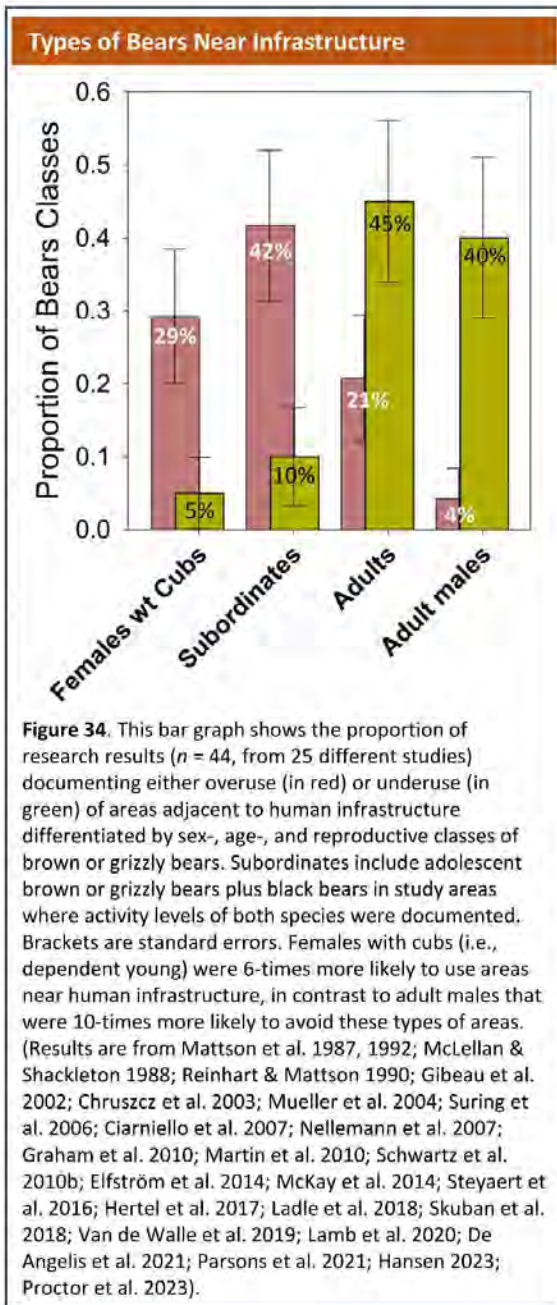
Figure 33 illustrates not only the uniformly negative response of brown and grizzly bears to road density, but also the considerable variability among studies in both research methods and magnitude of response. Of the five illustrative studies, three used selection ratios (observed use/expected null use; Wakkinen & Kasworm 1997, Suring et al. 2006, Proctor et al. 2017), one used observed bear sign along transects (Elgmork 1978), and one used statistical support for models that employed different road density cutpoints to explain bear densities (Lamb et al. 2018). Thresholds between overuse and underuse varied from approximately 0.5 to 1.0 km/km² for the illustrative studies that used selection ratios (Figures 33a and 33b), which trended higher than the range of 0.1-0.8 km/km² estimated using model support, and far higher than the 0.2 km/km² estimated from the single transect-based study (Figure 33a).

For all six studies reporting a threshold³, the median road density at which comparative overuse of an area by bears transitioned to comparative underuse was 0.4 km/km², with an interquartile range of 0.3-0.6 km/km² (i.e., median = 0.64 miles/mile²; range = 0.55-0.96 miles/mile²). This median threshold is an ecologically meaningful 33% less than the 0.6 km/km² (c. 1 mile/mile²) threshold recommended by Proctor et al. (2019). Perhaps even more important, impacts on aggregate habitat use by grizzly bears consistently declined as road densities declined, with optimal conditions for bears occurring where there was no motorized access – much like documented effects of road density on grizzly bear survival (Section 4.2.2).

Collectively, this information shows that most bears in most places at most times underuse areas near roads, townsites, and major recreational developments – presumably because most bears avoid people and human infrastructure (Mattson 2021a). However, given the evident variability in bear behaviors among study areas, habitat managers intent on minimizing adverse effects of human access on bear

³ Elgmork 1978, Mace et al. 1996, Wakkinen & Kasworm 1997, Suring et al. 2006, Proctor et al. 2017, Lamb et al. 2018.

behavior could, at one extreme, eliminate all roads or, less conservatively, require that road densities be $<0.3 \text{ km/km}^2$ ($0.55 \text{ miles/mile}^2$) and that secure habitat be defined as $>800\text{-m}$ distant from the nearest motorized access. By contrast, managers willing to propagate conditions creating unsustainable risk of human-caused mortality could allow average road densities in bear habitat to be as high as 0.6 km/km^2 (0.96 mile/mile^2) and define “secure” habitat as any area $>250\text{-m}$ distant from a road. The point here is that this range of management approaches would be more reflective of history, risk tolerance on the part of humans, and broader-scale environments rather than any irreducible or fixed bear behaviors.



Section 6.2. Differences Among Bears

The differences in aggregate responses of bears to people, roads, and residences summarized in Section 6.1 arise for numerous reasons complex enough to make any contextualized explanation inherently messy. The interdependency of relevant dynamics confounds the creation of clearcut demarcations among explanatory factors, which in turn creates fuzzy boundaries among the topics covered in the following sections. Even so, although all bear behaviors are ultimately individualistic, they nonetheless share commonalities that arise from dynamics associated with the shared exigencies of different sex and age classes, intraspecific interactions, distributions of productive habitats vis-à-vis human infrastructure, and learned strategies that reduce proximal exposure to people.

This section focuses on summarizing evidence for variation in responses of bears to human infrastructure that are predominantly intrinsic to bears rather than the environment, whether for idiopathic reasons, class-specific vulnerabilities and imperatives, or the amplifying effects of intraspecific interactions. Section 6.2.1 emphasizes the perhaps self-evident point that all bears are different – at least to some extent – and then begins to gather this disarray of individuality into coherent patterns related to differences among different sex-, age-, and reproductive classes of bears. Section 6.2.2 attempts to explain these differences in terms of class-specific patterns of learned behaviors as well as vulnerabilities associated with whether bears are young, old, male, female, or accompanied by dependent offspring.

Section 6.2.1. Differences Among Individuals and Bear Classes

Numerous studies have documented sometimes substantial variation in responses of individual bears to human infrastructure, including avoidance, attraction, and ambivalence – all during the same seasons and in the same locales (e.g., Wielgus et al. 2002, Cristescu et al. 2016a, Hertel et al. 2017, Ladle et al. 2019, Parsons et al. 2021, Sells et al. 2022). This diversity of behaviors among individuals is not only unsurprising (Mattson 2021a), but also a necessary precursor to the scale-dependent variability of *aggregate* responses by bears to human infrastructure evident in different studies and study areas (Section 6.1).

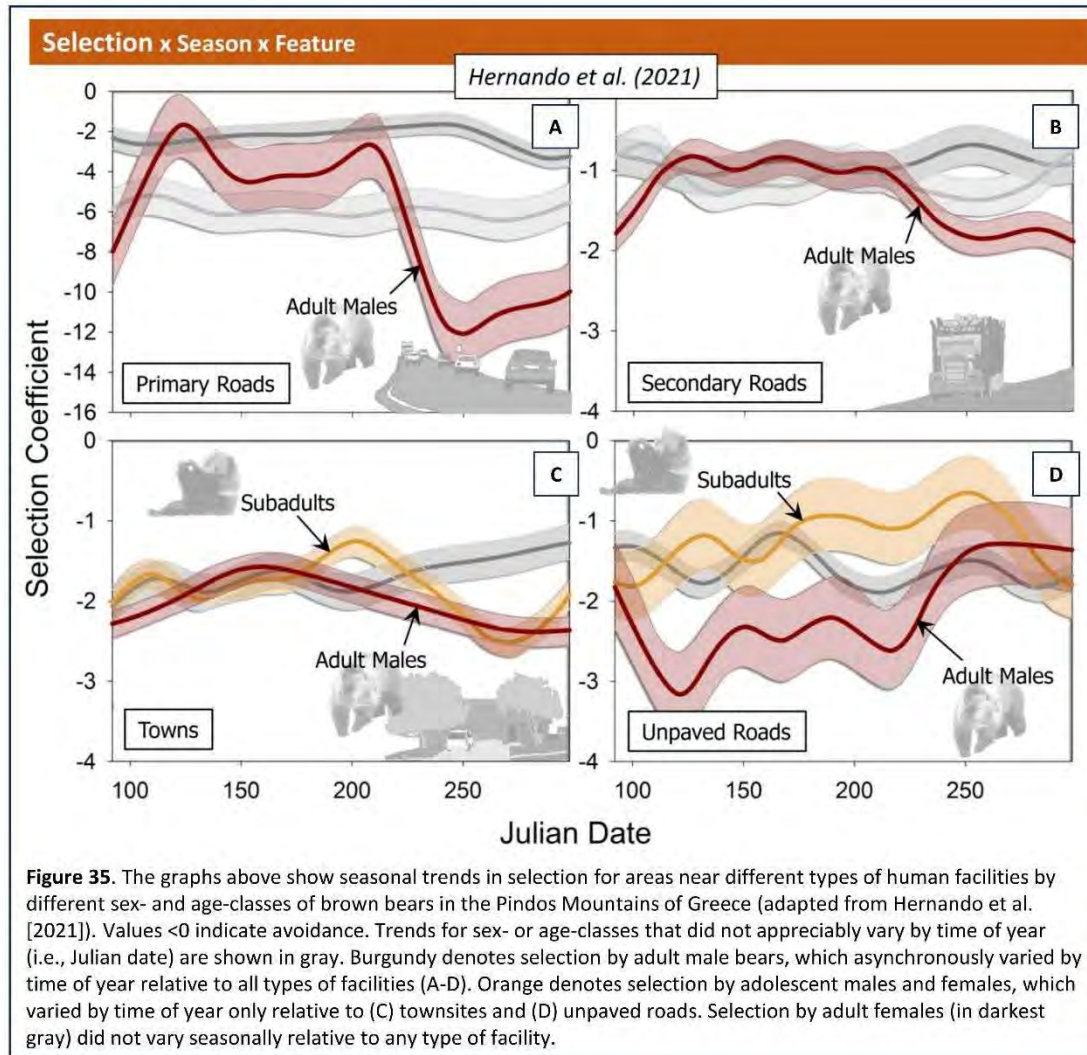
Even so, this individual-level variability is neither random nor inexplicable. Allowing for personality traits such as docility or agreeableness (Mattson 2021a), much of what bears do arises from shared modalities of physical size, susceptibility to conspecific aggression, care of vulnerable offspring, nutritional need, individual learning, and lineages of transmitted behavior. Of relevance to this section, males are typically larger than females of comparable age (e.g., Hilderbrand et al. 1999, Ferguson & McLoughlin 2000, McDonough & Christ 2012), able to dominate concentrated patches of high-quality food (e.g., Hornocker 1962, Craighead et al. 1995, Ben-David et al. 2004, Gende & Quinn 2004, Bourbonnais et al. 2014), and inclined to eat diets richer in animal fat and protein (e.g., Mattson 1997b, Jacoby et al. 1999, Hobson et al. 2000, Schwartz et al. 2014) – all of which reflects life strategies fundamentally different than those of female bears. These differences lead, in turn, to adult males not only often selecting distinctive foods and habitats, but also posing a threat to other bears (Mattson 2021a).

These patterns predictably lead to systematic differences in selection of habitats near people by bears of different sexes, ages, and reproductive states based on the vulnerability of dependent young and whether human environs provide access to food or refuge from threatening conspecifics (a human shield, Sections 4.3.2 and 4.3.3). Compared to other bears, adolescents and females with cubs-of-the-year are more likely to use areas adjacent to human infrastructure, especially if wary adult males are concentrated in the backcountry (Section 1.1, Figure 1) – which is precisely the pattern that emerges from the inevitable variation among 44 results of 25 studies where significant differences in use of areas near human infrastructure were observed for various sex, age, and reproductive classes. Females with dependent young and subordinate (e.g., adolescent) bears were 5.8- and 4.2-times more likely, respectively, to have exhibited overuse rather than underuse of areas near human infrastructure, in contrast to adult males and undifferentiated lone adults that were 9.6- and 2.2-times more likely to exhibit the opposite pattern (Figure 34; see caption for referenced studies). Not surprisingly, there is evidence that females selecting for areas avoided by predatory adult males more often have offspring that survive to adolescence (e.g., Steyaert et al. 2016, Van de Walle et al. 2019).

Section 6.2.2. Complexities of Inter-Class Variation in Avoidance

The results summarized in Section 6.2.1 are plausible evidence of the extent to which intraspecific interactions can potentially dominate choices made by bears regarding where and when to be active, especially in comparison to often benign interactions with people (Mattson 2021a). Use of human-impacted environs by bears plausibly arises from circumstances where lucid cues associated with accessing food and gaining security from conspecifics swamp opaque cues regarding longer-term risks of human-caused death (e.g., Bourbonnais et al. 2013). The culmination of risk that occurs when a human *does* kill a bear obviously debars learning that would otherwise lead the involved animal to avoid future

interactions with people – which begs the question of how bears learn avoidance in the first place. Without being exhaustive, much of this process likely arises from matrilineal transmission of learned behaviors (Mattson 2021a) as well as comparatively high death rates among at-risk tolerant bears, notably adolescent males⁴, with this last process predictably leading to the selective recruitment of wary adult males into backcountry areas (Sections 1.1 and 2).



Adding yet more nuance and complexity, an absence of differential responses to human infrastructure by any class of bear during a study could paradoxically arise in situations where either all bears are

⁴ Adolescent male grizzly bears in North America die at annual rates that are on average 1.8-times higher than those of adolescent females and 2.2- and 3.2-times higher than those of adult males and females, respectively, which comports with adolescent males being 1.4-, 2.9-, and 11.1-times more likely to be involved in and die from conflicts with humans for the same respective sex and age classes. References for mortality rates are: Eberhardt et al. (1994), Wielgus et al. (1994), Hovey & McLellan (1996), Miller (1997), Mace & Waller (1998), McLellan et al. (1999), Sellers et al. (1999), McLoughlin et al. (2003), Wakkinen & Kasworm (2004), Garshelis et al. (2005), Kovach et al. (2006), Schwartz et al. (2006), and Costello et al. (2016). References for conflicts are: McLellan et al. (1999), Mace & Chilton (2009), Mace & Roberts (2011, 2012a, 2012b, 2013, 2014, 2015), Costello & Roberts (2016, 2017, 2018, 2019, 2020, 2021), and Kasworm et al. (2022a, 2022b).

relentlessly persecuted or, alternatively, diligently protected. In the first scenario, there would be little opportunity for individual bears to learn tolerance or, if a female, transmit tolerance to her offspring, resulting in aggregate avoidance of people and human infrastructure by all classes of bears (Figure 1a, Section 1.1). In the second scenario, young tolerant males would survive at roughly the same rate as tolerant females, and thus be equally recruited as adults into front country environs, resulting in approximately equal proportional use of human-impacted areas by all types of bears (Figure 1d, Section 1.1). Under a more pronounced version of this latter scenario, the balance of activity near human infrastructure could be tipped in favor adult males if rich food sources were concentrated near human infrastructure, resulting in comparative overuse by adult males (Section 6.4).

All these scenarios potentially contribute to explaining the diversity of results summarized here and in Section 6.1. Unfortunately, few studies report information that comprehensively addresses relevant explanatory factors, including distributions of food-rich habitats vis-à-vis human infrastructure, prevalence of tolerant versus wary bears either among different sex- age-classes or population-wide, and histories of protection for different bear classes or the population they belong to. Absent this information, explanations for a specific set of results can only be speculative, with support for generalization being relegated to probabilistic summaries of results from different studies, as in Figures 32 and 34.

The results of Hernando et al. (2021), featuring responses of brown bears to human infrastructure in Greece, are emblematic of the imponderables affecting interpretation of complex bear behaviors when adequate contextual information is unavailable. Adult males in this study area exhibited pronounced seasonal variation in use of areas near primary paved roads and unpaved tertiary roads (Figure 35a and 35b) but evidenced little variation in use of areas near settlements and secondary paved roads. Adolescent bears exhibited a seasonal pattern of selection relative to unpaved tertiary roads that was the opposite of adult males (Figure 35d), while at the same time evincing little seasonal variation in use of areas near settlements or primary and secondary paved roads. By contrast, adult females demonstrated comparatively little seasonal variation in use of areas near roads while tending to be less averse to the vicinity of settlements during fall and the vicinity of primary paved roads year-round (Figure 35a). This complex pattern of results could be speculatively interpreted, but the absence of information regarding distributions of foods near different human facilities, individual histories for the handful ($n = 18$) of radio-tracked bears in this study, and past patterns of population-wide human exploitation makes any interpretation or related generalizations little more than conjecture.

Section 6.3. Bear Behaviors that Affect Avoidance

Grizzly and brown bears are not automatons that interact with their environment in mechanistic ways. Bears that survive interactions with people predictably learn from their experiences, giving rise to behaviors that tend to increase perceived rewards and decrease perceived risks, with rewards typically in the form of increased opportunities to reproduce, greater access to material resources, or avoidance of circumstances associated with threats. Because bear-centric assessments of risk and reward are axiomatically either subjective or instinctual (Mattson 2021a), bear behaviors rarely have a 1:1 correlation with outcomes or environmental features commonly measured by researchers, who consequently have inherently limited insight into the full spectrum of learning processes and learned behaviors that bears use to optimize navigation of their environments. By default, investigators tend to

relegate ostensible risk-reducing bear behaviors to a few easily measured but crude categories, notably activity levels, speed of movements, degree of nocturnality, and selection for visual or audio screens.

Section 6.3.1. Nocturnality

In common with numerous other species, perhaps the most prevalent tactic employed by bears to reduce risks associated with exploiting human-impacted environs is to increase levels of night-time activity (e.g., Burton et al. 2024) – at least among bears that survive initial interactions with humans (see Section 4.3.1). This pattern has been observed among brown bears in Europe (e.g., Ordiz et al. 2011, 2017; Hertel et al. 2017; Oberosler et al. 2020; Hernando et al. 2021; Jonsson 2023) and Asia (Seryodkin et al. 2013) as well as grizzly bears in Canada (McLellan & Shackleton 1988, Gibeau 2000, Gibeau et al. 2002, Mueller et al. 2004, Graham et al. 2010, Roever et al. 2010, Cristescu et al. 2013) and the United States (Waller & Servheen 2005, Schwartz et al. 2010b), vis-à-vis both roads and human settlements (e.g., Hernando et al. 2021, Schwartz et al. 2010b, Figure 36). Even so, this pattern is not universal.

Naïve, subordinate, and human-tolerant bears tend to be comparatively more day-active when near human infrastructure, presumably to facilitate exploitation of resources in a diel niche under-used by or vacated by more dominant bears, notably adult males (Mueller et al. 2004, Graham et al. 2010, Schwartz et al. 2010b, Lamb et al. 2020; see Section 6.2.1).

Increased nocturnality by bears is tantamount to avoiding encounters with people given that almost all human activity, regardless of type, tends to be concentrated during day-light hours (e.g., Waller & Servheen 2005, Mace et al. 2011, Kautz et al. 2021). From a plausible bear's perspective, the footprint functionally associated with human infrastructure is thus lessened at night, along with perceptions of risk associated with using food or other resources in human environs. Regardless of presumed motivation, bears that are more diurnal near roads and settlements tend to die at higher rates compared to preponderantly nocturnal bears (Section 4.3.1), with this differential predictably generating aggregate population-level underuse of human environs (e.g., Lamb et al. 2020).

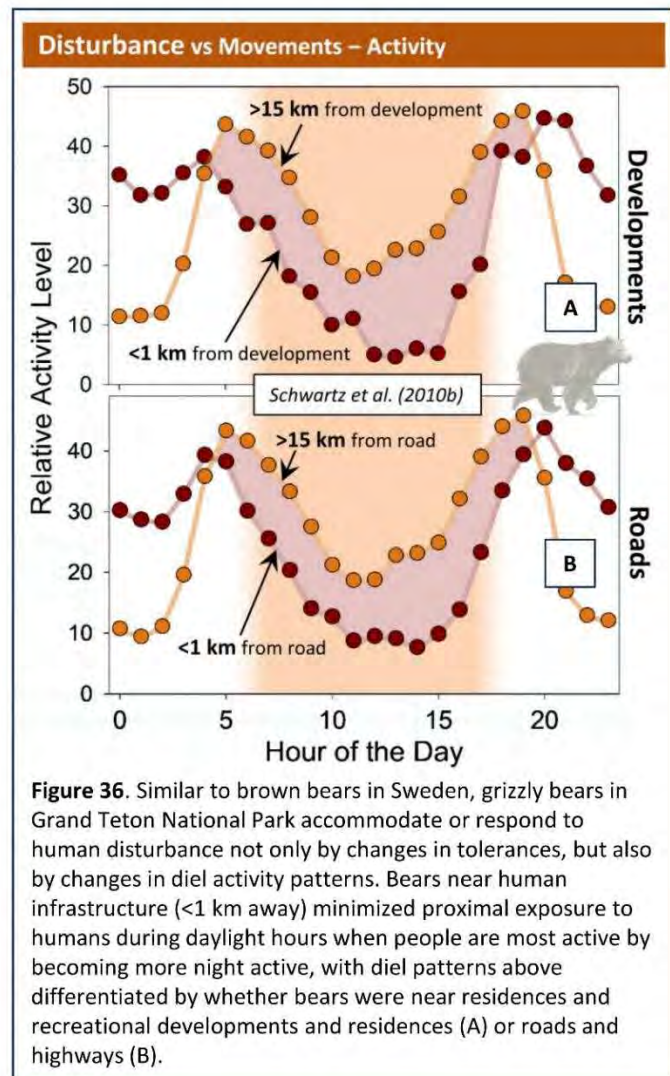


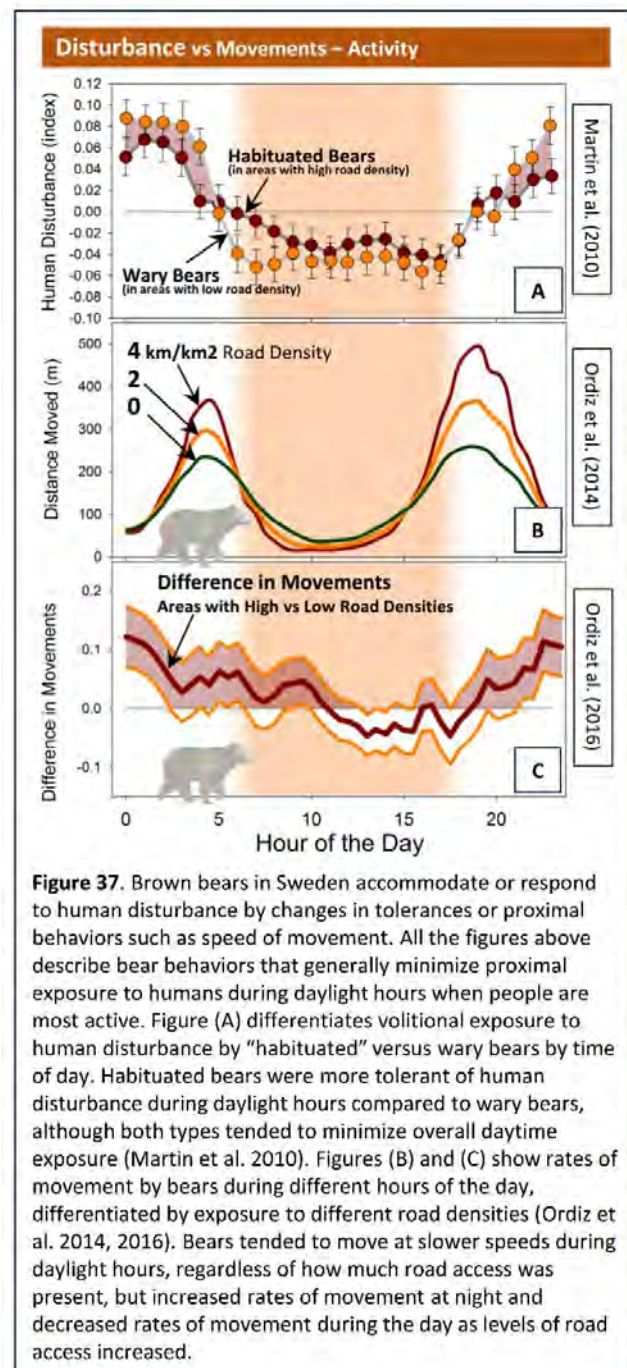
Figure 36. Similar to brown bears in Sweden, grizzly bears in Grand Teton National Park accommodate or respond to human disturbance not only by changes in tolerances, but also by changes in diel activity patterns. Bears near human infrastructure (<1 km away) minimized proximal exposure to humans during daylight hours when people are most active by becoming more night active, with diel patterns above differentiated by whether bears were near residences and recreational developments and residences (A) or roads and highways (B).

Section 6.3.2. Speed of Movement

The speed at which bears move and the likelihood that they will be active (i.e., non-stationary) are positively correlated, although the extent of this correlation likely decays as speed increases given that reckonings of ‘active’ versus ‘inactive’ from tilt or tip-switches on radio-collars are categorical rather than continuous (e.g., Garshelis et al. 1982). With the availability of more advanced technology that allows for high resolution temporal and spatial measurement of movement (see Section 3.1), researchers have consequently gravitated toward assessing responses of bears to human facilities by estimating rates of movement, whether as a function of nearness to the facility or proximal densities of features such as roads. Alternatively, various responses such as selection for areas near human infrastructure can be reckoned in terms of whether bears are stationary or moving.

In general, brown and grizzly tend to move more quickly at a perpendicular when near human infrastructure, with this tendency more evident during daylight hours when people are active (Gibeau 2000, Roevers et al. 2010, Linke et al. 2013, Ladle et al. 2019, Whittington et al. 2019, Kautz et al. 2021, Parsons et al. 2021, Falcinelli et al. 2024; Figure 47c). Accelerated directional movement by bears during daylight hours when near human facilities can be plausibly interpreted as a means of reducing temporal exposure to human-related hazards. Even so, results reported by Ordiz et al. (2014, 2016) in a Scandinavian study area complicate this relatively straight forward conclusion. Bears in this study area moved longer distances at night and shorter distances during daylight hours in areas with high versus low road densities, with greatest differences in movement evident at night (Figure 37b and 37c).

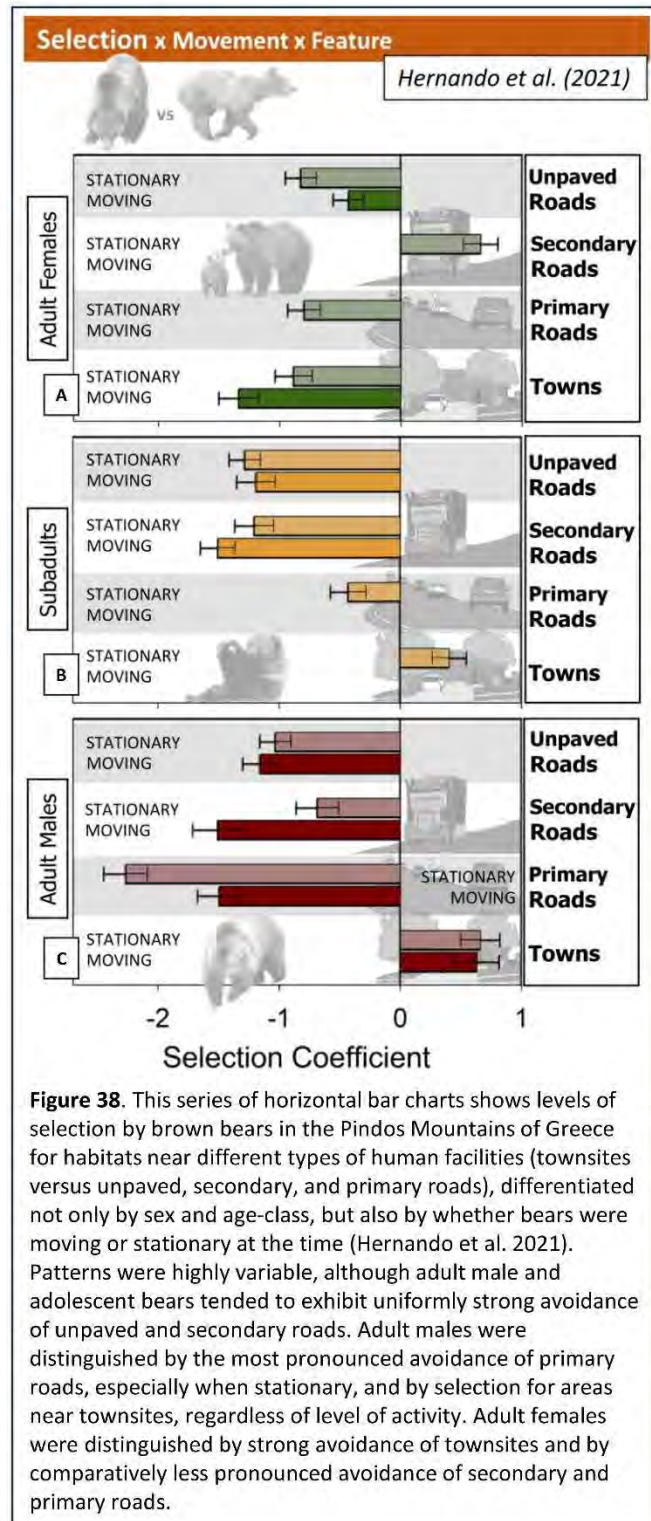
These results collectively suggest that when reactions of bears to human features are compared at coarse and fine grains, bears in the first case tend to minimize diel-averaged exposure to human-related hazards by becoming more night-active, whereas bears in the second case tend to minimize exposure for periods of minutes or hours by accelerating



movements when near or crossing discrete human features such as paved highways. This distinction suggests that bears employ different behavioral strategies to minimize exposure to human-related hazards when occupying dense networks of roads compared to when near linear or point human features embedded in a wildland matrix, which cautions against extrapolating research results across these different domains. The results of Hernando et al. (2021) and Whittington et al. (2022) further caution against unqualified extrapolation of research results for analysis of human impacts.

Hernando et al. (2021) found complex patterns of selection by different sex and age classes for areas near different types of human facilities. Notably, bears in this Balkan study area tended to avoid human facilities of all types – with the exception that adult males selected for areas near settlements, adult females selected for areas near secondary paved roads (Figures 38c and 38a), and selection among all classes of bears varied depending on whether focal animals were stationary or moving (Figure 38). As might be expected, selection of human environs by bears while moving versus stationary tended to be positively correlated, but with important outliers (Figure 39) suggesting that adult females were more likely to avoid secondary paved roads and be attracted to primary paved highways while stationary compared to while moving, with the opposite pattern true for adult males (Figures 38a and 38c).

There is no way to confidently interpret these patterns (see Section 6.2.2), although they suggest that variation in speed of movements may have been an artifact of adult females using immobility to avoid comparatively more mobile (and actively foraging?) adult males when near secondary paved roads. Conversely, adult females may have not only preferentially selected areas near major highways (Figure 38a), but also been more actively

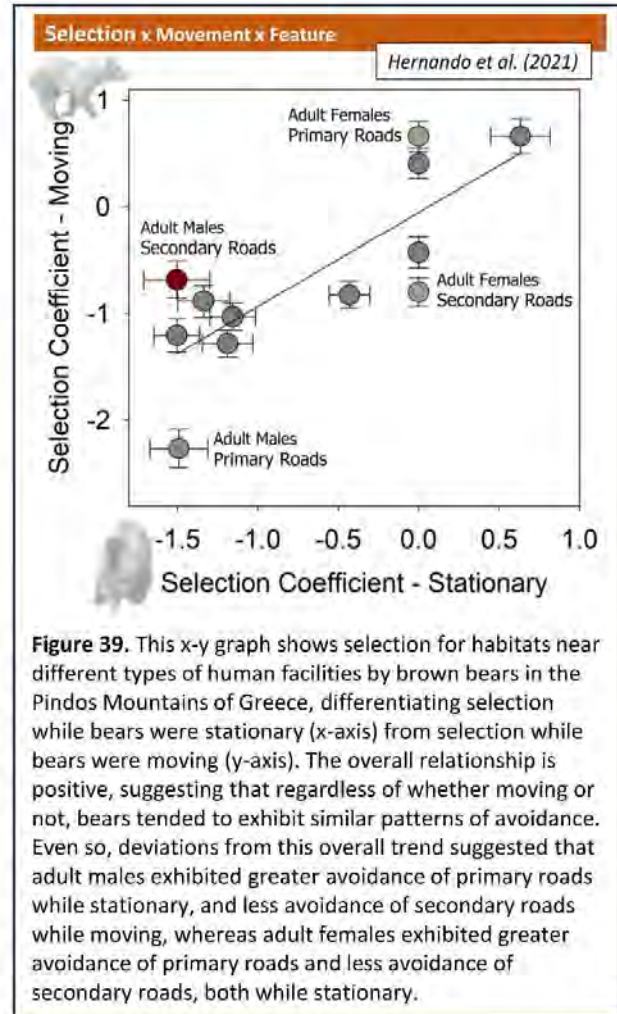


foraging while there, especially given that these areas were strongly avoided by adult males when stationary. The main conclusion to be drawn from these complex albeit imponderable results is that differential rates of movement together with interactions among conspecifics confound any simple interpretation of how bears in this study area responded to human features.

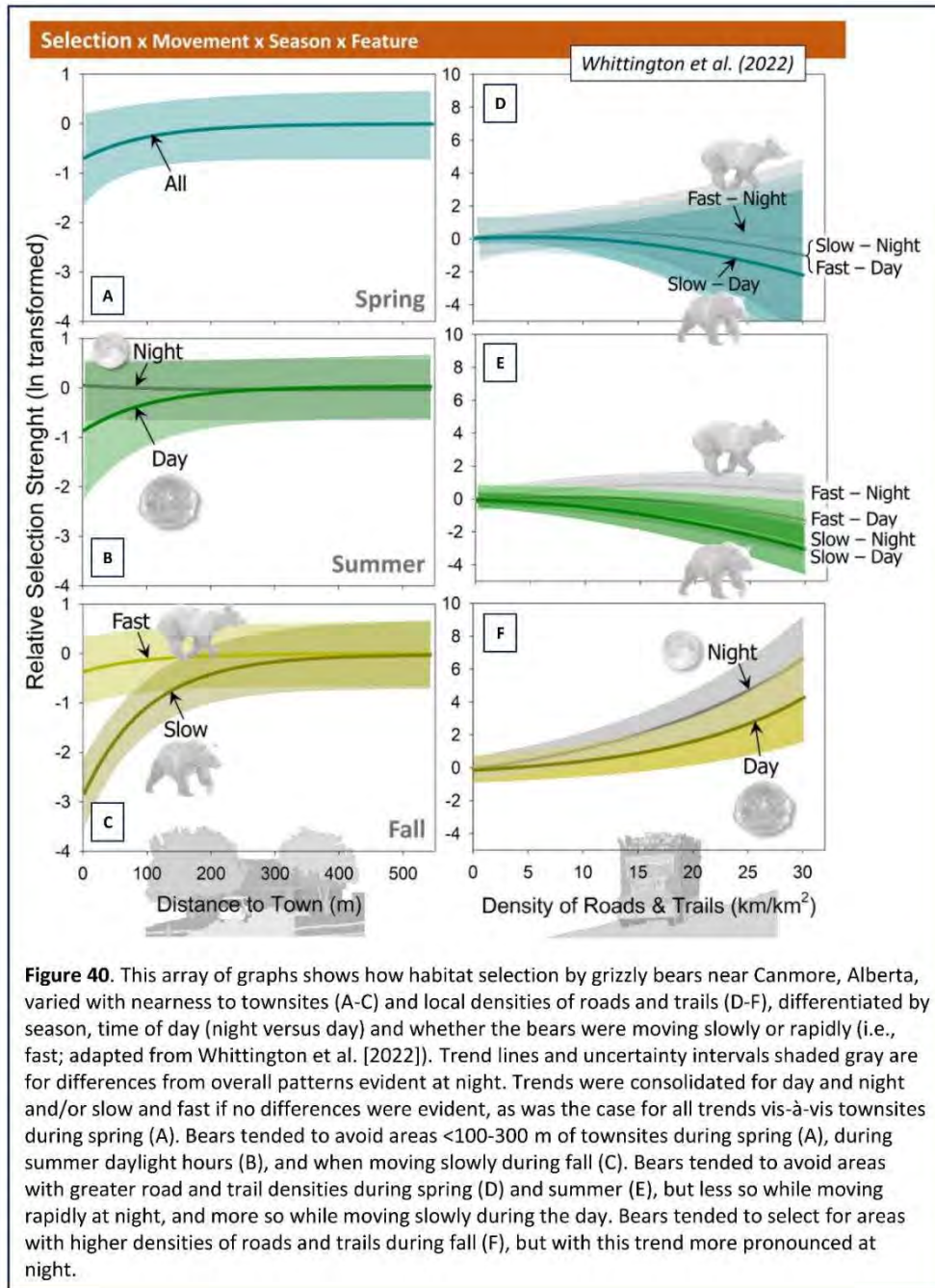
This cautionary point is reinforced by the results of Whittington et al. (2022). Here again, these researchers stratified their analysis of selection by different types of human features (i.e., townsites versus roads and trails) and whether bears were moving slowly (i.e., 'stationary') or quickly (i.e., 'moving'), but with additional stratifications that accounted for season (i.e., spring, summer, and fall) and time of day (i.e., day versus night), resulting in 24 total strata that all potentially demanded some sort of explanation. This interpretational exigency was further complicated by the fact that results were reckoned in terms of both densities when it came to the effects of roads and trails and distances when it came to the effects of townsites.

The authors of this study were able to statistically differentiate variation among only 13 of the 24 strata, especially those related to season, time of day, and rate of speed for bears exposed to a range of access densities (Figures 40d, 40e, and 40f). Without being exhaustive, bears in this study area tended to avoid higher densities of roads when moving slowly or during daylight hours – at least during spring and summer (Figures 40d and 40e) – and underuse areas near townsites during spring (Figure 40a), during daylight hours in summer (Figure 40b), and while moving slowly during fall (Figure 40c). In an exception to what would otherwise be generalized diurnal avoidance of human features by slow-moving bears, areas associated with high densities of road and trails were overused by bears during fall regardless of rate of speed (Figure 40f). This exception to an apparent rule was presumably attributable to bears being attracted to high-quality fall foods concentrated near roads and trails (Whittington et al. 2022) – a circumstance that distinguishes this study area from many others (see Section 6.4.2).

These tangles of complex imponderable results caution against rote extrapolations of research focused on bear movements from specific study areas without accounting for conspecific interactions, season, time of day, type of human facility, or – even more importantly – singular environmental conditions. Even so, despite some uninterpretable complexities, the results summarized in this section – including those



of Ordiz (2014, 2016), Hernando et al. (2021), Whittington et al. (2022), and Falcinelli et al. (2024) – support provisionally concluding that bears not only tend to exhibit greater avoidance of human facilities during daylight hours (Section 6.3.1), but also while moving slowly.



Section 6.3.3. Tolerance of Humans

In addition to learning tolerance for certain stimuli and cues from mothers, bears can also develop tolerance through a process of habituation under circumstances where they do not associate stimuli with painful or other adverse outcomes (Mattson 2021a). Habituation reduces stressful reactions to stimuli that have not been previously associated with harm, in turn allowing bears to improve their

navigation of perceived environmental risks and rewards. Notably, habituation is a function of visceral reactions as well as cognitive perceptions, which makes the development of tolerance intrinsically subjective and prone to error, at least vis-à-vis what some human observers might consider objective measures of risk. Habituation can thus lead to tolerance for people using human infrastructure driven by avoidance of palpable risks posed by conspecifics in the backcountry or immediate rewards associated with access to food resources near human facilities (Mattson 2021a) – despite the increase in associated risks of premature death from interactions with people (Section 4.3.2). Learned tolerance for humans can be thus viewed as part of an adaptive process by which bears reduce risk, but only vis-à-vis more immediately tangible cues and stimuli.

Despite the widespread occurrence of bears able to tolerate humans (Mattson 2021a), relatively little research has focused on how tolerance explicitly affects aggregate use of human impacted areas, plausibly because subjective tolerance is difficult for humans to directly judge, much less reliably measure. Nonetheless, several researchers have speculated that certain seasonal or multi-annual distributional patterns in their study areas can be partly explained by levels of fear or resource-driven tolerance for people (e.g., Mattson et al. 1987, 1992; Gibeau 2000; Mueller et al. 2021; see Section 6.4.2). A few studies have even shown that some (but certainly not all [Støen et al. 2015]) bears exhibit less rather than more measurable stress in the form of hair cortisol or fecal cortisol metabolites when using human impacted environs, plausibly because they feel safer or better provisioned (Bourbonnais et al. 2013, Ditmer et al. 2015, Babic et al. 2023) – all of which predictably fuels habituation to people and human-associated cues.

A handful of studies, notably Mattson et al. (1992) and Martin et al. (2010), have tackled the challenge of categorizing radio-collared bears as either human-tolerant (i.e., ‘habituated’) or intolerant (i.e., ‘wary’). Mattson et al. (1992) found that tolerant bears were three-times more likely than wary bears to use areas <4-km from recreational developments and nearly twice as likely to use areas <2-km from highways in Yellowstone National Park (Figures 42c, 42d, 43b, and 43c; see below). This differential resulted in human-tolerant bears accounting for most activity in these human-impacted areas, although not enough to offset population-level underuse (Mattson et al. 1987) plausibly because tolerant bears were killed by people at three-times the rate that wary bears were killed (Mattson et al. 1992, Pease & Mattson 1999; see Section 1.2 and Figure 1b).

On a related note, Martin et al. (2010) not surprisingly found that human-tolerant bears tended to be more common and more day-mobile in areas typified by high road densities, whereas human-intolerant bears were more common and night- active in areas typified by low road densities (Figure 37a). This pattern can be plausibly interpreted as arising from functional responses of bears exposed to people for sustained periods of time at a scale disallowing ready escape, in turn fueling habituation to human-associated stimuli and cues (Mattson 2021a).

More descriptively, functional responses are evident when animal behaviors – notably selection for habitats and foods – correlate with availability of these resources at the scale of seasonal or annual ranges (e.g., Mauritzen et al. 2003, LeClerc et al. 2016, Holbrook et al. 2019). More specific to human infrastructure, there is ample evidence in addition to that of Martin et al. (2010) suggesting that bears chronically exposed to roads and human residences are more likely to use human-impacted areas (Beringer et al. 1990, Ciarniello et al. 2007, Duquette et al. 2017, McKay et al. 2014, Zeller et al. 2019) – plausibly because they have few other options. But bears evincing this kind of compensatory even

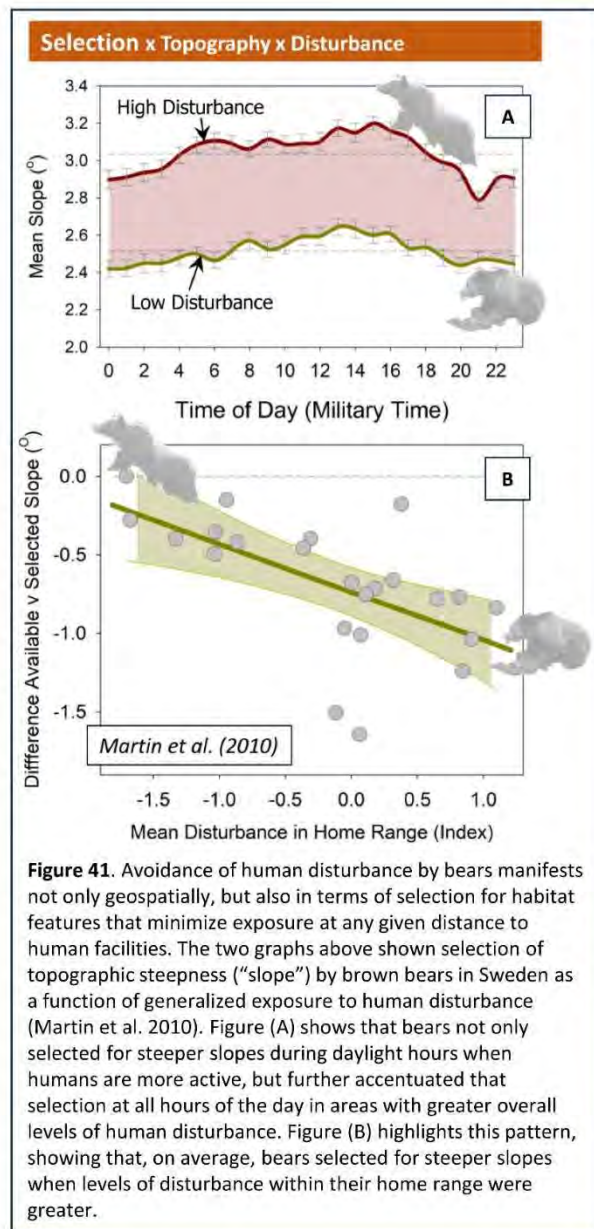
necessary habituation-driven behavior are only those that have survived encounters with humans long enough to be radio-collared, tracked, and subsumed in a database.

Section 6.4. Environmental Effects

Functional responses of bears to the prevalence of human features within their seasonal and annual ranges provides a logical bridge to the effects of physical features of the environment on distributions of bears vis-à-vis roads, residences, and other human infrastructure. The physical environment can have major effects on bear behaviors by decreasing exposure of bears to people when they are near human facilities, heightening the impact of human features, or increasing the attractiveness of habitats that would otherwise be alienated by human impacts. These temporizing or exacerbating physical features include those that impede peoples' mobility or create visual and audio screening (Section 6.4.1); enhance the comparative seasonal or annual productivity of habitats near people (Section 6.4.2); or increase audio and visual impacts of specific human facilities (Section 6.4.3). As a preview, few environmental features have discrete cleanly differentiated mechanisms by which they may affect bears. Notably, physical screening can facilitate the use of productive habitats *and* temporize the impact of heavy traffic. Conversely, lack of screening can magnify the perceptual impacts of traffic, facilitate offroad human activity, *and* exacerbate the alienation of productive habitats.

Section 6.4.1. Physical Obstructions

Only a handful of researchers have explicitly studied the effects of physical concealment or obstructions on the behavior of bears near human facilities. Even so, these researchers have consistently found that bears near roads either select for environs with greater audio muffling (Archibald et al. 1987), decelerate and vary their movements when there is greater audio and visual interference between themselves and roads (Parsons et al. 2020, 2021; Figure 45d; see below), or, more simply, stay farther away from roads that lack screening vegetation (González-Bernardo et al. 2022). Ordiz et al. (2011) and Cristescu et al. (2013) similarly found that brown and grizzly select for microsites with greater vertical screening and overhead vegetation cover when bedded near human features.



More specific to the effects of topographic exposure on bear behaviors, Nellemann et al. (2007), Martin et al. (2010), De Angelis (2019), Ladle et al. (2019), and Hernando et al. (2021) all found evidence that bears in their study areas tended to select for more rugged terrain or steeper slopes when near roads and human settlements. Martin et al. (2010) further found that bears in their Scandinavian study area used steeper slopes not only during daylight hours (as per Section 6.3.1), but also when exposed to higher road densities and related human disturbances within their home ranges (Figure 41).

This consistent gravitation by bears near human facilities to habitats with greater visual or audio screening and related impediments to offroad human activity is not surprising. Grizzly bears that routinely expose themselves to visual detection by people during daylight hours and under circumstances where obscuring vegetation or terrain are lacking tend to die at higher rates compared to bears that are more secretive (e.g., Kite et al. 2016; Sections 4.2.4, 4.3).

This greater attrition of bold or unguarded bears could arise for several reasons. People tend to be less active at night or in more rugged terrain with thicker vegetation, and thus less likely to encounter bears under these conditions (Sections 4.2.4 and 4.3.1). Of more direct relevance to bear behavior, premature deaths of bears that expose themselves to people would predictably result in a preponderance of survivors that had either been averse to detection in the first place or learned to be more guarded after stressful encounters with people. In either case, researchers would find aggregate avoidance of circumstances that bears presumably associate with detection by humans.

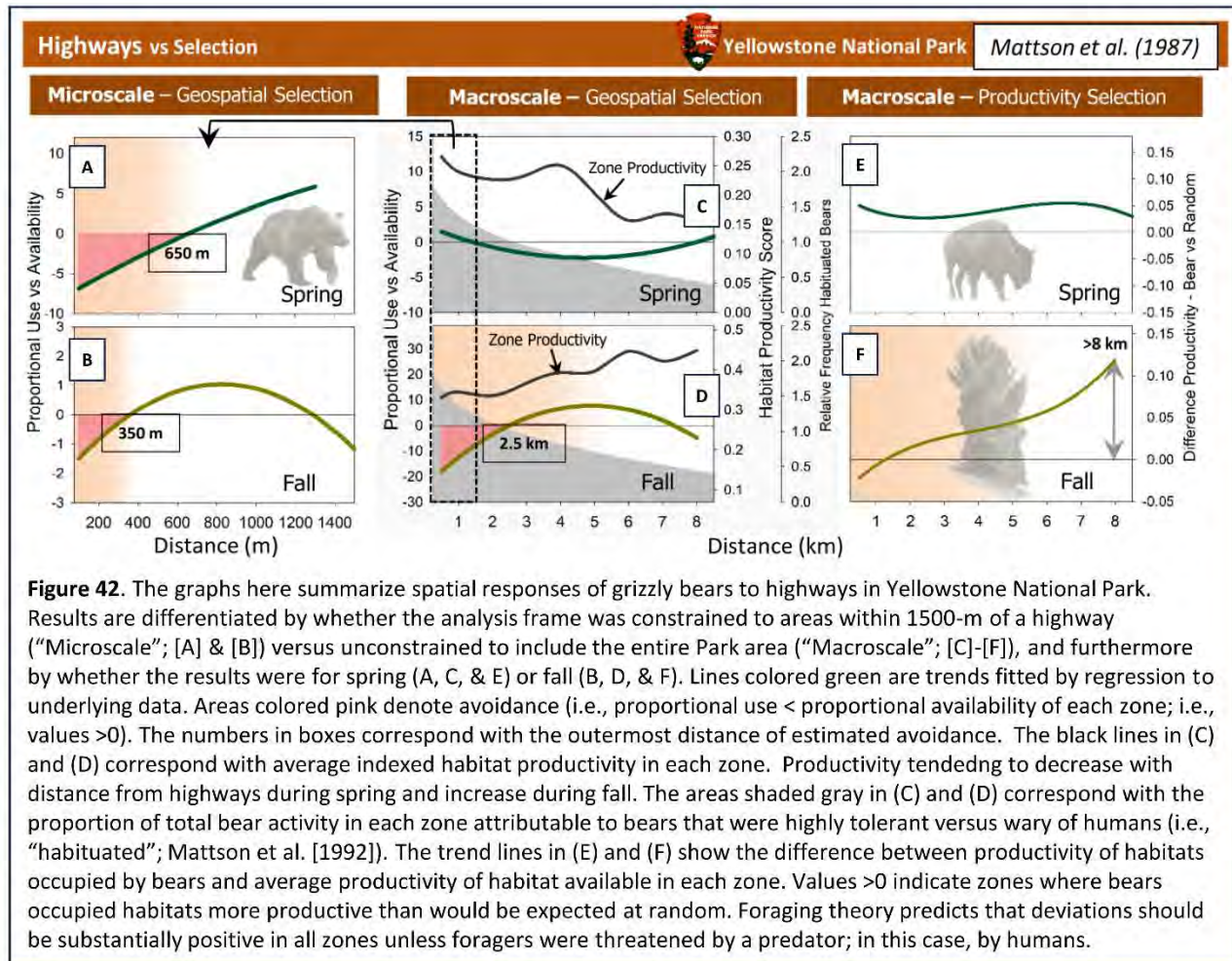
Of more direct relevance to habitat managers, these results strongly suggest that adverse effects of human infrastructure – notably tertiary roads – will be magnified by placement of these features in areas that have been or will be denuded of vegetation cover, especially where there is little topographic relief. These adverse effects arising from lack of cover predictably include not only increased odds of human-caused mortality (Section 4.2.4), but also increased alienation of habitat because of avoidance behavior among surviving bears (see also Box 3).

Section 6.4.2. Distributions of Productive Habitat

Bears are highly motivated to consume nutrient-rich foods in productive habitats, especially during their pre-hibernation hyperphagic quest for calories. Yet, like all animals, bears balance perceived risks and rewards of exploiting foods and habitats, leading to what can seem like the paradoxical avoidance of productive habitats or willful acceptance of life-threatening hazards (e.g., Bunnell & Tait 1981, Stirling & Derocher 1990, Ferguson & McLoughlin 2000, Herrero 2018). Given that humans are the cause of most adolescent and adult bear deaths worldwide (Section 2), it would be reasonable to assume that bears will avoid humans and human infrastructure, even if it means foregoing access to concentrations of nutritionally valuable foods. Yet there is compelling evidence that brown and grizzly bears routinely do the opposite, and embrace substantial collateral risk while exploiting high-quality natural and anthropogenic foods that are seasonally or annually concentrated near human infrastructure.

Some of the first research investigating effects of human infrastructure on habitat use by bears was also amongst the first to query how these patterns were affected by seasonal as well as annual distributions of habitat productivity – all in context of bear tolerances (i.e., habituation) and related differences in age, sex, and reproductive status (Mattson et al. 1987, 1992). Productive habitats in this Yellowstone National Park study area were concentrated near roads and recreational developments during spring and in backcountry areas during fall (Figures 42c, 42d, 43b, and 43c), with spring productivity defined largely by

availability of carrion from ungulates on lower-elevation winter ranges (Green et al. 1997) and fall productivity defined largely by whitebark pine seeds that bears obtained from high-elevation caches of cones made by red squirrels (Mattson & Reinhart 1997, Mattson et al. 2004).



Geospatial distributions of grizzly bears in this Yellowstone Park study area relative to human infrastructure, productive habitats, and other types of bears highlight complexities that potentially confound straight-forward interpretations of bear behaviors in response to roads and human settlements. Despite the concentration of productive habitats near human infrastructure during spring, bears in Yellowstone Park under-utilized carrion and other resources as far away as 2.5-4.5 km from recreational developments (Figures 43b and 43d), yet more fully exploited foods and resources near park roads (Figures 42c and 42e; Green et al. 1997), plausibly because concentrations of human-tolerant and adult female bears attracted to ungulate carrion near roads offset avoidance by adult males (Mattson et al. 1987, Mattson 2000).

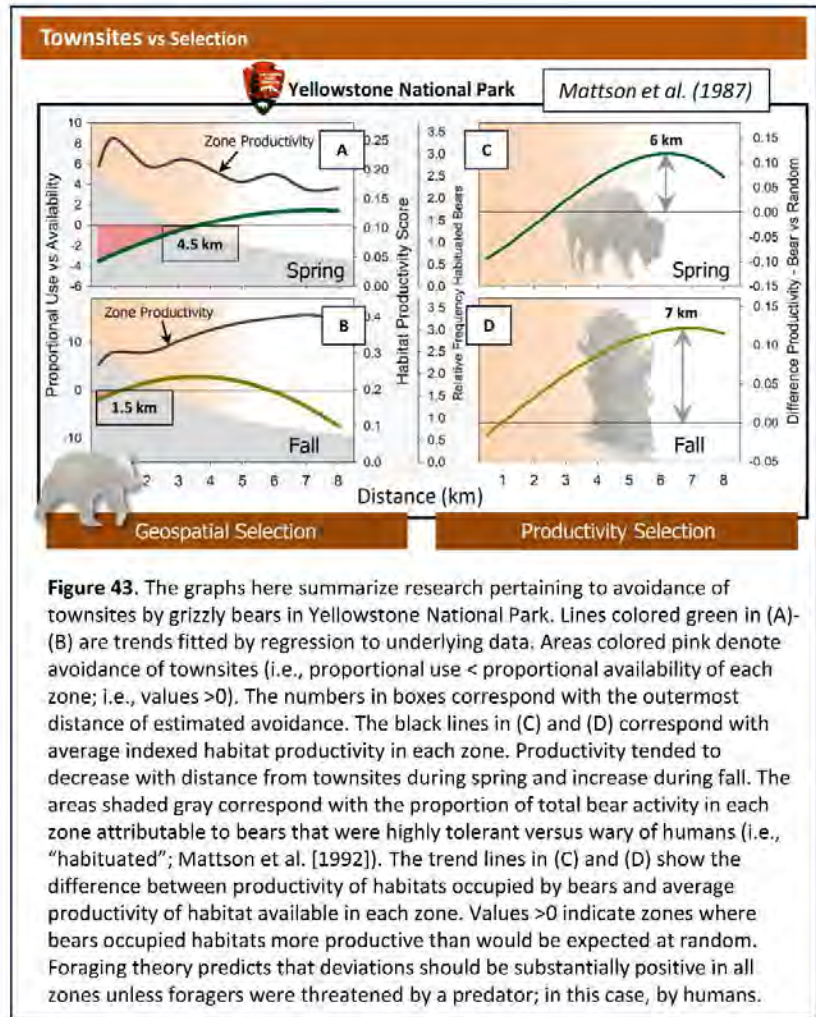
In contrast to spring, bears during fall more uniformly avoided areas near both roads and developments plausibly because rich foods were concentrated in the backcountry (Figures 42d, 42f, 43d, and 43e), but with this pattern complicated by the fact that adolescent and adult female bears gravitated to front-country areas to avoid adult males that dominated productive backcountry habitats (Mattson et al. 1987). These intraspecific interactions conceivably offset what would otherwise have been even greater

aggregate avoidance of human infrastructure. Adding yet more complexity, fall bear activity near roads and developments varied substantially from one year to the next depending on the size of whitebark pinecone crops, with under-use of areas near human infrastructure at a nadir during years when large cone crops attracted bears to remote backcountry areas (Mattson et al. 1992, 2001; Figures 24a and 24b).

These patterns from Yellowstone Park emphasize the extent to which seasonal and annual variation in distributions of high-quality foods, tolerance for humans, and avoidance of threatening conspecifics can jointly affect whether and to what extent bears avoid human infrastructure – a point reinforced by results from multiple study areas in Europe and North America. Mace et al.

(1999), Gibeau et al. (2002), Lamb et al. (2017), Lodberg-Holm et al. (2019), Parsons et al. (2021), Clarke (2022), and Proctor et al. (2023) all found that bears in their study areas selected for naturally productive human-impacted environs, but with the proviso that human-tolerant or socially subordinate bears were more likely to use these areas, presumably either because of naivete or as a means of minimizing exposure to adult males (Reinhart & Mattson 1990; Chruszcz et al. 2003; Mueller et al. 2004; Nellemann et al. 2007; Lamb et al. 2020, 2023; De Angelis et al. 2021; Hansen 2023). Other studies additionally found that bears gravitated to areas near roads and human settlements in pursuit of anthropogenic or lower-quality natural foods during years when high-quality foods in the backcountry were scarce (Mattson 1990, Merkle et al. 2013, Cristescu et al. 2016b, Skuban et al. 2018, De Angelis et al. 2021).

These geospatial motifs were further conditioned on the natural productivity of a given region and the extent to which humans had modified the distribution and extent of productive habitats through activities such as timber harvest and control of wildfires. Most evidence for this proposition comes from relatively austere environments in Alberta, Canada, where suppression of fires together with extensive clearcutting and oil and gas development had resulted in the superimposition of productive bear habitats with road and motorized trail systems (Roever et al. 2008b; Souliere 2023). This human-manufactured concentration of bear foods near tertiary roads resulted in studies from this region



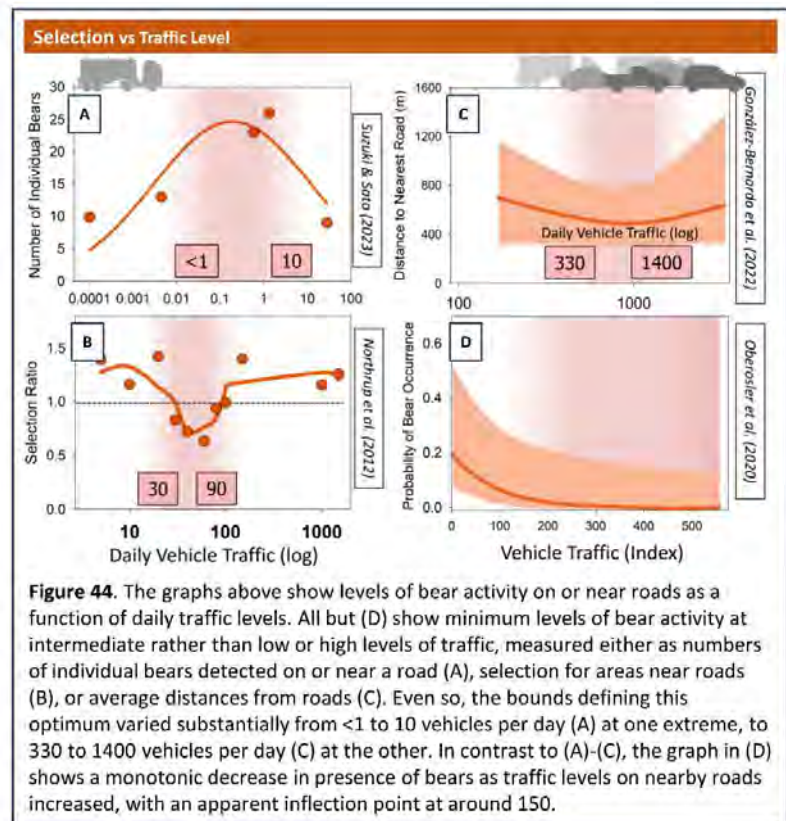
routinely showing that grizzly bears selected for human-modified habitats, with associated selection of productive microsites near roads and well sites (Roever et al. 2008a, 2010; Berland et al. 2013; Linke et al. 2013; McKay et al. 2014; Colton et al. 2021; Sorenson et al. 2021; Clarke 2022).

The main conclusion to be drawn from these Alberta-specific results is that people can create widespread habitat conditions that lure brown and grizzly bears into hazardous human-impacted environs. As several researchers have noted (e.g., Roever et al. 2008a, 2010; Lodberg-Holm et al. 2019; Proctor et al. 2020, 2023; Souliere 2023), these conditions predictably produce ecological traps where the heightened odds of a premature death almost invariably offset any benefits arising from greater access to food-rich habitats, especially if bears do not adopt risk-mitigating behaviors such as increased nocturnality (see Sections 4.3.1 and 4.3.4).

Of relevance to habitat management, the large body of research reviewed here clearly shows that locating roads, recreational development, or permanent residences in productive bear habitats amplifies human impacts by attracting bears into hazardous situations where they are more likely to be killed by people. Any planning process that fails to consider this amplifying effect when building or maintaining roads and other infrastructure will predictably lead to unforeseen harm to bears. This basic fact makes the deliberate neglect of habitat productivity in management of habitat security for grizzly bears in the United States a bemusing as well as scientifically unjustifiable choice (for example, see U.S. Fish & Wildlife Service [2007], Greater Yellowstone Ecosystem Grizzly Bear Subcommittee [2016], Northern Continental Divide Ecosystem Grizzly Bear Subcommittee [2019]).

Section 6.4.3. Traffic Effects

The design, site-specific footprint, and related types and levels of human activity on roads and highways are all features of the physical environment that affect bear behaviors. Speeds and volumes of vehicular traffic are some of the most consequential features of a given road or highway segment (e.g., Zeller et al. 2020), dictated largely by whether road design, surfacing, maintenance, and sight distances allow for higher speed-limits and heavier traffic. Increased vehicular speeds and volumes can jointly affect bear behaviors as well as mortality rates – the former by triggering greater avoidance or decreased numbers of road crossings and the latter through increased likelihood of fatal collisions between bears and vehicles (Bennett 2017; Section 7).



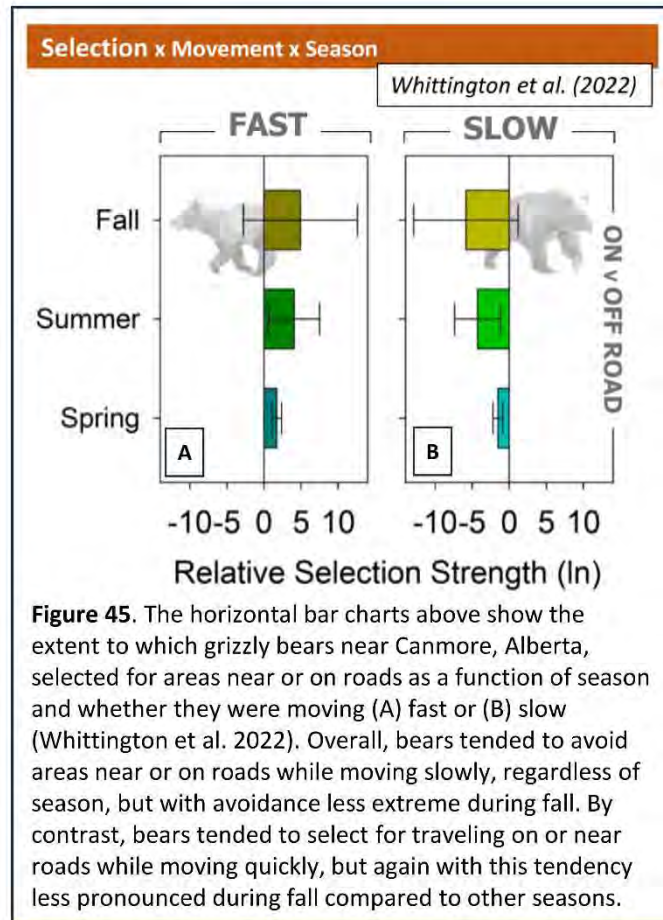
In this section I address behavioral responses of bears to traffic on roads and highways, emphasizing roadways that are not designed for high-speed high-volume traffic and thus not a significant source of bear fatalities caused by vehicles operating as potentially lethal projectiles. The emphasis here is on avoidance and road crossings as behavioral phenomena varying as a function of traffic volume. Section 7 focuses on highways where vehicles are a direct source of mortality, in turn a function of whether bears are willing to attempt a crossing in the first place – realizing, yet again, that these distinctions are matters of degree rather than kind.

Multiple studies have shown that bears exhibit greater avoidance of roads as traffic levels increase, regardless of whether the road is an isolated feature surrounded by wildlands or part of a motorized network (e.g., Mace et al. 1999, Chruszcz et al. 2003, Donelon 2004, Waller & Servheen 2005, Roever et al. 2010, Northrup et al. 2012a, Ladle et al. 2018, Whittington et al. 2019, Oberosler et al. 2020, González-Bernardo et al. 2022; Figures 44d). That having been said, there are not only lower thresholds at which avoidance is evident, but also higher traffic levels at which avoidance begins to wane.

Several studies have found that bears exhibit little or no avoidance of roads and highways when traffic is <10-20 vehicles *per day* (McLellan & Shackleton 1988, Mace et al. 1999, Waller & Servheen 2005, Northrup et al. 2012a), including the visually unobstructed main access road to Denali National Park (Singer & Beattie 1986, Burson et al. 2000, Yost & Wright 2001, Mace et al. 2011).

Not surprisingly, some studies—including ones focused on black bears – have found that bears will even use lightly-trafficked roads as travel routes, with this proclivity greatest during hyperhagia and nocturnal hours (Whittington et al. 2022, Suzuki & Sato 2023; Figures 44a and 45). At the other extreme, there is also evidence from several study areas that aversion to areas near paved highways paradoxically wanes when traffic levels exceed >100-1,400 vehicles *per day* (Northrup et al. 2012a, González-Bernardo et al. 2022), but with the important proviso that crossings of heavily trafficked highways concurrently decline.

Perhaps one of the most consistent behavioral responses of bears to increased vehicular traffic is a monotonic decline in road crossings (Figure 47f; see below), often congruent with diel increases in human activity on highways (Figures 46a-46c and 47; Waller & Servheen 2005, Graves et al. 2006, Skuban et al. 2017, Kautz et al. 2021). That having been said, crossings declined at substantially different



rates depending on the study area, approaching zero at traffic levels ranging anywhere from around 100 to 500 vehicles *per hour*, indicating that there is substantial variation in how populations of bears will respond to risks posed by passing traffic (Figure 47f; Percy 2003, Alexander et al. 2005, Waller & Servheen 2005, Graves et al. 2006, Barrueto et al. 2014, Skuban et al. 2017).

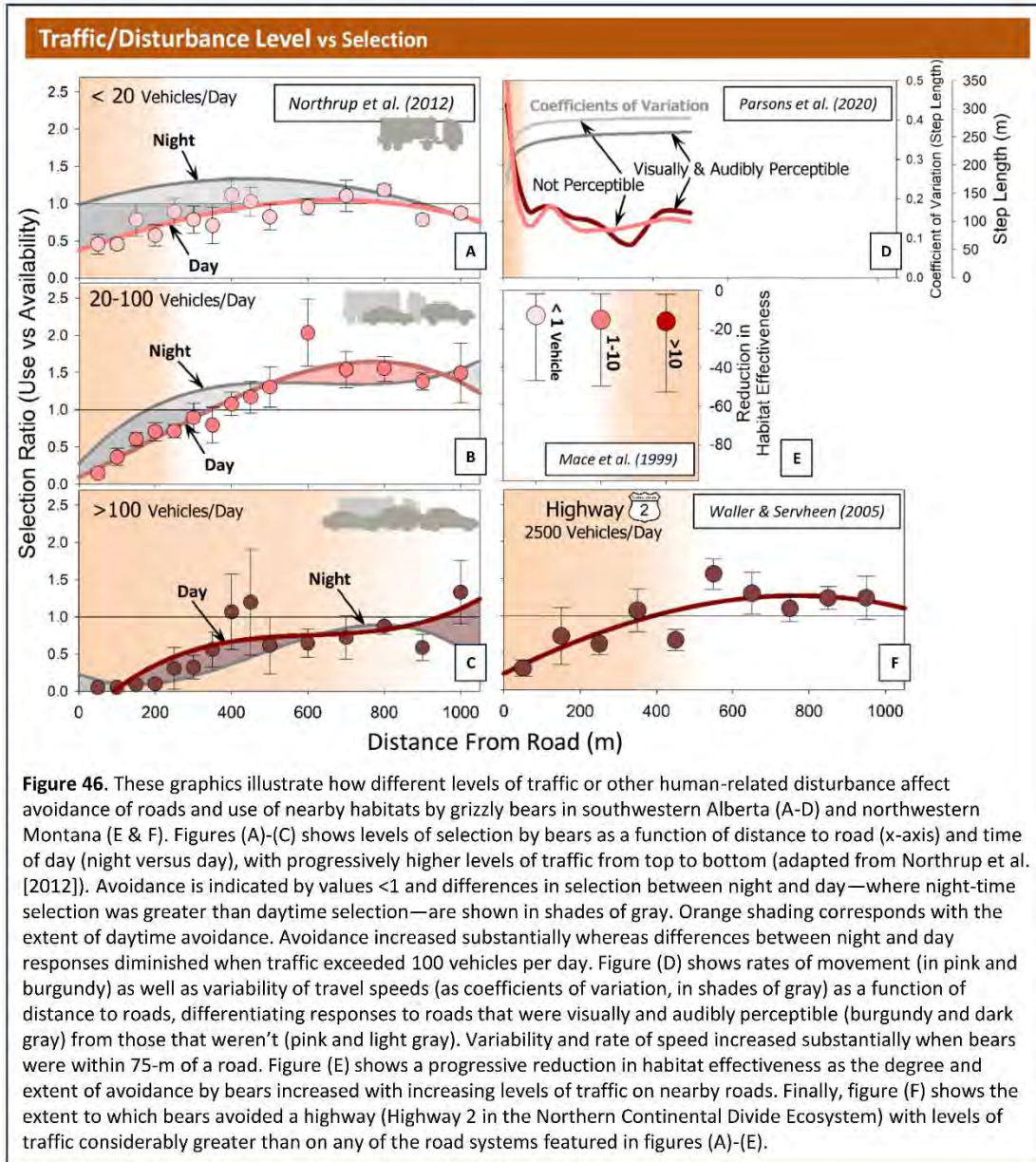
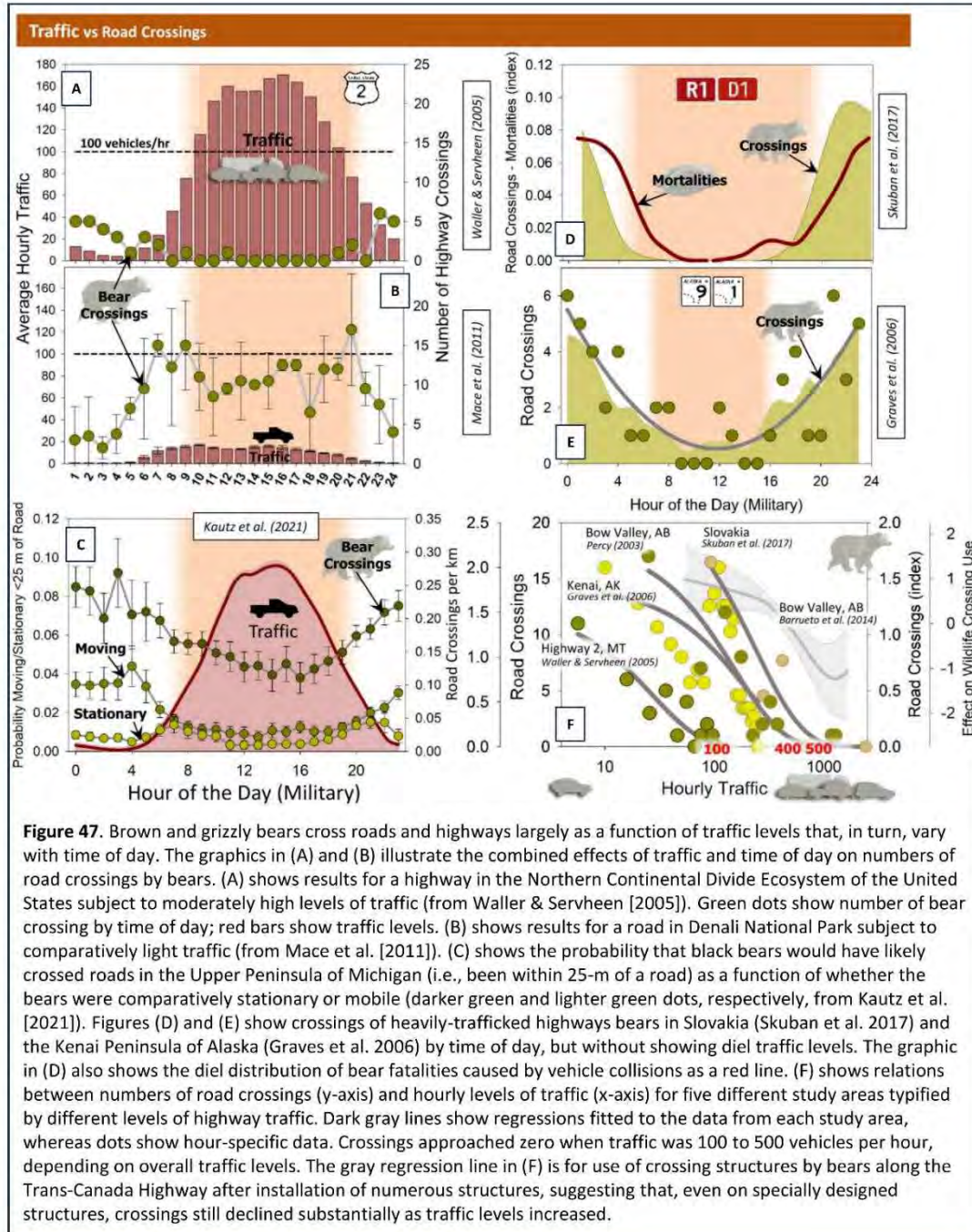


Figure 46. These graphics illustrate how different levels of traffic or other human-related disturbance affect avoidance of roads and use of nearby habitats by grizzly bears in southwestern Alberta (A-D) and northwestern Montana (E & F). Figures (A)-(C) shows levels of selection by bears as a function of distance to road (x-axis) and time of day (night versus day), with progressively higher levels of traffic from top to bottom (adapted from Northrup et al. [2012]). Avoidance is indicated by values <1 and differences in selection between night and day—where night-time selection was greater than daytime selection—are shown in shades of gray. Orange shading corresponds with the extent of daytime avoidance. Avoidance increased substantially whereas differences between night and day responses diminished when traffic exceeded 100 vehicles per day. Figure (D) shows rates of movement (in pink and burgundy) as well as variability of travel speeds (as coefficients of variation, in shades of gray) as a function of distance to roads, differentiating responses to roads that were visually and audibly perceptible (burgundy and dark gray) from those that weren't (pink and light gray). Variability and rate of speed increased substantially when bears were within 75-m of a road. Figure (E) shows a progressive reduction in habitat effectiveness as the degree and extent of avoidance by bears increased with increasing levels of traffic on nearby roads. Finally, figure (F) shows the extent to which bears avoided a highway (Highway 2 in the Northern Continental Divide Ecosystem) with levels of traffic considerably greater than on any of the road systems featured in figures (A)-(E).

The contrast of research results from Highway 2 along the south boundary of Glacier National Park (Waller & Servheen 2005) and the main access road to Denali NP (Mace et al. 2011) illustrates the extent to which interacting effects of traffic levels and time of day can affect road crossings by bears (Figures 47a and 47b; see below). Highway 2 crossings peaked at night coincident with a nadir in traffic, with essentially no crossings occurring once daytime traffic levels exceeded 100 vehicles *per hour*. By contrast, bear crossings of the Denali NP access road peaked during daylight hours, coincident with peak traffic – albeit traffic that never exceeded 20 vehicles *per hour*, roughly 9-times less than peak traffic on Highway

2. A quick perusal of results from Denali NP might lead an undiscerning reader to conclude that vehicular traffic, in general, does not impede road crossings by bears, and that most crossings occur during the day – which would have not been applicable anywhere other than in Denali NP.



The differences in how brown and grizzly bears react to vehicular traffic within and among study areas is yet more evidence that multiple interacting factors affect bear behavior, and that responses by bears to human disturbances and infrastructure always happen in context of a broad-scale physical environment, longer-term histories of interactions with people, and transmitted or individually learned tolerances for

human-associated risks (Section 2.2). Insofar as avoidance *per se* is concerned, maximum aversion to roadside habitats at intermediate rather than peak levels of traffic is probably an artifact of vehicle speeds and the related likelihood that vehicles will be associated with people who are active along roadways. Few people stop along major high-speed transportation routes, especially on a *per capita* basis (Billion 1959), whereas people are more likely to be active outside their vehicles where discretionary parking is easier, safer, and otherwise more rewarding, as along tertiary roads transecting wildlands. Bears thus plausibly perceive intermediate levels of traffic as a threat simply because the time-specific likelihood of encountering people on foot is likely to be comparatively high. By contrast, the likelihood that vehicles will strike a bear predictably increases monotonically as a joint function of traffic volume and speed (e.g., Gunther et al. [1998], Waller et al. [2005], and Section 7).

Section 6.6. Making Sense of Habitat Alienation

The research reviewed in this section (Section 6) unambiguously demonstrates not only substantial variation in behavioral responses of brown and grizzly bears to human infrastructure, but also the dependence of this variation on intrinsic and extrinsic factors. The magnitude of this variation could lead uncritical readers to conclude there are only a few generalizable patterns and, of these, that most are inexplicable. They would be wrong on both counts.

Untangling the complexity of how bears respond to human infrastructure necessarily starts with making key conceptual as well as pragmatic distinctions, including between behavioral responses of individual bears and patterns evident for individuals aggregated to the scale of a population, region, or research sample. Behaviors of individuals are typified by avoidance, attraction, or indifference to human features during finite lifetimes – sometimes at variance with responses exhibited by other bears in the same population at the same time. Population-level patterns subsume these diverse individual responses to the point where underlying themes can be obscured, especially when the demographic consequences of behavioral lineages are ignored. Attraction to human facilities and tolerance for human-associated stimuli often truncates the lives of individual bears (Section 5) and leads to the withering of human-tolerant behavioral lineages (Section 2). Occasionally the opposite is true. Regardless of which pattern prevails, longer-term dynamics are almost invariably central to a useful explanation of population-level geospatial patterns.

Ambulatory people driven by diverse motivations are also not the same as the concrete, steel, gravel, or wood that physically comprise human infrastructure. Roads are explicitly designed to expedite travel through a landscape, which not only serves human purposes, but can also attract bears. Human-altered environments such as lawns, pipeline routes, and highway verges can create flushes of attractive bear food – in addition to the rubbish and food stocks that typify human residences. Absent all people, one could reasonably speculate that certain types of human infrastructure would attract and benefit bears. However, there is no evidence that this hypothetical often exists, especially given that people predictably use infrastructure that is built for human purposes. The question is, in what numbers, at what times, and with what attitudes towards bears.

With these distinctions in mind, there are several themes that are both explicable and generalizable evident in behavioral responses of bears to human infrastructure at the scale of populations, study areas, and research samples:

- 👤 Most bears in most places underuse areas near townsites, highways, and unpaved roads, but with this tendency most pronounced near tertiary roads at the scale of populations rather than individual home ranges, presumably because population-scale patterns better reflect the demographic accumulation of hazards resulting from exposure to humans (Section 6.1.1).
- 👤 Where evident, habitat alienation tends to be more spatially extensive around townsites compared to around highways and roads, although the extent of this effect can vary widely from one area to another (Section 6.1.1).
- 👤 Alienation of habitat progressively increases as road densities increase, although the rate at which alienation occurs varies widely from one area to another. Even so, areas where there are no roads are consistently the least compromised for bears (Section 6.1.2).
- 👤 All else equal, adolescent bears and females with dependent young tend to make comparatively heavier use of areas near human facilities plausibly because human environs provide access to competition-free resources as well as security from threats posed by adult males often concentrated in backcountry areas (Sections 6.2.1 and 6.2.2).
- 👤 All else equal, when bears are active near human facilities, they tend to be more nocturnal and/or use sites where physical features impede human foot travel and provide visual or audio screening, presumably as a means of minimizing detection and likelihood of encounters with people (Sections 6.3.1 and 6.4.1).
- 👤 All else equal, bears tend to move at a faster pace in a more overtly directional manner when near human infrastructure to presumably minimize the duration of their exposure to perceived human-associated hazards (Section 6.3.2).
- 👤 All else equal, human-tolerant rather than wary bears tend to be more active near human facilities, presumably both as an impetus for and reflection of more frequent exposure to people (6.3.3).
- 👤 All else equal, bears tend to be more active near human facilities located in naturally productive habitats or in areas where human disturbances have created comparatively more productive habitat conditions (Section 6.4.2).
- 👤 All else equal, bears tend to be less active in areas near roads with intermediate levels of traffic compared to in areas near lightly-trafficked roads or heavily-trafficked highways – typified by <10-100 vehicles *per day* and >100-1,000 vehicles *per hour*, respectively – and only rarely attempt to cross highways when traffic levels exceed 100-500 vehicles *per hour* (Section 6.4.3).

Section 7. Highways, Roadkill, and Fragmentation

Heavily trafficked (>1,000-2,000 vehicles/day) high-speed (>45 mph/70 kph) highways (hereafter highways) not only have major impacts on bear populations, but also entrain singular interactions between humans and bears. Brown and grizzly bear fatalities caused by collisions with vehicles are almost exclusively confined to highways⁵, where vehicles effectively function as lethal projectiles. However, unlike people who kill bears near residences and secondary roads, people driving vehicles virtually never intend to kill a bear (see Section 5). Almost all collisions are accidental, but nonetheless usually fatal for involved bears, largely because high speeds limit distances at which drivers and bears can react (e.g., Arts & Van Schagen 2006, Wang et al. 2013), and maximize blunt force trauma. The tempo of high-velocity threats and stimuli on highways also predictably exceeds what most bears can cognitively and physically navigate (Mattson 2021a). We can only speculate what bears perceive when they attempt to cross highways, but if objective audio and visual stimuli and risk of death were a determinant, bears would very likely rarely, if ever, attempt a crossing.

Even so, there are several predictable reasons why bears might attempt to cross a highway. For one, dispersing adolescent males – more so than females – often venture into unknown hazardous environs (e.g., Zedrosser et al. 2007, Jerina & Adamič 2008, Shirane et al. 2019, Karamanlidis et al. 2021, Hansen 2023), including areas transected by highways where odds of encountering and attempting to cross a novel landscape feature predictably mount (e.g., Kaczensky et al. 2003). For another, adult males undertake extended movements during breeding season with the intent of encountering reproductively available females (e.g., Dahle et al. 2003a, 2003b; Krofel et al. 2010; Sato et al. 2011; Steyaert et al. 2012), plausibly leading them to likewise encounter and attempt to cross highways. Finally, given that brown and grizzly bear populations less often exhibit underuse of areas near primary highways compared to other human features (Section 6.1), there are probably numerous incentivized and unforeseeable opportunities for bears to attempt a highway crossing, especially where populations are small and isolated, as in southern Europe (e.g., Huber et al. 1998, Krofel et al. 2012, Skuban et al. 2017, Psaralexi et al. 2022), or where previous crossings were successful and yielded a reward.

The following sections describe factors that predictably govern the impacts of roadkill on populations of carnivores, including bears (Section 7.1); the documented toll that fatal collisions with vehicles take on brown and grizzly bear populations wherever there is exposure to heavily trafficked highways (Section 7.2); the aggregate effect of major transportation corridors on fragmentation and viability of regional bear meta-populations (Section 7.3); and the degree to which physical infrastructure along and over highways designed to facilitate crossings can mitigate this toll (Section 7.4).

Section 7.1. Factors Governing Carnivore Roadkill

Roadkill has been a major focus of attention for wildlife researchers operating under the broader rubric of road ecology since this discipline was formally established in the late 1990s, spawning numerous field

⁵ Regional traffic levels affect how regional researchers perceive and define secondary roads versus highways. For example, Skuban et al. 2017 and Find'o et al. 2018 defined highways traversed by >2,000 or even 4,000 vehicles per day as “secondary roads,” which considerably exceeds traffic levels on roads defined as “secondary” by grizzly bear researchers in North America. Here, I adopt a threshold for defining heavily trafficked highways that comports with definitions used in North America and better reflects the full range of traffic levels on roads transecting brown and grizzly bear ranges.

studies as well as review books and articles (e.g., Forman 1998, Forman et al. 1998, Fahrig & Rytwinski 2009, Beckmann et al. 2010, Van der Ree et al. 2015). This profusion of research has clarified both the extent to which roadkill jeopardizes the conservation of carnivores as well as major factors governing impacts on different species in different physical settings.

Roadkill takes a non-trivial toll on carnivores worldwide. Annually, roughly 4% of all carnivores die from collisions with vehicles, accounting for an average 25% of all recorded deaths (Moore et al. 2023). As important for conservation purposes, roadkill is often an additive source of mortality, especially among large carnivores such as bears (e.g., Hill et al. 2019, Barrientos et al. 2021, Logan & Runge 2021, Dyck et al. 2023). Even so, a minority of carnivore species and populations predictably bear the brunt of roadkill because of predisposing life histories and features of the natural and human environment, with roadkill accounting for >15% of all mortality in only 28% of studies where overall mortality patterns have been studied (Moore et al. 2023).

Of life history traits, there are a handful that render some species more than others vulnerable to the effects of fatal collisions. Of these, many apply to brown and grizzly bears. Populations of omnivorous large-bodied species typified by low reproductive rates and greater mobility are especially impacted by deaths associated with human infrastructure (Ford et al. 2007; Fahrig & Rytwinski 2009; Hostetler et al. 2009; Rytwinski & Fahrig 2011, 2012; Cook et al. 2013; Grilo et al. 2015) – to the extent that small populations can be put at demonstrably greater risk of extirpation (Cardillo et al. 2005, 2008; Bennett et al. 2017; Hill et al. 2020). As might be expected, wide-ranging animals such as bears are more likely to encounter highways and be killed by cars, especially during hyperphagia and the breeding season (Bertwistle 2001, Grilo et al. 2015, Waller & Miller 2015, Sidorovich et al. 2020, Psaralexi et al. 2022, Bénard et al. 2023). This risk is predictably compounded for omnivorous scavengers when carrion or spilled edibles such as grain attracts them to highways (Fahrig & Rytwinski 2009, Quiles & Barrientos 2024).

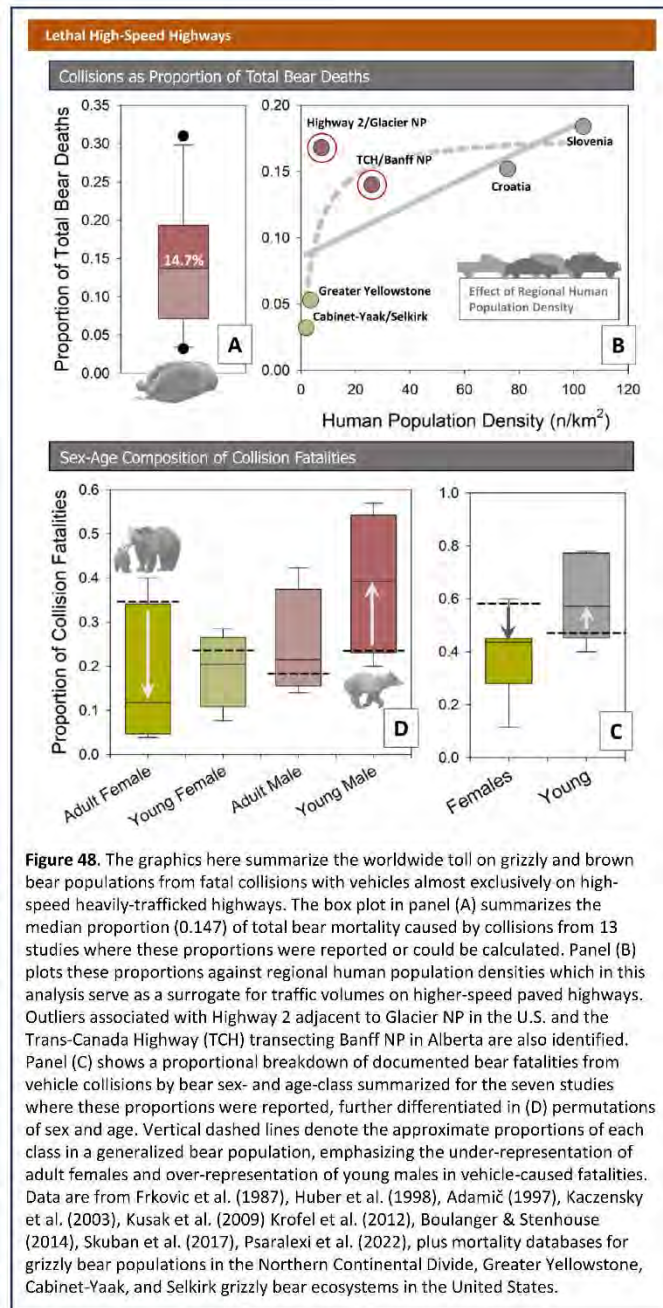
Other factors related to the highway design, traffic management, and physical setting have well-documented effects on rates of roadkill. Of these, traffic levels are perhaps the most important, with roadkill predictably mounting with increasing traffic (Lodé 2000, Bertwistle 2001, Hostetler et al. 2009, Waller & Miller 2015, Sidorovich et al. 2020, Lee et al. 2021), often as a function of greater densities of resident humans (Rutherford et al. 2014, Vistin et al. 2015, Hill et al. 2020, Barrientos et al. 2021, Ha 2022). Even so, highway features and management policies that reduce sighting distances and reaction times can exacerbate roadkill – notably higher speed limits, greater road curvature, and intrusion of roadside vegetation (Gunther et al. 1998, Benítez-López et al. 2010, Neumann et al. 2012, Israel 2018). Not surprisingly, collisions are also often more frequent when there is inclement weather or reduced ambient light, which also coincides with when large carnivores often attempt to cross highways (Section 6.4.4; Waller & Servheen 2005, Neumann et al. 2012).

All these exacerbating factors potentially apply to brown and grizzly bears. They are large-bodied wide-ranging omnivores with the lowest reproductive rate of any terrestrial mammal, barring pachyderms (Pacifi et al. 2013). Differences in population trajectory are consequently often determined by very small changes in survival rates of especially adult females (see Section 4.2.2). Bears are also attracted to roadkill carrion along transportation routes with often fatal consequences for the involved bears (Huber et al. 1998, Waller & Servheen 2005, Mattson 2019a), especially where high speed limits, low visibility, and heavy traffic limit reaction times of both drivers and bears (Waller et al. 2005, Skuban et al. 2017,

Psaralexi et al. 2022, Zarco-González et al. 2023, Zarco-González & Monroy-Vilchis 2024). More to the point, brown and grizzly bear populations exposed to heavily trafficked highways predictably incur consequential levels of roadkill, with resulting adverse demographic consequences.

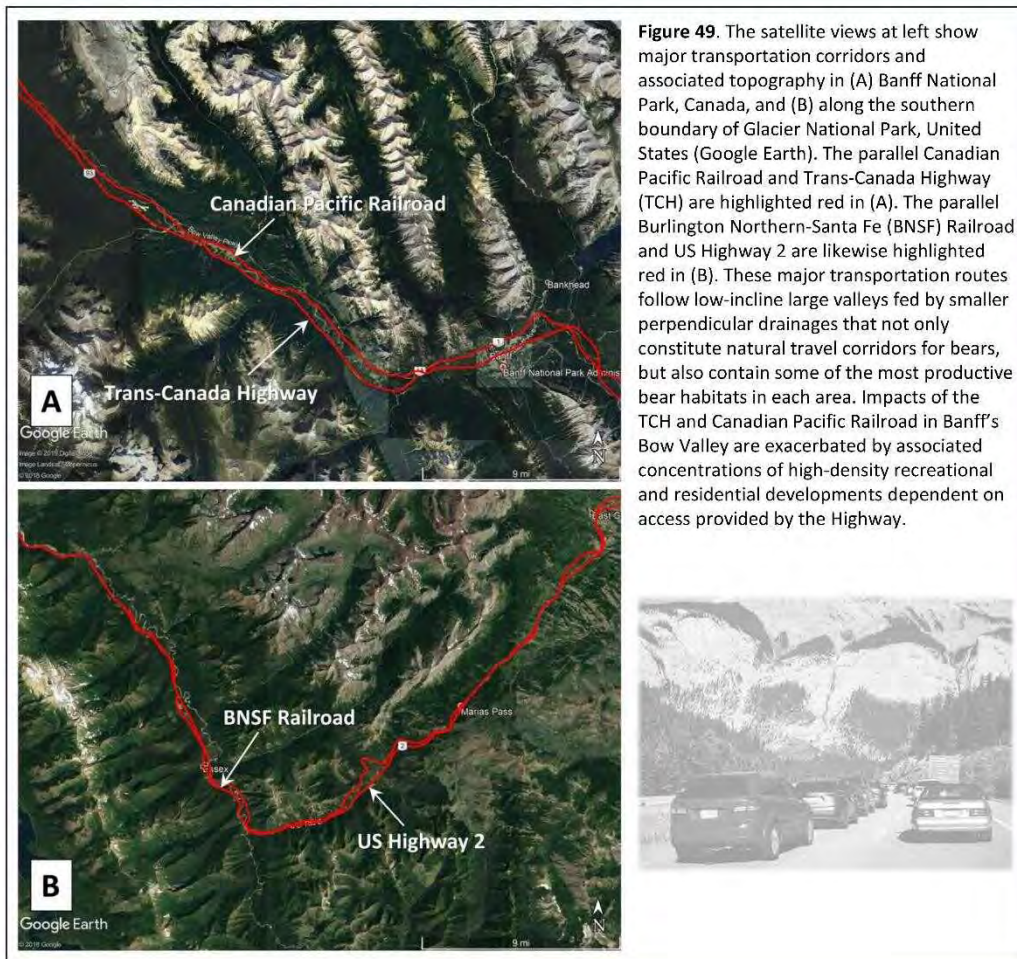
Section 7.2. The Demography of Bear Roadkill

Brown and grizzly bears are exposed to the adverse effects of roads in 65% of their global distribution (Ceia-Hasse et al. 2017), with most impacts attributable to heavily trafficked highways concentrated in a mid-latitude band encompassing North America and Europe. Within this band of greatest exposure, a median 14% of all recorded bear mortalities are attributable to vehicle collisions, albeit with an interquartile range of 8-19% and minimum-maximum range of 3-30% (the U.S. Selkirk and Cabinet-Yaak ecosystems and Slovenia, respectively⁶; Figure 48a). Of these deaths, a disproportionately large number are young bears (i.e., adolescents or cubs; Figure 48c), notably adolescent males (Figure 48d). By contrast, adult females are disproportionately under-represented (Figure 48d), which comports with their smaller ranges and likely greater familiarity with environmental hazards vis-à-vis less experienced dispersing young males (Section 7 introduction, Section 7.1).



⁶ Frkovic et al (1987), Adamič (1997), Huber et al, (1998), Benn & Herrero (2002), Kaczensky et al. (2003), Kusak et al. (2009), Krofel et al. (2012), Boulanger & Stenhouse (2014), Skuban et al. (2017), Kasworm et al. (2022), Interagency Grizzly Bear Study Team Annual Reports (2014-2023), Northern Continental Divide Ecosystem Annual Monitoring Reports (2014-2023).

Although researchers have not comprehensively addressed factors driving regional variation in levels of roadkill in brown and grizzly bear populations, there are several of perhaps self-evident importance, including a convincing correlation between collisions and levels of traffic (Waller et al. 2015, Gilhooly et al. 2019; Figures 51a and 51d), as well as a similar, not surprising, relationship between traffic and regional human population densities (as per Section 7.1; Figure 48b). Even so, there is an equal if not greater effect plausibly attributable to elevated traffic associated with visitation to high-profile protected areas or travelers using national transportation corridors, with both features exemplified by the Trans-Canada Highway (TCH) in Banff National Park and Highway 2 along the southern border of Glacier National Park in the United States (Figure 48b). Mountainous terrain along these and other highways – typical of mid-latitude brown bear distributions – predictably further increases the odds of lethal collisions by funneling bears onto hazardous highways and nearby railways (see Figure 49; Gibeau 2000, Waller & Servheen 2005, Skuban et al. 2017, Gilhooly et al. 2019, Fedorca et al. 2021, Psaralexi et al. 2022).

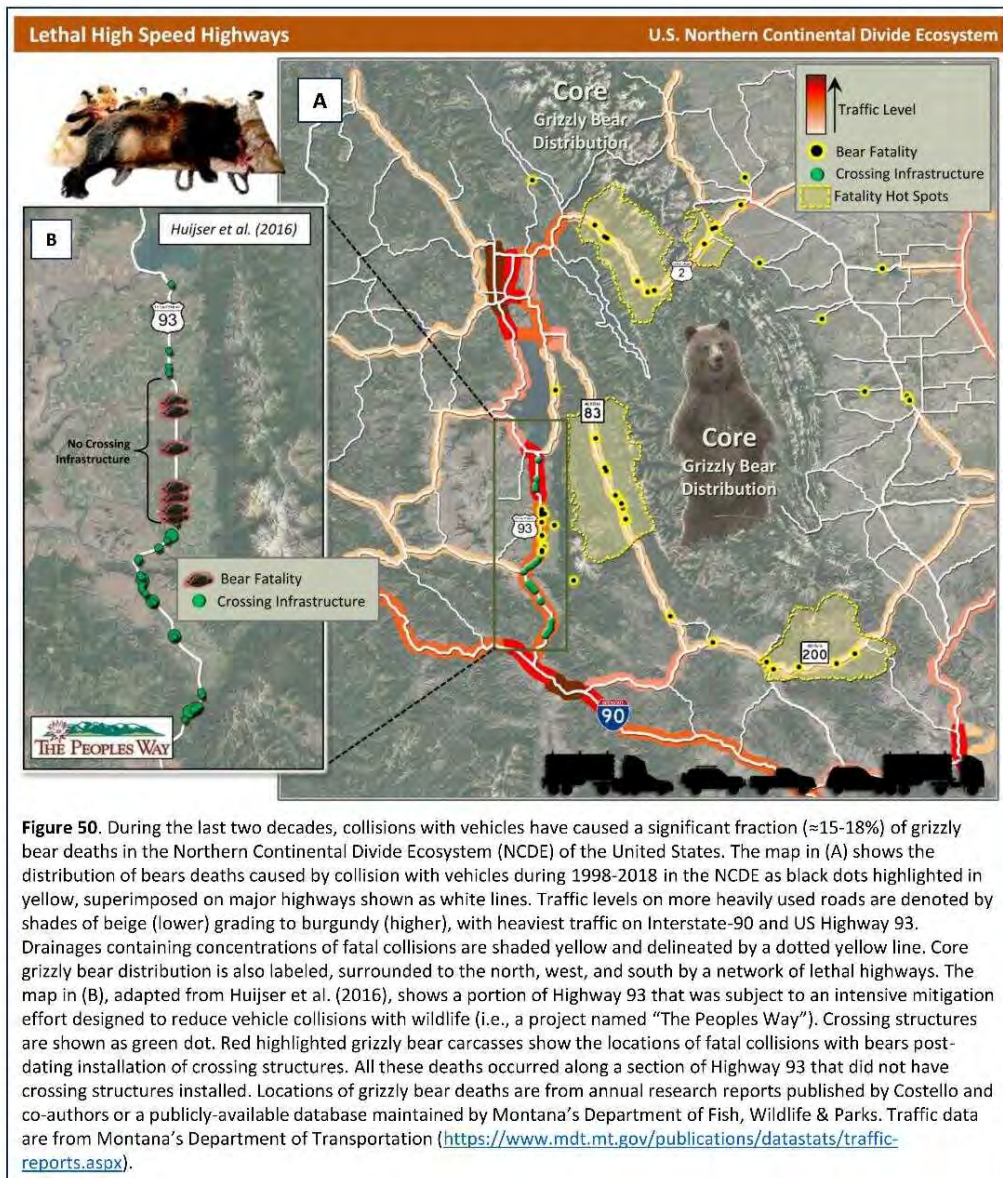


Section 7.3. Transportation Corridors and Population Fragmentation

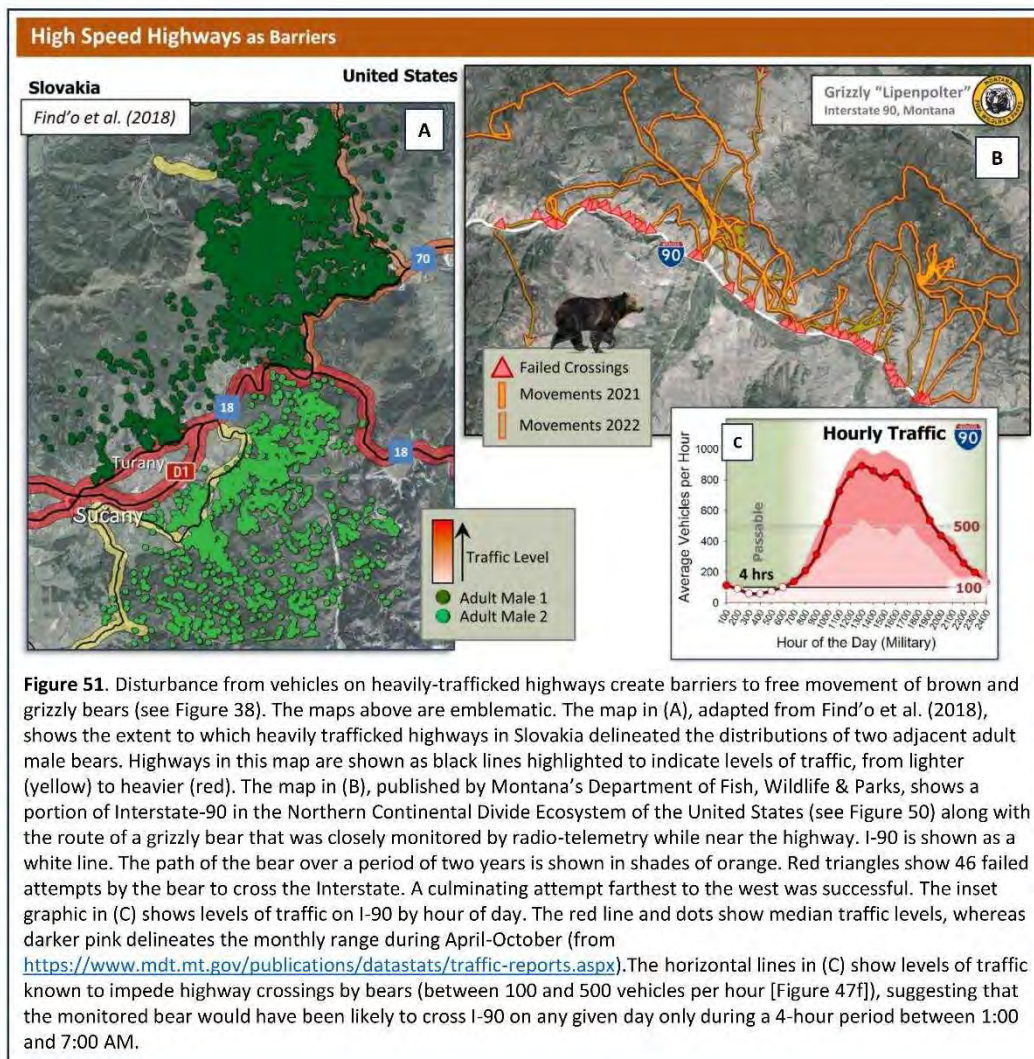
Not surprisingly, small (<250), isolated populations of brown and grizzly bears typical of mid-latitudes are less resilient and more vulnerable to changes in human and natural environments compared to the large contiguous populations ubiquitous at higher latitudes. This greater vulnerability has led to a focus of

conservation concern on small bear populations worldwide, even when only isolated by relatively narrow fracture zones, as with grizzly bears in the Cabinet Mountains of the United States (Committee on the Status of Endangered Wildlife in Canada 2012, McLellan et al. 2017, International Union for the Conservation of Nature 2018, U.S. Fish & Wildlife Service 2021).

The current isolation of bear populations arose almost invariably from historical fracturing and fragmentation caused by unsustainable human-caused mortality concentrated in areas where access was provided by the spread of transportation infrastructure and related encroachment of human settlements (Mattson & Merrill 2002, Albrecht et al. 2017, Benazzo et al. 2017; Section 5.1.1). Unfortunately, this historical isolation has been perpetuated by on-going corrosive effects attributable to mortality as well as visual and audio disturbances associated with major transportation corridors and adjacent human settlements (see Section 6.4.1) – most of which are concentrated in major drainages transecting mountainous terrain (e.g., Gibeau & Herrero 1998, Lamb et al. 2023; Figure 49).



Figures (50a & 51) are illustrative of the barrier effect caused by heavily trafficked highways in the United States and Europe. This effect is attributable not only to impeded cross-highway movements (Section 6.5) but also heavy mortality among bears that do attempt a crossing (Section 7.2). These maps exemplify not only the concentration of mortality along valley-bottom transportation routes encompassing some bear populations, as in the Northern Continental Divide Ecosystem of the United States (Figure 50a), but also the difficulties confronting bears residing adjacent to and attempting to cross heavily trafficked highways, resulting in numerous thwarted crossing attempts (Figure 51b) and home ranges with hard edges defined by concentrations of roads and settlements (Figure 51a). Although bears can clearly navigate highways such as these, they do so far less often than they traverse more areas less impacted by humans (e.g., Gibeau & Herrero 1998, Waller & Servheen 2005, Kusak et al. 2009, Proctor et al. 2015).



Sustained isolation takes a demonstrable toll on the genetic health and viability of small bear populations. Historical fracturing and fragmentation has not only resulted in lessened demographic resilience but also increased genetic differentiation and impoverishment of population isolates, especially those subject to unsustainable killing of reproductive-aged bears by people (Miller & Waits 2003; Dixon et al. 2007; Kendall et al. 2009, 2016; Cushman et al. 2010; Mikle et al. 2016; Israel 2018;

Mattson 2019c; Palm et al. 2023). This problematic syndrome is widespread among mid-latitude brown and grizzly bear populations (e.g., Proctor et al. 2002, 2005, 2012), exemplified by the plight of isolated populations of bears with limited genetic or demographic connectivity in southern British Columbia (Proctor et al. 2012, Morgan et al. 2019; Figure 52), Cantabria, Spain (González et al. 2016), the Pyrenees Mountains of Europe (Kervellec et al. 2023), and the Cabinet Mountains of the United States (Kasworm et al. 2021a).

Section 7.4. Effects of Mitigation Infrastructure

Threats posed by the isolating effects of highways and associated human settlements have predictably led numerous researchers and managers to call for measures that increase the permeability of human-related barriers, prominently including construction of physical infrastructure to facilitate safe passage across highways (Peters et al. 2015, Morgan et al. 2019, Vaeokhaw et al. 2020, Recio et al. 2021, Bogdanović et al. 2023, Kervellec et al. 2023, Khosravi et al. 2023).

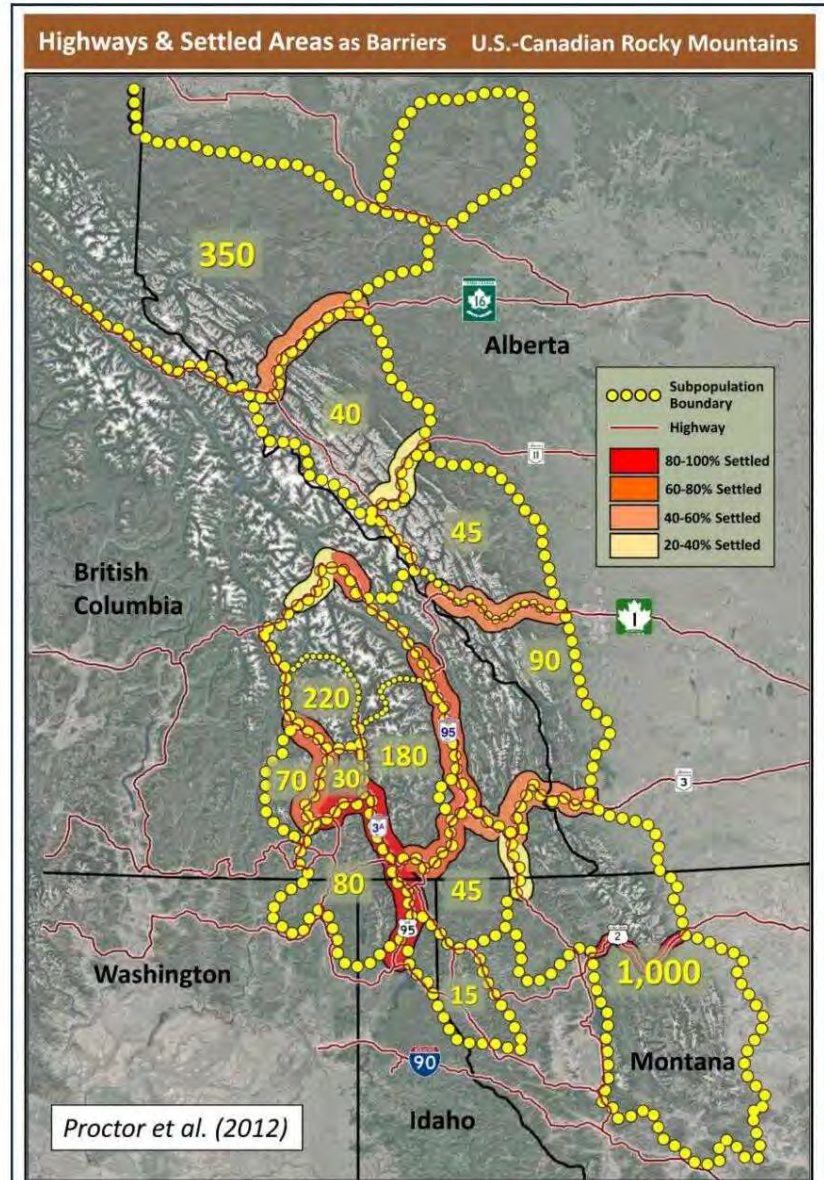
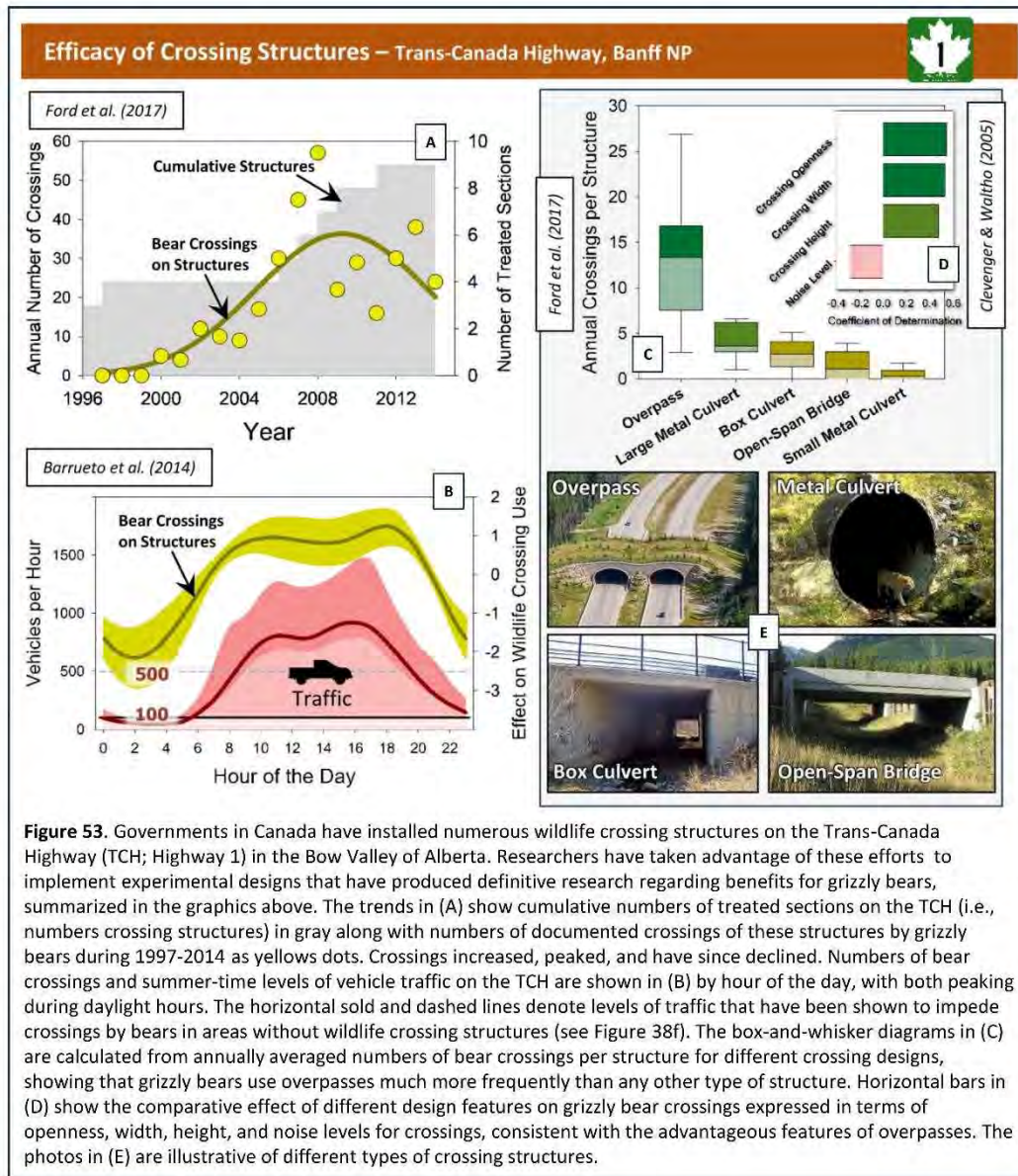


Figure 52. The map above is adapted from Proctor et al. (2012) showing fragmentation of grizzly bear populations in the Rocky Mountains of southern Canada and the northern United States. The dotted yellow lines delimit subpopulations of bears exhibiting a significant level of genetic differentiation from adjoining subpopulations. Major highways are shown as red lines, together with buffers shading from beige to red denoting levels of human development and permanent residential areas adjoining each highway segment. Estimated numbers of grizzly bears for each subpopulation are given in yellow, which in some instances include only numbers estimated for some portion of the total subpopulation (e.g., between Highways 95 and 3A in British Columbia and spanning the spine of the Rocky Mountains defining the border of Alberta and British Columbia). Only 3 of the 12 identified subpopulations likely number >300 and all but one are <1000.



Section 7.4.1. Use and Selection of Crossing Structures

Although limited in number, several jurisdictions in Canada, the United States, and eastern Europe have attempted to increase permeability of barriers aligned with major transportation corridors by not only attempting to reduce human-bear conflicts near human settlements, but also by constructing purpose-built highway crossing infrastructure or by evaluating existing features that serve as *de facto* passages to determine whether they are sufficient for the purpose. Increasingly, efforts have also been made to predict locations where crossing structures will likely provide the greatest benefits using models ranging in sophistication from those based on subjective scorings (notably in the United States, e.g., Mietz [1994], Sandstrom [1996], Walker & Craighead [1997], Servheen et al. [2001], and Singleton et al. [2004]) to those empirically derived from pre-construction bear locations and movements (e.g., Clevenger et al.

2002, Roesch 2010, Short Bull et al. 2011, Lewis et al. 2011, Proctor et al. 2015, Zeller et al. 2021) or distributions of roadkills (Zarco-González et al. 2024).

Regardless of whether purpose-built or legacy structures, evaluations of effectiveness have consistently found that although brown and grizzly bears will utilize underpasses and box culverts (Andis et al. 2017, Ford et al. 2017), they nonetheless strongly select for crossing structures that are high, wide, and short, including overpasses and open-span bridges (Clevenger & Waltho 2005, Sawaya et al. 2013, Ford et al. 2017, Denneboom 2021; Figures 53c, 53d, & 53d), with the proviso that extensive fencing on the flanks of crossing structures are essential to promoting wildlife use (Huijser et al. 2016b, Denneboom et al. 2021). Perhaps not surprisingly, little or no use of smaller-dimensioned drainage culverts by bears has been documented (Clevenger et al. 2001b). Researchers have also found that grizzly bears less often use structures influenced by elevated levels of nearby human activity (Clevenger & Waltho 2000, 2005; although see Barrueto et al. 2014) or where structures such as bridges or road underpasses are concurrently used by people (Kusak et al. 2009). Encouragingly, researchers in Banff National Park demonstrated that overall use of crossing structures by grizzly bears tends to increase as spatial coverage of crossing infrastructure expands (Ford et al. 2017; Figure 53a).

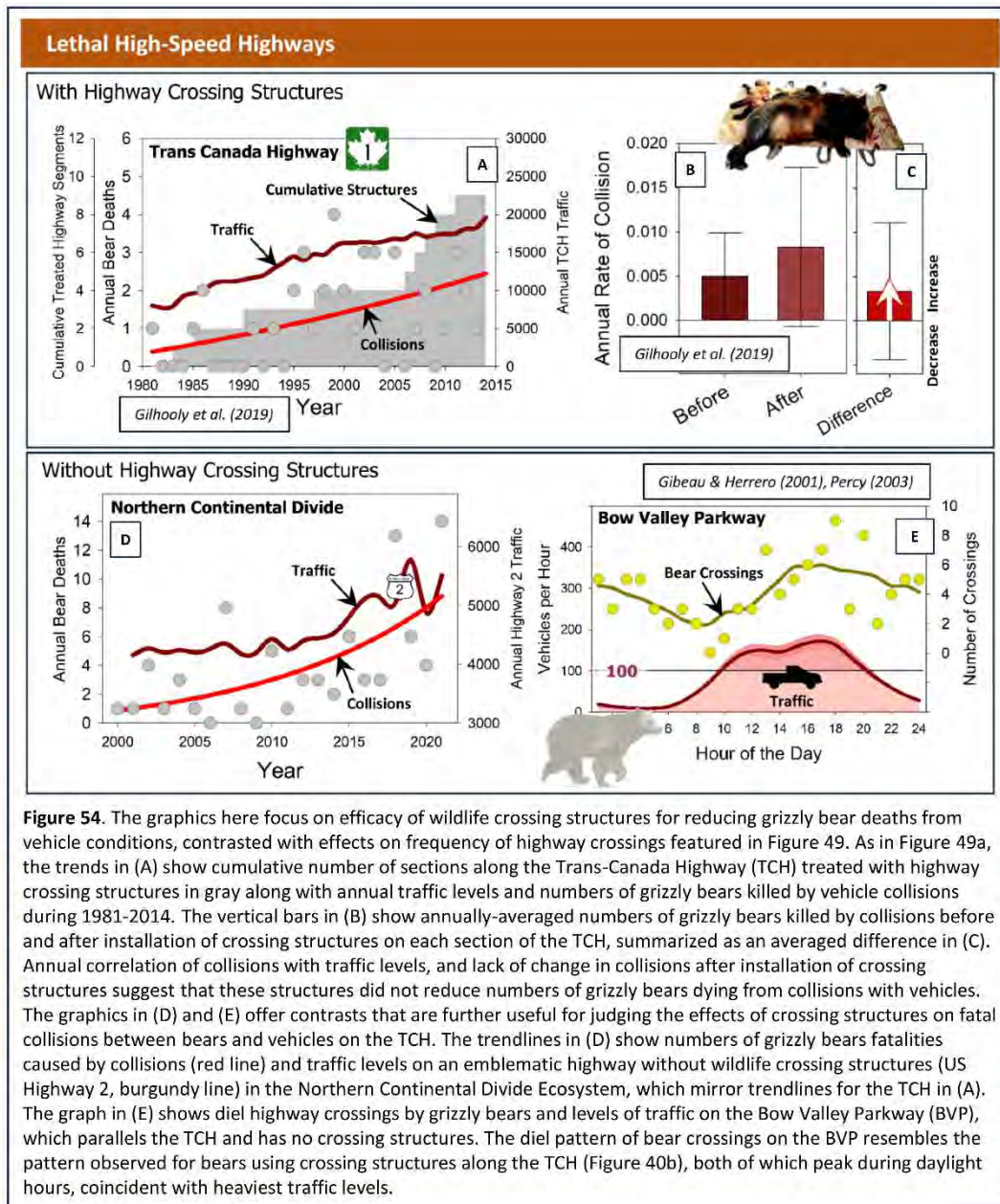
Section 7.4.2. Effects on Roadkill

Most evaluations of crossing structure effectiveness have focused on the number of detected crossings and related evidence of genetic diffusion, with evidence of use or even small amounts of genetic exchange considered to be proof of net efficacy by nearly all researchers (i.e., all the previously referenced literature plus Van Manen et al. [2012] and Sawaya et al. [2014]). However, Van der Grift (2013) and Soanes et al. (2024) made the important point that evaluations should ideally distinguish between use and effectiveness, with the former representing a low bar of evaluation and the latter requiring that researchers clearly define in advance how they define effectiveness and the currency by which they reckon it.

This distinction matters when assessing whether there is evidence that crossing structures reduce numbers of fatal vehicle collisions with bears. Unfortunately, the available evidence suggests road crossing structures *do not* reduce roadkill of bears, including more conclusive studies using controls or before- and after comparisons from Canada and the United States (Clevenger et al. 2001a, Van Manen et al. 2012, Huijser et al. 2016a, Gilhooly et al. 2019, Ford et al. 2022; Figures 54a-54c). Researchers have speculated that lack of statistical evidence for any reduction in roadkill is attributable to small sample sizes and related limited statistical power to detect change (Hardy et al. 2006, Ford et al. 2022), although the consistency of non-effects among studies calls these sorts of claims into question.

The invocation of low statistical power to explain a lack of conclusive evidence is also called into question by the similarity in the relationships between traffic levels and roadkill of bears contrasting a highway with extensive road-crossing infrastructure (the Trans-Canada Highway, Figure 54a) and a highway in a similar topographic setting farther south with no dedicated crossing structures (Highway 2, Figure 54d). In both instances, roadkill increased apace with increasing vehicle traffic. Moreover, the very similar diel peaks in daytime crossings of both the Bow Valley Parkway (Figure 54e) – which lacked crossing structures – and the nearby Trans-Canada Highway (Figure 53b) – which was comprehensively treated with crossing infrastructure – begs the question of whether and to what extent crossing structures in Bow Valley of Banff National Park facilitated a shift in hourly crossings.

A final instructive piece of evidence regarding the prospectively limited effectiveness of road crossing infrastructure for reducing bear fatalities comes from Highway 93 in the Mission Valley of Montana on the western periphery of the Northern Continental Divide Ecosystem. As in Banff National Park, studies here contrasted roadkill of bears before and after construction of localized road-crossing structures on stretches of highway flanking a longer high-speed portion of highway transecting the valley and associated agricultural bottomlands. Overall, there was no reduction in deaths of bears caused by vehicle collisions (Huijser et al. 2016a). More importantly, all the post-construction roadkill occurred along a stretch of Highway 93 that lacked crossing structures or fencing (Figure 50b), suggesting that unless there is comprehensive treatment of problematic stretches of highway with structures specifically tailored to bear behavior, there may be no decrease in fatal collisions.



Section 7.5. An Interpretation

At some level, fatal collisions between bears and vehicles on heavily trafficked high-speed highways are a phenomenon dictated by physics. Greater numbers of potentially lethal projectiles traveling at high velocities along a linear feature predictably increase the time-specific odds that any animals attempting to cross the feature will end up struck and killed. This holds for everything from bears to frogs (e.g., Rytwinski et al. 2016, Denneboom et al. 2021). Most bears seem to mitigate this risk by crossing highways when there is less traffic (Section 6.4.3) presumably because they are repelled by negative sensory stimuli and perceived danger when confronted by heavy traffic. Even so, a substantial number of brown and grizzly bears die from fatal collisions in populations exposed to this hazard (Section 7.2).

Intuitively, installing infrastructure that facilitates safe passage and channels bears towards crossing structures should reduce fatal highway collisions. This makes the disappointing performance of crossing structures on this front all the more difficult to explain, especially given that major reductions in roadkill have been repeatedly demonstrated for ungulates such as deer and elk (Glista et al. 2009, Benitez-Lopez et al. 2010, Rytwinski et al. 2016), and also because bears readily use crossing structures (Section 7.4.1) and are otherwise averse to crossing unmitigated highways.

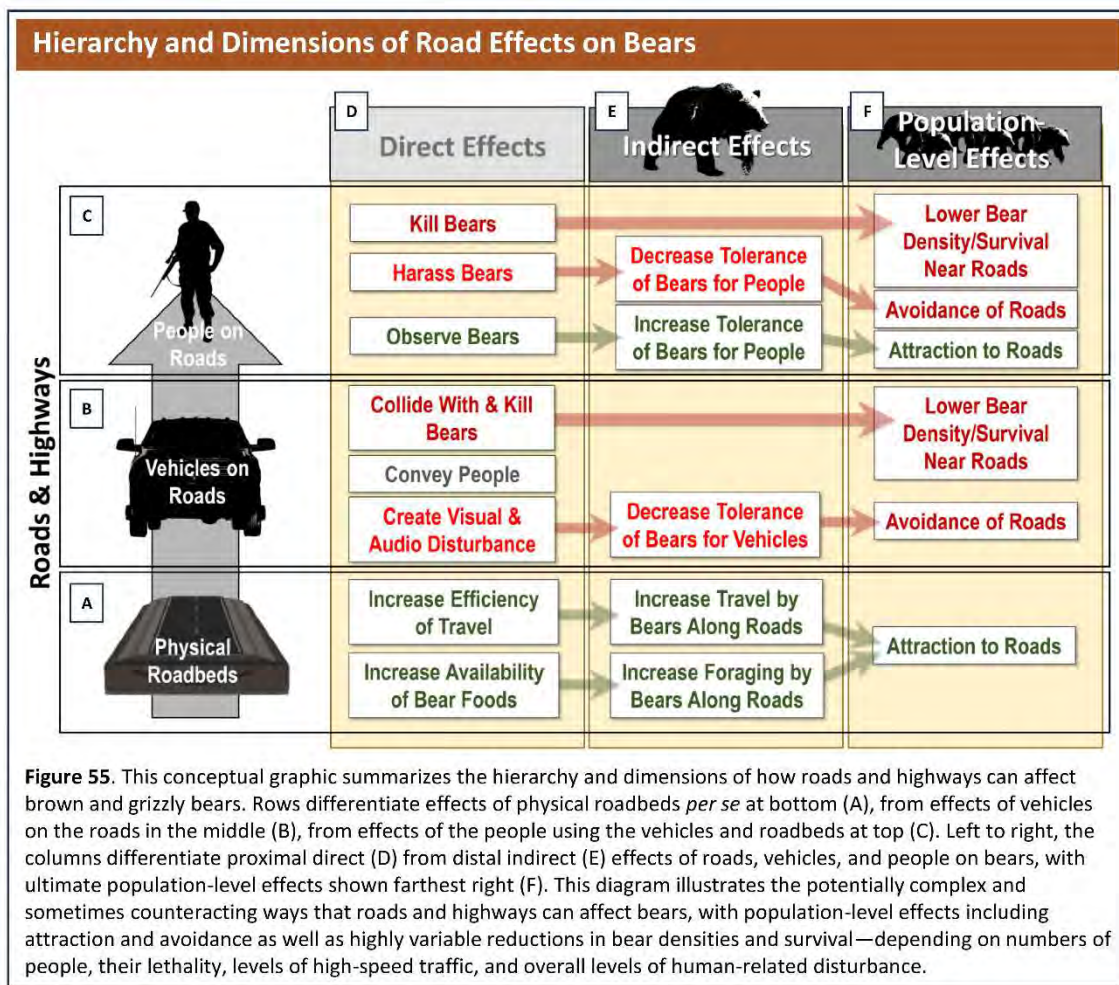
In part, this anomaly could have arisen from the lack of controlled studies investigating effects of crossing structures on bear roadkill. There have effectively been only two, leaving open the possibility that crossing structures are more effective in other areas. But another explanation could arise from the fact that bears and other large carnivores are dissimilar enough morphologically and behaviorally from ungulates to cause divergent responses to fences and crossing structures. Unlike unguligrade herbivores, the claws and plantigrade or digitigrade posture of most carnivores would allow them to potentially dig under roadside fences that otherwise channel animals to crossing structures. Plantigrade animals such as bears could, moreover, climb barrier fences more readily than either unguligrade herbivores or digitigrade carnivores. These morphological differences alone might explain the ineffectiveness of road-crossing infrastructure when it comes to reducing fatal collisions involving bears and most other carnivores, especially when compared to the substantial benefits evident for ungulates.

Wildlife and highway managers should not construe the apparent ineffectiveness of highway-crossing infrastructure for reducing bear roadkill as cause for dismissing the potential benefits of crossing structures. Rather, the equivocal evidence described in Section 7.4.2 suggests that infrastructure built to mitigate hazards for bears may need to use design criteria or strategies that are different from those employed when building infrastructure focused on reducing vehicle collisions with ungulates. Regardless of which conclusion is best supported, the review in this section suggests that anyone consulting research on efficacies of road crossing infrastructure should use caution when extrapolating ungulate-specific results to bears and be skeptical of the many articles that adopt a promotional stance (Soanes et al. 2024).



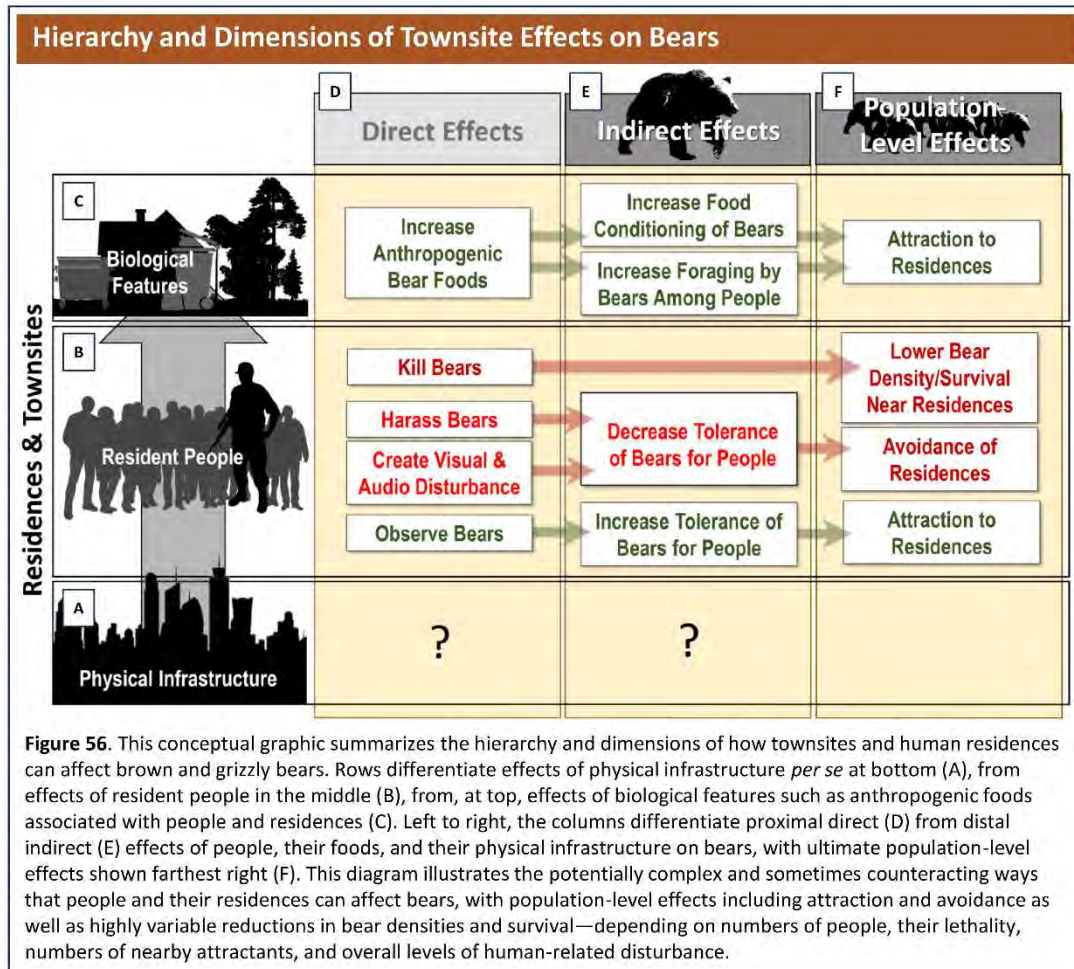
Section 8. Conclusions

Humans build roads, highways, residences, and recreational facilities for people to use, which makes it difficult to isolate the effects of people from effects attributable solely to physical structures and associated environmental alterations. Roadbeds and nearby environs predictably have different effects on bears compared to vehicles on highways – or the people using access features (Figure 55). Physical features of townsites and residences likewise have effects that are different from human-associated attractants or resident people (Figure 56). Adding more complexity yet, direct effects differ from indirect effects on individual bears, with both, in turn, differing from cumulative temporal and spatial effects on bear populations. Muddying these distinctions, human infrastructure almost invariably comes with a certain amount of human activity. The question is, how many (if any) people, during what seasons or time of day, with what attitudes and intentions, and engaged in what sorts of activities?



Figures 55 and 56 attempt to organize these considerations in a two-dimensional matrix, with effects of static physical features, moving vehicles, and people differentiated along the vertical axis, and direct, indirect, and population-level effects differentiated along the horizontal axis. As the populated cells of these matrices suggest, highways and residential areas can have a mix of both positive and negative effects on bears depending on the scale considered and whether physical features or people are the focus of attention.

These figures conceptually and visually recast the same factors featured in Sections 1.1-1.2 and 2.1-2.3 to place greater emphasis on distinctions between effects of people and effects of physical features as well as the different scales at which effects play out. Importantly, managers and researchers who fail to keep these distinctions in mind are vulnerable to misinterpreting or misrepresenting research results and inappropriately extrapolating research from one area to another. The attraction of bears to productive habitats near human facilities (Section 6.4.2) or the energetic savings of traveling on roads (Section 6.4.3) are not equivalent to bears being indifferent to disturbances or unaffected by mortality caused by people; nor are all people equal in their effects on bears (Section 5).



In fact, as I emphasize in Section 1.1, most of the variation and valence in how human infrastructure affects bears is arguably attributable to human choices and behaviors, with most responses by bears to human infrastructure being ultimately driven by where and how people chose to build infrastructure and their behaviors vis-à-vis bears while utilizing these physical features. All else equal, bears will predictably be killed by humans in greater numbers if people either build infrastructure in naturally productive habitats or proceed to create attractive conditions (e.g., timber harvest units in Alberta; Section 4.3.4) – and then populate this infrastructure with numerous armed and intolerant people (Sections 4.2.3 and 5.2). By contrast, if human infrastructure is well sanitized, built in areas that are naturally unproductive, and used by benign tolerant people, regional impacts on bears will be predictably small (Sections 4.3.4, 5.2, and 5.3).

Of relevance to this last point, there is ample evidence that brown and grizzly bears are not intrinsically afraid of humans or, if fearful and intolerant, likely to become more tolerant after a history of benign interactions with people (Stringham & Rogers 2017; Mattson 2019b, 2021a). Importantly, fear, intolerance, or the converse can emerge not only during individual lifetimes, but also cumulatively over multiple generations as a consequence of different learned behaviors being selectively transmitted from mothers to offspring (Mattson 2021a) – with much of this dynamic driven by whether rates of human-caused mortality vary among different types of bears over periods of years, decades, centuries, or even millennia (Section 5). Generalized human antipathy towards all bears or lethal actions that selectively target male bears (e.g., through male-biased conflicts or hunting) will have predictably powerful configuring effects on whether and how bears respond to human infrastructure (Figure 1; Sections 4.3.3., 5, 6.2.1, and 6.2.2).

8.1. Some Generalizations

As I observe in the Introduction (Section 1), the upshot of these considerations is that there are no universal or invariant thresholds governing the nature and extent of human infrastructure compatible with conserving brown and grizzly bear populations – unless a person does not what to deal with complexity or is promoting a political agenda, as too often seems to be case for bear managers and researchers (Mattson 2022a, 2023). Even so, there are several generalizable propositions that can be distilled from the literature reviewed in this report:

-  Humans have taken and invariably continue to take a consequential, if not catastrophic, toll on brown and grizzly bear populations worldwide (Sections 2 and 5).
-  Humans kill bears at higher rates near human infrastructure, but with substantial variation in the magnitude of this toll (Section 4).
-  Brown and grizzly bear populations fare best in the absence of all people and human infrastructure (Sections 4, 5, 6, and 7).
-  As a corollary, fewer roads are better than more roads if the goal is to conserve bear populations, with no roads being best of all (Box 1; Sections 4.2, 6.1).
-  Few people are better than more people, especially when in the form of little or no traffic on roads and few if any resident humans (Sections 4.2.4, 6.4.3, and 7.2).
-  Bears in most populations underuse areas near human infrastructure, but with considerable variation in the extent of this underuse (Section 6).
-  Bears exposed to humans and human infrastructure invariably fare better when subsidized by immigration from nearby large source areas free of human impacts (Box 2; Sections 4.2.2, 4.2.3, 4.3.4, and 7.3).



All else equal, the extent of areas secure from human impacts needs to be greater where people are armed, intolerant, and likely to violate wildlife protection laws (Box 5; Sections 5.1.2, 5.1.3, 5.2, and 5.3).



Major transportation corridors often constitute fracture zones in what would otherwise be regional meta-populations, with mountainous terrain typically exacerbating this effect (Section 7.4).



Highways are less lethal for bears when there is less traffic, lower speed limits, fewer attractants, and designs that facilitate detection of bears by drivers (Section 7.1 and 7.2).



Human infrastructure located in naturally productive environments or associated with unsecured attractants often lures bears into fatal conflicts with people (Sections 4.3.4, 4.3.5, and 6.4.2).



Bears are more vulnerable to disturbance and human-caused mortality in areas that lack visual and audio screening or protective rugged topography (Box 2; Sections 4.2.5 and 6.4.1).



Most bears in most places mitigate the hazards of human infrastructure by accelerating and directing their movements to minimize the duration of their exposure to human-related hazards (Section 6.3.2).



When near humans, nocturnal bears experience less human-caused mortality compared to diurnal bears and are consequently more common among bears that survive interactions with people (Sections 4.3.1 and 6.3.1).



Human-tolerant bears are better able to use human environs, but also die at higher rates compared to less tolerant bears (Sections 4.3.2 and 6.3.3).



The disproportionate killing of human-tolerant male bears by people often leads to security-conscious adolescents and females with dependent young concentrating near human infrastructure, typically with problematic outcomes (Sections 4.3.3 and 6.3).



Bear managers in the United States neglect impacts attributable to locating infrastructure in productive habitats without screening cover (Box 3; Sections 4.3.4).



Most standards employed by bear managers in the United States for managing grizzly bear habitat security lack scientific justification. Some are arbitrary and capricious (Sections 4.2.2 and 4.2.3).

Section 8.2. A Range of Possible Standards

The complexities described in this report debar simple-minded conclusions regarding the management of human infrastructure and grizzly bear habitat security. Even so, there is scientific support for adopting a range of specific management thresholds for promoting grizzly bear conservation, but with several important provisos. For one, adopted thresholds invariably reflect whether those who apply them are

precautionary or willing to embrace significant risk when managing habitat security for bears (e.g., Shrader-Frechette & McCoy 1994, Peel 2005). Stringent thresholds provide a buffer against unknowns and uncertainties whereas lax thresholds incur greater risk of irreversible harm. For another, even given consensus on an approach to risk, the adoption of conservative versus liberal thresholds ideally depends on the lethality of people using the affected human infrastructure. Lethal people require more constraints on their access to bear habitat, whereas benign people require fewer, if managers are to achieve conservation goals (e.g., Section 5 and Box 5).

With those provisos in mind, I have distilled two sets of standards or thresholds for managing grizzly and brown bear habitat security from the research reviewed in this report, one of which is conservative (i.e., nearer the quartiles of results from relevant studies) and the other middle of the road (i.e., nearer the mean or median), both of which can be considered rules of thumb. I have expressed criteria for adopting one or the other of these two sets in terms of independent contingencies (i.e., x, or y, or z), largely because there is not enough evidence to assess the efficacy of applying various thresholds under permuted circumstances. Prudence would dictate that if any one contingency is met a precautionary approach is warranted.

The **Conservative Set** is appropriate for regions where either <50% of bear distributions are in roadless protected areas (Section 4.2.3); regional human population densities are $>3/\text{km}^2$ ($>1.2/\text{mile}^2$); >30% of known and probable human-caused mortalities are malicious, under investigation, or attributable to suspect causes (Section 5.2.2); or humans cause >80% of known (>90% of known plus probable) adolescent and adult bear deaths (Section 2). Thresholds or standards appropriate for these conditions are:

-  **Road densities** $<0.4 \text{ km}/\text{km}^2$ (0.6 miles/mile²) (Sections 4.2.2 and 6.1.2)
-  **Buffers for defining patches of secure habitat along roads** >815 m (0.5 miles) (Section 6.1.2)
-  **Buffers for defining patches of secure habitat around townsites** >5,000 m (3 miles) (Section 6.1.2)
-  **Individual patches of secure habitat** >870 ha (2,150 acres) in size >815 m from the nearest road and >5,000 m from the nearest townsite (Section 4.2.3)
-  **Secure habitat** >75% of the regional bear distribution (Section 4.2.3)
-  **Population source areas** >4,000 km² in size (1,550 miles²) (Box 2)

The **Middle of the Road Set** is appropriate for regions where >50% of bear distributions are in protected areas; regional human densities are $<3/\text{km}^2$ ($<1.2/\text{mile}^2$); <30% of human-caused mortalities implicate intolerant or otherwise lethal humans; or where humans cause <75% of known (<87% of known plus probable) adolescent and adult bear deaths. Thresholds or standards appropriate for these conditions are:

-  **Road densities** $<0.7 \text{ km}/\text{km}^2$ (1.1 miles/mile²) (Sections 4.2.2 and 6.1.2)
-  **Buffers for defining patches of secure habitat along roads** >400 m wide (0.25 miles) (Section 6.1.2)



Buffers for defining patches of secure habitat around townsites >3,000 m wide (2 miles)
(Section 6.1.2)



Individual patches of secure habitat >490 ha (1,200 acres) in size >400 m from the nearest road
and >3,000 m from the nearest townsite (Section 4.2.3)



Secure habitat >65% of the regional bear distribution (Section 4.2.3)



Population source areas >1,000 km² in size (390 miles²) (Box 2)

More concretely, the conservative set of standards presented here would be appropriate for managing bear habitat security where populations are small, partially isolated, and exhibiting little or no absolute growth. Prime examples include the Selkirk and Cabinet-Yaak populations in the United States (U.S. Fish & Wildlife Service 2021); the Garibaldi-Pitt, North Cascades, South Selkirk, Stein-Nahatlatch, and Yahk population units in British Columbia (Morgan et al. 2019); and the Castle, Clearwater, Swan Hills, and Yellowhead population units in Alberta (Festa-Bianchet 2010). That having been said, the constraints imposed by extant human infrastructure and populations in areas occupied by these sorts of at-risk population probably make conservative standards for managing habitat security largely aspirational. Even so, conservative standards are more appropriate and effective than middle of the road standards for rescuing and recovering vulnerable brown and grizzly bear populations.



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Section 9. Cited and Other Relevant Literature

- Adamič, M. (1997). The analysis of key source of mortality of the brown bear (*Ursus arctos* L.) In Slovenia in the last 6 years. *Ljubljana*, 53, 5-28.
- Ahmadipari, M., Yavari, A., & Ghobadi, M. (2021). Ecological monitoring and assessment of habitat suitability for brown bear species in the Oshtorankooh protected area, Iran. *Ecological Indicators*, 126, 107606.
- Albrecht, J., Bartoń, K. A., Selva, N., Sommer, R. S., Swenson, J. E., & Bischof, R. (2017). Humans and climate change drove the Holocene decline of the brown bear. *Scientific Reports*, 7(1), 10399.
- Alexander, S. M., Waters, N. M., & Paquet, P. C. (2005). Traffic volume and highway permeability for a mammalian community in the Canadian Rocky Mountains. *Canadian Geographer*, 49(4), 321-331.
- Allen, M. L., Krofel, M., Yamazaki, K., Alexander, E. P., & Koike, S. (2022). Cannibalism in bears. *Ursus*, 33(10), 1-9.
- Ambarlı, H., & Bilgin, C. C. (2008). Human–brown bear conflicts in Artvin, northeastern Turkey: Encounters, damage, and attitudes. *Ursus*, 19(2), 146-153.
- Andis, A. (2016). Performance measures of road crossing structures from relative movement rates of large mammals. M.S. Thesis, University of Montana, Missoula, Montana.
- Andis, A. Z., Huijser, M. P., & Broberg, L. (2017). Performance of arch-style road crossing structures from relative movement rates of large mammals. *Frontiers in Ecology & Evolution*, 5, Article 122.
- Apps, C. D., McLellan, B. N., Woods, J. G., & Proctor, M. F. (2004). Estimating grizzly bear distribution and abundance relative to habitat and human influence. *Journal of Wildlife Management*, 68(1), 138-152.
- Apps, C. D., McLellan, B. N., Proctor, M. F., Stenhouse, G. B., & Servheen, C. (2016). Predicting spatial variation in grizzly bear abundance to inform conservation. *The Journal of Wildlife Management*, 80(3), 396-413.
- Archibald, W. R., Ellis, R., & Hamilton, A. N. (1987). Responses of grizzly bears to logging truck traffic in the Kimsquit River Valley, British Columbia. *International Conference on Bear Research & Management*, 7, 251-257.
- Ardö, J., & Pilesjö, P. (1992). On the accuracy of the global positioning system—a test using a hand-held receiver. *International Journal of Remote Sensing*, 13(16), 3229-3233.
- Aarts, L., & Van Schagen, I. (2006). Driving speed and the risk of road crashes: A review. *Accident Analysis & Prevention*, 38(2), 215-224.
- Aune, K., & Kasworm, W. (1989). East Front grizzly studies: final report. Montana Department of Fish, Wildlife & Parks, Helena, Montana.
- Babic, N. L., Johnstone, C. P., Reljić, S., Sergiel, A., Huber, D., & Reina, R. D. (2023). Evaluation of physiological stress in free-ranging bears: current knowledge and future directions. *Biological Reviews*, 98(1), 168-190.
- Barton, K. A., Zwijacz-Kozica, T., Zieba, F., Sergiel, A., & Selva, N. (2019). Bears without borders: long-distance movement in human-dominated landscapes. *Global Ecology and Conservation*, 17, Article e00541.
- Barrientos, R., Ascensão, F., D'Amico, M., Grilo, C., & Pereira, H. M. (2021). The lost road: Do transportation networks imperil wildlife population persistence?. *Perspectives in Ecology & Conservation*, 19(4), 411-416.
- Barrueto, M., Ford, A. T., & Clevenger, A. P. (2014). Anthropogenic effects on activity patterns of wildlife at crossing structures. *Ecosphere*, 5(3), 1-19.

- Baruch-Mordo, S., Breck, S. W., Wilson, K. R., & Theobald, D. M. (2008). Spatiotemporal distribution of black bear-human conflicts in Colorado, USA. *Journal of Wildlife Management*, 72(8), 1853-1862.
- Basile, J. V., & Lonner, T. N. (1979). Vehicle restrictions influence elk and hunter distribution in Montana. *Journal of Forestry*, 77(3), 155-159.
- Battin, J. (2004). When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology*, 18(6), 1482-1491.
- Bechtold, T., Havlick, D., & Stockman, K. (1996). Analysis of road densities in selected Bear Management Units in the Northern Rockies. *Proceedings of the 16th ESRI User's Conference*, Palm Springs, California.
- Beckmann, J. P., Clevenger, A. P., Huijser, M. P., & Hilty, J. A. (2010). *Safe passages: Highways, wildlife, and habitat connectivity*. Island Press, Washington, D.C.
- Bellemain, E., Swenson, J. E., & Taberlet, P. (2006). Mating strategies in relation to sexually selected infanticide in a non-social carnivore: the brown bear. *Ethology*, 112(3), 238-246.
- Ben-David, M., Titus, K., & Beier, L. R. (2004). Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide?. *Oecologia*, 138, 465-474.
- Bénard, A., Lengagne, T., & Bonenfant, C. (2023). A biologically realistic model to predict wildlife-vehicle collision risks. *bioRxiv*, 2023-02.
- Benazzo, A., Trucchi, E., Cahill, J. A., Maisano Delser, P., Mona, S., Fumagalli, M., ... & Bertorelle, G. (2017). Survival and divergence in a small group: The extraordinary genomic history of the endangered Apennine brown bear stragglers. *Proceedings of the National Academy of Sciences*, 114(45), E9589-E9597.
- Benítez-López, A., Alkemade, R., & Verweij, P. A. (2010). The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. *Biological Conservation*, 143(6), 1307-1316.
- Benn, B., & Herrero, S. (2002). Grizzly bear mortality and human access in Banff and Yoho National Parks, 1971-98. *Ursus*, 13, 213-221.
- Bennett, V. J. (2017). Effects of road density and pattern on the conservation of species and biodiversity. *Current Landscape Ecology Reports*, 2, 1-11.
- Berger, J., Swenson, J.E., & Persson, I.-L. (2001). Recolonizing carnivores and naive prey: Conservation lessons from Pleistocene extinctions. *Science*, 291, 1036-1039.
- Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters*, 3(6), 620-623.
- Beringer, J. J., Seibert, S. G., & Pelton, M. R. (1990). Incidence of road crossing by black bears on Pisgah National Forest, North Carolina. *International Conference on Bear Research & Management*, 8, 85-92.
- Berland, A., Nelson, T., Stenhouse, G., Graham, K., & Cranston, J. (2008). The impact of landscape disturbance on grizzly bear habitat use in the Foothills Model Forest, Alberta, Canada. *Forest Ecology & Management*, 256(11), 1875-1883.
- Bertwistle, J. (2001). Description and analysis of vehicle and train collisions with wildlife in Jasper National Park, Alberta Canada, 1951-1999. Pages 433-434 in *Proceedings of the 2001 International Conference on Ecology & Transportation Proceedings*. North Carolina State University, Raleigh, North Carolina.

Bevan, A., Colledge, S., Fuller, D., Fyfe, R., Shennan, S., & Stevens, C. (2017). Holocene fluctuations in human population demonstrate repeated links to food production and climate. *Proceedings of the National Academy of Sciences*, 114(49), E10524-E10531.

Billion, C. E. (1959). Shoulder Occupancy on Rural Highways. In *HRB Proc* (Vol. 38).

Bischof, R., Swenson, J. E., Yoccoz, N. G., Mysterud, A., & Gimenez, O. (2009). The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. *Journal of Animal Ecology*, 78(3), 656-665.

Bischof, R., Steyaert, S. M., & Kindberg, J. (2017). Caught in the mesh: Roads and their network scale impediment to animal movement. *Ecography*, 40(12), 1369-1380.

Bischof, R., Bonenfant, C., Rivrud, I. M., Zedrosser, A., Friebe, A., Coulson, T., ... & Swenson, J. E. (2018). Regulated hunting re-shapes the life history of brown bears. *Nature Ecology & Evolution*, 2(1), 116-123.

Bischof, R., Milleret, C., Dupont, P., Chipperfield, J., Tourani, M., Ordiz, A., ... & Kindberg, J. (2020). Estimating and forecasting spatial population dynamics of apex predators using transnational genetic monitoring. *Proceedings of the National Academy of Sciences*, 117(48), 30531-30538.

Bjerke, T., & Kaltenborn, B. P. (1999). The relationship of ecocentric and anthropocentric motives to attitudes toward large carnivores. *Journal of Environmental psychology*, 19(4), 415-421.

Blanchard, B. M., & Knight, R. R. (1991). Movements of Yellowstone grizzly bears. *Biological Conservation*, 58(1), 41-67.

Bogdanović, N., Zedrosser, A., Hertel, A. G., Zarzo-Arias, A., & Ćirović, D. (2023). Where to go? Habitat preferences and connectivity at a crossroad of European brown bear metapopulations. *Global Ecology & Conservation*, 43, e02460.

Boitani, L., Ciucci, P., Corsi, F., & Dupre, E. (1999). Potential range and corridors for brown bears in the Eastern Alps, Italy. *Ursus*, 11, 123-130.

Bombieri, G., Naves, J., Penteriani, V., Selva, N., Fernández-Gil, A., López-Bao, J. V., ... & Delgado, M. M. (2019). Brown bear attacks on humans: a worldwide perspective. *Scientific Reports*, 9(1), 8573.

Bombieri, G., Penteriani, V., Almasieh, K., Ambarlı, H., Ashrafzadeh, M. R., Das, C. S., ... & del Mar Delgado, M. (2023). A worldwide perspective on large carnivore attacks on humans. *PLoS biology*, 21(1), e3001946.

Boulanger, J., Cattet, M., Nielsen, S. E., Stenhouse, G., & Cranston, J. (2013). Use of multi state models to explore relationships between changes in body condition, habitat and survival of grizzly bears *Ursus arctos horribilis*. *Wildlife Biology*, 19(3), 274-288.

Boulanger, J., & Stenhouse, G. B. (2014). The impact of roads on the demography of grizzly bears in Alberta. *PloS One*, 9(12), e115535.

Boulanger, J., Nielsen, S. E., & Stenhouse, G. B. (2018). Using spatial mark-recapture for conservation monitoring of grizzly bear populations in Alberta. *Scientific Reports*, 8(1), 1-15.

Boyce, M. S., & Waller, J. S. (2003). Grizzly bears for the Bitterroot: predicting potential abundance and distribution. *Wildlife Society Bulletin*, 31(3), 670-683.

Boyce, M. S. (2006). Scale for resource selection functions. *Diversity & Distributions*, 12(3), 269-276.

- Braunstein, J. L., Clark, J. D., Williamson, R. H., & Stiver, W. H. (2020). Black bear movement and food conditioning in an exurban landscape. *Journal of Wildlife Management*, 84(6), 1038-1050.
- Brody, A. J., & Pelton, M. R. (1989). Effects of roads on black bear movements in western North Carolina. *Wildlife Society Bulletin*, 17(1), 5-10.
- Brown, D. E. (1996). *The grizzly in the Southwest: Documentary of an extinction*. University of Oklahoma Press, Norman, Oklahoma.
- Brown, L., Zedrosser, A., Arnemo, J. M., Fuchs, B., Kindberg, J., & Pelletier, F. (2023). Landscape of fear or landscape of food? Moose hunting triggers an antipredator response in brown bears. *Ecological Applications*, 33(4), e2840.
- Brown, L., Zedrosser, A., Kindberg, J., & Pelletier, F. (2024). Behavioural responses of brown bears to roads and hunting disturbance. *Ecology & Evolution*, 14(6), e11532.
- Bunnell, F. L., & Tait, D. E. N. (1981). Population dynamics of bears – Implications. Pages 75-98 in Fowler, C. W., & Smith, T. D. (eds). *Dynamics of large mammal populations*. John Wiley & Sons, New York, New York.
- Brunner, B. (2007). *Bears: A brief history*. Yale University Press, New Haven, Connecticut.
- Burson III, S. L., Belant, J. L., Fortier, K. A., & III, W. T. (2000). The effect of vehicle traffic on wildlife in Denali National Park. *Arctic*, 53(2), 146-151.
- Burton, A. C., Beirne, C., Gaynor, K. M., Sun, C., Granados, A., Allen, M. L., ... & Oberosler, V. (2024). Mammal responses to global changes in human activity vary by trophic group and landscape. *Nature Ecology & Evolution*, 8(5), 924-935.
- Byrd, K. (2002). Mirrors and metaphors: Contemporary narratives of the wolf in Minnesota. *Ethics, Place & Environment*, 5(1), 50-65.
- Can, Ö. E., D'Cruze, N., Garshelis, D. L., Beecham, J., & Macdonald, D. W. (2014). Resolving human-bear conflict: A global survey of countries, experts, and key factors. *Conservation Letters*, 7, 501–513.
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J., & Mace, G. M. (2004). Human population density and extinction risk in the world's carnivores. *PLoS Biology*, 2(7), e197.
- Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R., Sechrest, W., ... & Purvis, A. (2005). Multiple causes of high extinction risk in large mammal species. *Science*, 309(5738), 1239-1241.
- Cardillo, M., Mace, G. M., Gittleman, J. L., Jones, K. E., Bielby, J., & Purvis, A. (2008). The predictability of extinction: biological and external correlates of decline in mammals. *Proceedings of the Royal Society B: Biological Sciences*, 275(1641), 1441-1448.
- Carroll, C., Noss, R. F., & Paquet, P. C. (2001). Carnivores as focal species for conservation planning in the Rocky Mountain region. *Ecological Applications*, 11(4), 961-980.
- Carroll, C., Noss, R. F., Paquet, P. C., & Schumaker, N. H. (2003). Use of population viability analysis and reserve selection algorithms in regional conservation plans. *Ecological Applications*, 13(6), 1773-1789.
- Ceia-Hasse, A., Borda-de-Água, L., Grilo, C., & Pereira, H. M. (2017). Global exposure of carnivores to roads. *Global Ecology & Biogeography*, 26(5), 592-600.
- Chapron, G., Kaczensky, P., Linnell, J. D., Von Arx, M., Huber, D., Andrén, H., ... & Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, 346(6216), 1517-1519.

- Chetkiewicz, C. L. B., & Boyce, M. S. (2009). Use of resource selection functions to identify conservation corridors. *Journal of Applied Ecology*, 46(5), 1036-1047.
- Chevin, L. M., Lande, R., & Mace, G. M. (2010). Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. *PLoS Biology*, 8(4), e1000357.
- Chruszcz, B., Clevenger, A. P., Gunson, K. E., & Gibeau, M. L. (2003). Relationships among grizzly bears, highways, and habitat in the Banff-Bow Valley, Alberta, Canada. *Canadian Journal of Zoology*, 81(8), 1378-1391.
- Ciarniello, L.M., Boyce, M.S., Heard, D.C., & Seip, D.R. (2007) Components of grizzly bear habitat selection: Density, habitats, roads, and mortality risk. *Journal of Wildlife Manage*, 71, 1446–1457.
- Ciarniello, L. M., Boyce, M. S., Seip, D. R., & Heard, D. C. (2009). Comparison of grizzly bear *Ursus arctos* demographics in wilderness mountains versus a plateau with resource development. *Wildlife Biology*, 15(3), 247-265.
- Cisneros-Araujo, P., Goicolea, T., Mateo-Sánchez, M. C., García-Viñás, J. I., Marchamalo, M., Mercier, A., & Gastón, A. (2021). The role of remote sensing data in habitat suitability and connectivity modeling: Insights from the Cantabrian brown bear. *Remote Sensing*, 13(6), 1138.
- Clark, T. W., & Casey, D. (1992). *Tales of the grizzly: Thirty-nine stories of grizzly bear encounters in the wilderness*. Homestead Publishing, Moose, Wyoming.
- Clarke, M. J. (2022). Quantifying grizzly bear (*Ursus arctos*) habitat selection for a seasonal resource, the Canadian buffaloberry (*Shepherdia canadensis*) in southern British Columbia. M.S. Thesis, University of British Columbia – Okanagan, Okanagan, British Columbia.
- Clevenger, A. P., Purroy, F. J., & Campos, M. A. (1997). Habitat assessment of a relict brown bear *Ursus arctos* population in northern Spain. *Biological Conservation*, 80(1), 17-22.
- Clevenger, A. P., & Waltho, N. (2000). Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. *Conservation Biology*, 14(1), 47-56.
- Clevenger, A. P., Chruszcz, B., & Gunson, K. E. (2001a). Highway mitigation fencing reduces wildlife-vehicle collisions. *Wildlife Society Bulletin*, 29(2), 646-653.
- Clevenger, A. P., Chruszcz, B., & Gunson, K. (2001b). Drainage culverts as habitat linkages and factors affecting passage by mammals. *Journal of Applied Ecology*, 38(6), 1340-1349.
- Clevenger, A. P., Wierchowski, J., Chruszcz, B., & Gunson, K. (2002). GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. *Conservation Biology*, 16(2), 503-514.
- Clevenger, A. P., & Waltho, N. (2005). Performance indices to identify attributes of highway crossing structures facilitating movement of large mammals. *Biological Conservation*, 121(3), 453-464.
- Clevenger, A. P. (2012). Mitigating continental-scale bottlenecks: How small-scale highway mitigation has large-scale impacts. *Ecological Restoration*, 30(4), 300-307.
- Cole, G. F. (1974). Management involving grizzly bears and humans in Yellowstone National Park, 1970–73. *BioScience*, 24(6), 335-338.

Colton, C. P., Coops, N. C., & Burton, A. C. (2021). Grizzly bear (*Ursus arctos*) responses to forest harvesting: A review of underlying mechanisms and management recommendations. *Forest Ecology & Management*, 497, 119471.

Committee on the Status of Endangered Wildlife in Canada (2012). COSEWIC assessment and status report on the Grizzly Bear *Ursus arctos* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Canada. www.registrelep.sararegistry.gc.ca/default_e.cfm

Coogan, S. C., Raubenheimer, D., Stenhouse, G. B., Coops, N. C., & Nielsen, S. E. (2018). Functional macronutritional generalism in a large omnivore, the brown bear. *Ecology & Evolution*, 8(4), 2365-2376.

Cook, T. C., & Blumstein, D. T. (2013). The omnivore's dilemma: Diet explains variation in vulnerability to vehicle collision mortality. *Biological Conservation*, 167, 310-315.

Costello, C. M., Mace, R. D. & Roberts, L. (2016). Grizzly bear demographics in the Northern Continental Divide Ecosystem, Montana: research results (2004–2014) and suggested techniques for management of mortality. Montana Department of Fish, Wildlife & Parks. Helena, Montana.

Costello, C.M., & Roberts, L. L. (2017). Northern Continental Divide Ecosystem grizzly bear monitoring team annual report, 2016. Montana Fish, Wildlife & Parks, Kalispell, Montana.

Costello, C.M., & Roberts, L. L. (2018). Northern Continental Divide Ecosystem grizzly bear monitoring team annual report, 2017. Montana Fish, Wildlife & Parks, Kalispell, Montana.

Costello, C.M., & Roberts, L. L. (2019). Northern Continental Divide Ecosystem grizzly bear monitoring team annual report, 2018. Montana Fish, Wildlife & Parks, Kalispell, Montana.

Costello, C.M., & Roberts, L. L. (2020). Northern Continental Divide Ecosystem grizzly bear monitoring team annual report, 2019. Montana Fish, Wildlife & Parks, Kalispell, Montana.

Costello, C.M., & Roberts, L. L. (2021). Northern Continental Divide Ecosystem grizzly bear monitoring team annual report, 2020. Montana Fish, Wildlife & Parks, Kalispell, Montana.

Costello, C.M., & Roberts, L. L. (2022). Northern Continental Divide Ecosystem grizzly bear monitoring team annual report, 2021. Montana Fish, Wildlife & Parks, Kalispell, Montana.

Cox, D. T., Gardner, A. S., & Gaston, K. J. (2023). Diel niche variation in mammalian declines in the Anthropocene. *Scientific Reports*, 13(1), Article 1031.

Craighead, F. C., Jr., & Craighead, J. J. (1965). Tracking grizzly bears. *BioScience*, 15(2), 88-92.

Craighead, F. C., Jr., Craighead, J. J., Cote, C. E., & Beuchner, H. K. (1972). Satellite and ground radio tracking of elk. Pages 99-111 in Galler, S. R., Schmidt-Koenig, K., Jacobs, G. J., & Belleville, R. E. (eds). *Proceedings of a conference on animal orientation and navigation*. NASA Scientific Publications, 262.

Craighead, J. J., Varney, J. R., & Craighead Jr, F. C. (1974). A population analysis of the Yellowstone grizzly bears. University of Montana, Montana Forest & Conservation Experiment Station Bulletin 40. <https://scholarworks.umt.edu/cgi/viewcontent.cgi?article=1024&context=umforestrybulletin>

Craighead, J. J., Craighead, F. C., & Sumner, J. (1976). Reproductive cycles and rates in the grizzly bear, *Ursus arctos horribilis*, of the Yellowstone ecosystem. *International Conference on Bear Research & Management*, 3, 337-356.

Craighead, J. J., Sumner, J. S., & Mitchell, J. A. (1995). The grizzly bears of Yellowstone: Their ecology in the Yellowstone ecosystem, 1959-1992. Island Press, Washington, D.C.

Craighead, L., & Olenicki, T. (2005). Modeling highway impacts related to grizzly bear core, living, and connectivity habitat in Idaho, Montana, and Wyoming using a two-scale approach. Pages 287-291 in *On the road to stewardship: Wildlife impacts and conservation solutions*.

Cristescu, B., Stenhouse, G. B., & Boyce, M. S. (2013). Perception of human-derived risk influences choice at top of the food chain. *PLoS One*, 8(12), e82738.

Cristescu, B., Stenhouse, G. B., & Boyce, M. S. (2016a). Large omnivore movements in response to surface mining and mine reclamation. *Scientific Reports*, 6(1), 19177.

Cristescu, B., Stenhouse, G. B., Goski, B., & Boyce, M. S. (2016b). Grizzly bear space use, survival, and persistence in relation to human habitation and access. *Human–Wildlife Interactions*, 10(2), 240-257.

Curveira-Santos, G., Marion, S., Sutherland, C., Beirne, C., Herdman, E. J., Tattersall, E. R., ... & Burton, A. C. (2024). Disturbance-mediated changes to boreal mammal spatial networks in industrializing landscapes. *Ecological Applications*, e3004.

Cushman, S. A., & Lewis, J. S. (2010). Movement behavior explains genetic differentiation in American black bears. *Landscape ecology*, 25, 1613-1625.

Cushman, S. A., Lewis, J. S., & Landguth, E. L. (2013). Evaluating the intersection of a regional wildlife connectivity network with highways. *Movement Ecology*, 1, 1-11.

Custer Gallatin National Forest (2014). Occupancy and Use Order #01-14-11-00-02.

Dahle, B., & Swenson, J. E. (2003a). Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos*. *Journal of Animal Ecology*, 72(4), 660-667.

Dahle, B., & Swenson, J. E. (2003b). Home ranges in adult Scandinavian brown bears (*Ursus arctos*): effect of mass, sex, reproductive category, population density and habitat type. *Journal of Zoology*, 260(4), 329-335.

Dai, Y., Hacker, C. E., Zhang, Y., Li, Y., Li, J., Xue, Y., & Li, D. (2020). Conflicts of human with the Tibetan brown bear (*Ursus arctos pruinosus*) in the Sanjiangyuan region, China. *Global Ecology & Conservation*, 22, e01039.

Dalerum, F., Selby, L. O., & Pirk, C. W. (2020). Relationships between livestock damages and large carnivore densities in Sweden. *Frontiers in Ecology & Evolution*, 7, 507.

Danuta, F. (2018). Resting site selection by brown bears (*Ursus arctos*) in the Bieszczady Mountains, Poland. M.S. Thesis, Jagiellonian University, Cracow, Poland.

De Angelis, D. (2019). Moving in a crowded world: Ecological and human related factors affecting brown bear space-use patterns. Ph.D. Dissertation, Sapienza University of Rome, Rome, Italy.

Denneboom, D., Bar-Massada, A., & Shwartz, A. (2021). Factors affecting usage of crossing structures by wildlife—A systematic review and meta-analysis. *Science of the Total Environment*, 777, Article 146061.

Diamond, E. P. (2023). Understanding rural identities and environmental policy attitudes in America. *Perspectives on Politics*, 21(2), 502-518.

Diefenbach, D. R., Finley, J. C., Luloff, A. E., Stedman, R., Swope, C. B., Zinn, H. C., & San Julian, G. J. (2005). Bear and deer hunter density and distribution on public land in Pennsylvania. *Human Dimensions of Wildlife*, 10(3), 201-212.

Ditmer, M. A., Garshelis, D. L., Noyce, K. V., Laske, T. G., Iaizzo, P. A., Burk, T. E., ... & Fieberg, J. R. (2015). Behavioral and physiological responses of American black bears to landscape features within an agricultural region. *Ecosphere*, 6(3), 1-21.

Ditmer, M. A., Rettler, S. J., Fieberg, J. R., Iazzo, P. A., Laske, T. G., Noyce, K. V., & Garshelis, D. L. (2018). American black bears perceive the risks of crossing roads. *Behavioral Ecology*, 29(3), 667-675.

Dixon, B. G. (1997). Cumulative effects modeling for grizzly bears in the Greater Yellowstone Ecosystem. M.S. Thesis, Montana State University, Bozeman, Montana.

Dixon, J. D., Oli, M. K., Wooten, M. C., Eason, T. H., McCown, J. W., & Cunningham, M. W. (2007). Genetic consequences of habitat fragmentation and loss: the case of the Florida black bear (*Ursus americanus floridanus*). *Conservation Genetics*, 8, 455-464.

Doak, D. F. (1995). Source sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. *Conservation Biology*, 9(6), 1370-1379.

Donatelli, A., Mastrantonio, G., & Ciucci, P. (2022). Circadian activity of small brown bear populations living in human-dominated landscapes. *Scientific Reports*, 12(1), 15804.

Donelon, S. (2004). Fine scale spatial and temporal patterns of grizzly bears in the Bow Valley of Alberta. M.S. Thesis, Royal Roads University, Victoria, British Columbia.

Dood, A. R., Brannon, R. D., & Mace, R. D. (1986). Management of grizzly bears in the Northern Continental Divide Ecosystem. *Transactions of the North American Wildlife & Natural Resources Conference*, 51, 162-177.

Downey, S. S., Haas Jr, W. R., & Shennan, S. J. (2016). European Neolithic societies showed early warning signals of population collapse. *Proceedings of the National Academy of Sciences*, 113(35), 9751-9756.

Dunlap, R. E., & Mertig, A. G. (1991). The evolution of the US environmental movement from 1970 to 1990: An overview. *Society & Natural Resources*, 4(3), 209-218.

Dunn, J. A. (2023). A tangled path to extremism: desperation, resentment, and rebellion in rural Montana. Ph.D. Dissertation, Montana State University, Bozeman, Montana.

Duquette, J. F., Belant, J. L., Wilton, C. M., Fowler, N., Waller, B. W., Beyer Jr, D. E., ... & Beringer, J. (2017). Black bear (*Ursus americanus*) functional resource selection relative to intraspecific competition and human risk. *Canadian Journal of Zoology*, 95(3), 203-212.

Dyck, M. A., Shoemaker, K. T., Dennison, C. C., & Popescu, V. D. (2023). Simulated effects of roadkill and harvest on the viability of a recovering bobcat population. *Journal of Wildlife Management*, 87(7), e22460.

Egbert, A. L., & Stokes, A. W. (1976). The social behaviour of brown bears on an Alaskan salmon stream. *International Conference on Bear Research & Management*, 3, 41-56.

Eberhardt, L. L., Blanchard, B. M., & Knight, R. R. (1994). Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. *Canadian Journal of Zoology*, 72(2), 360-363.

Elfström, M., Zedrosser, A., Støen, O. G., & Swenson, J. E. (2012). Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: review and management implications. *Mammal Review*, 44(1), 5-18.

Elfström, M., Davey, M. L., Zedrosser, A., Müller, M., De Barba, M., Støen, O. G., ... & Swenson, J. E. (2014). Do Scandinavian brown bears approach settlements to obtain high-quality food?. *Biological Conservation*, 178, 128-135.

Elgmork, K. (1978). Human impact on a brown bear population (*Ursus arctos* L.). *Biological Conservation*, 13(2), 81-103.

- Eliason, S. L. (1999). The illegal taking of wildlife: Toward a theoretical understanding of poaching. *Human Dimensions of Wildlife*, 4(2), 27-39.
- Evans, M. J., Rittenhouse, T. A., Hawley, J. E., & Rego, P. W. (2017). Black bear recolonization patterns in a human-dominated landscape vary based on housing: New insights from spatially explicit density models. *Landscape & Urban Planning*, 162, 13-24.
- Fan, J., Li, J., Quan, Z., Wu, X., Hu, L., & Yang, Q. (2011). Impact of road construction on giant panda's habitat and its carrying capacity in Qinling Mountains. *Acta Ecologica Sinica*, 31(3), 145-149.
- Fahrig, L., & Rytwinski, T. (2009). Effects of roads on animal abundance: An empirical review and synthesis. *Ecology & Society*, 14, Article 21.
- Falcinelli, D., del Mar Delgado, M., Kojola, I., Heikkinen, S., Lamamy, C., & Penteriani, V. (2024). The use of anthropogenic areas helps explain male brown bear movement rates and distance travelled during the mating season. *Journal of Zoology*.
- Falcucci, A., Ciucci, P., Maiorano, L., Gentile, L., & Boitani, L. (2009). Assessing habitat quality for conservation using an integrated occurrence-mortality model. *Journal of Applied Ecology*, 46, 600-609.
- Fedorca, A., Russo, I. R. M., Ionescu, O., Ionescu, G., Popa, M., Fedorca, M., ... & Bruford, M. W. (2019). Inferring fine-scale spatial structure of the brown bear (*Ursus arctos*) population in the Carpathians prior to infrastructure development. *Scientific Reports*, 9(1), 9494.
- Ferguson, S. H., & McLoughlin, P. D. (2000). Effect of energy availability, seasonality, and geographic range on brown bear life history. *Ecography*, 23(2), 193-200.
- Festa-Bianchet, M. (2010). Status of the grizzly bear (*Ursus arctos*) in Alberta: Update 2010. *Alberta Wildlife Status Report*, 37, Alberta Sustainable Resource Development, Edmonton, Alberta.
- Find'ó, S., Skuban, M., Kajba, M., Chalmers, J., & Kalaš, M. (2018). Identifying attributes associated with brown bear (*Ursus arctos*) road-crossing and road-kill sites. *Carpathian Wildlife Society*, Zvolen, Slovakia.
- Ford, A. T., & Fahrig, L. (2007). Diet and body size of North American mammal road mortalities. *Transportation Research Part D: Transport and Environment*, 12(7), 498-505.
- Ford, A. T., Barrueto, M., & Clevenger, A. P. (2017). Road mitigation is a demographic filter for grizzly bears. *Wildlife Society Bulletin*, 41(4), 712-719.
- Ford, A. T., Dorsey, B., Lee, T. S., & Clevenger, A. P. (2022). A before-after-control-impact study of wildlife fencing along a highway in the Canadian Rocky Mountains. *Frontiers in Conservation Science*, 3, Article 935420.
- Fording, R. C., & Schram, S. F. (2017). The cognitive and emotional sources of Trump support: The case of low-information voters. *New Political Science*, 39(4), 670-686.
- Forman, R. T. (1998). Road ecology: A solution for the giant embracing us. *Landscape Ecology*, 13(4), III-V.
- Forsyth, C. J., Gramling, R., & Wooddell, G. (1998). The game of poaching: Folk crimes in southwest Louisiana. *Society & Natural Resources*, 11(1), 25-38.
- Frąckowiak, W., Theuerkauf, J., Pirga, B., & Gula, R. (2014). Brown bear habitat selection in relation to anthropogenic structures in the Bieszczady Mountains, Poland. *Biologia*, 69(7), 926-930.
- Frank, S. C., Ordiz, A., Gosselin, J., Hertel, A., Kindberg, J., Leclerc, M., ... & Swenson, J. E. (2017). Indirect effects of bear hunting: a review from Scandinavia. *Ursus*, 28(2), 150-164.

- Gangaas, K. E., Kaltenborn, B. P., & Andreassen, H. P. (2013). Geo-spatial aspects of acceptance of illegal hunting of large carnivores in Scandinavia. *PloS One*, 8(7), e68849.
- García, P., Lastra, J., Marquín, J., & Nores, C. (2007). Detailed model of shelter areas for the Cantabrian brown bear. *Ecological Informatics*, 2(4), 297-307.
- García-Sánchez, M. P., González-Ávila, S., Solana-Gutiérrez, J., Popa, M., Jurj, R., Ionescu, G., ... & Fedorca, A. (2021). Sex-specific connectivity modelling for brown bear conservation in the Carpathian Mountains. *Landscape Ecology*, 37, 1311-1329.
- Garshelis, D. L., Quigley, H. B., Villarrubia, C. R., & Pelton, M. R. (1982). Assessment of telemetric motion sensors for studies of activity. *Canadian Journal of Zoology*, 60(8), 1800-1805.
- Garshelis, D. L., Gibeau, M. L., & Herrero, S. (2005). Grizzly bear demographics in and around Banff National Park and Kananaskis Country. Alberta. *Journal of Wildlife Management*, 69(1), 277-297.
- Gaynor, K. M., Hohnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, 360(6394), 1232-1235.
- Gende, S. M., & Quinn, T. P. (2004). The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon. *Canadian Journal of Zoology*, 82(1), 75-85.
- Gervasi, V., Linnell, J. D., Berce, T., Boitani, L., Ciucci, P., Cretois, B., ... & Gimenez, O. (2021). Ecological correlates of large carnivore depredation on sheep in Europe. *Global Ecology & Conservation*, 30, e01798.
- Gibeau, M. L., & Herrero, S. (1998). Roads, rails and grizzly bears in the Bow River Valley, Alberta. Pages 104-108 in 1998 International Conference on Wildlife Ecology and Transportation. Fort Meyers, Florida.
- Gibeau, M. L. (2000). A conservation biology approach to management of grizzly bears in Banff National Park, Alberta. University of Calgary, Calgary, Alberta.
- Gibeau, M. L., Clevenger, A. P., Herrero, S., & Wierzchowski, J. (2002). Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. *Biological Conservation*, 103(2), 227-236.
- Gibeau, M., & Stevens, S. (2005). Grizzly bear response to human use. Pages 182-192 in Gibeau, M., & Herrero, S. (eds). Final report of the Eastern Slopes Grizzly Bear Study. University of Calgary, Calgary, Alberta.
- Gignoux, C. R., Henn, B. M., & Mountain, J. L. (2011). Rapid, global demographic expansions after the origins of agriculture. *Proceedings of the National Academy of Sciences*, 108(15), 6044-6049.
- Gilhooly, P. S., Nielsen, S. E., Whittington, J., & St. Clair, C. C. (2019). Wildlife mortality on roads and railways following highway mitigation. *Ecosphere*, 10(2), Article e02597.
- Gilroy, J. J., & Sutherland, W. J. (2007). Beyond ecological traps: perceptual errors and undervalued resources. *Trends in Ecology & Evolution*, 22(7), 351-356.
- González, E. G., Blanco, J. C., Ballesteros, F., Alcaraz, L., Palomero, G., & Doadrio, I. (2016). Genetic and demographic recovery of an isolated population of brown bear *Ursus arctos* L., 1758. *PeerJ*, 4, e1928.
- González-Bernardo, E., Delgado, M. D. M., Matos, D. G. G., Zarzo-Arias, A., Morales-González, A., Ruiz-Villar, H., ... & Penteriani, V. (2023). The influence of road networks on brown bear spatial distribution and habitat suitability in a human-modified landscape. *Journal of Zoology*, 319(1), 76-90.

- Gore, J. F., Claar, J. J., & Ruediger, B. (2001). Why did the bear cross the road? It didn't!. Pages 595-602 in Irwin, C. L., Garrett, P., & McDermott, K. P. (eds). *Proceedings of the 2001 International Conference on Ecology and Transportation*. North Carolina State University, Raleigh, North Carolina.
- Gosselin, J., Zedrosser, A., Swenson, J. E., & Pelletier, F. (2015). The relative importance of direct and indirect effects of hunting mortality on the population dynamics of brown bears. *Proceedings of the Royal Society B: Biological Sciences*, 282(1798), 20141840.
- Graham, K., Boulanger, J., Duval, J., & Stenhouse, G. (2010). Spatial and temporal use of roads by grizzly bears in west-central Alberta. *Ursus*, 21(1), 43-56.
- Graham, K., & Stenhouse, G. B. (2014). Home range, movements, and denning chronology of the grizzly bear (*Ursus arctos*) in west-central Alberta. *The Canadian Field-Naturalist*, 128(3), 223-234.
- Gratson, M. W., & Whitman, C. L. (2000). Road closures and density and success of elk hunters in Idaho. *Wildlife Society Bulletin*, 28, 302-310.
- Graves, T. A., Farley, S., & Servheen, C. (2006). Frequency and distribution of highway crossings by Kenai Peninsula brown bears. *Wildlife Society Bulletin*, 34(3), 800-808.
- Graves, T. A., Farley, S., Goldstein, M. I., & Servheen, C. (2007). Identification of functional corridors with movement characteristics of brown bears on the Kenai Peninsula, Alaska. *Landscape Ecology*, 22, 765-772.
- Graves, T. A., Kendall, K. C., Royle, J. A., Stetz, J. B., & Macleod, A. C. (2011). Linking landscape characteristics to local grizzly bear abundance using multiple detection methods in a hierarchical model. *Animal Conservation*, 14(6), 652-664.
- Greater Yellowstone Ecosystem Grizzly Bear Subcommittee (2016). 2016 Conservation Strategy for the grizzly bear in the Greater Yellowstone Ecosystem. Interagency Grizzly Bear Committee, U.S. Fish & Wildlife Service, Missoula, Montana.
- Green, G. I., Mattson, D. J., & Peek, J. M. (1997). Spring feeding on ungulate carcasses by grizzly bears in Yellowstone National Park. *Journal of Wildlife Management*, 61(4), 1040-1055.
- Greggor, A. L., Trimmer, P. C., Barrett, B. J., & Sih, A. (2019). Challenges of learning to escape evolutionary traps. *Frontiers in Ecology & Evolution*, 7, Article 408.
- Gregório, I., Barros, T., Pando, D., Morante, J., Fonseca, C., & Ferreira, E. (2020). Paths for colonization or exodus? New insights from the brown bear (*Ursus arctos*) population of the Cantabrian Mountains. *PLoS One*, 15(1), e0227302.
- Grilo, C., Smith, D. J., & Klar, N. (2015). Carnivores: struggling for survival in roaded landscapes. Pages 300-312 in Van der Ree, R., Smith, D. J., & Grilo, C. (eds). *Handbook of road ecology*. John Wiley & Sons, New York, New York..
- Gucinski, H., Furniss, M. J., Ziemer, R. R., & Brookes, M. H. (eds) (2001). *Forest roads: A synthesis of scientific information*. U.S. Forest Service, General Technical Report, PNW-GTR-509.
- Gude, P. H., Hansen, A. J., Rasker, R., & Maxwell, B. (2006). Rates and drivers of rural residential development in the Greater Yellowstone. *Landscape & Urban planning*, 77(1-2), 131-151.
- Gude, P. H., Hansen, A. J., & Jones, D. A. (2007). Biodiversity consequences of alternative future land use scenarios in Greater Yellowstone. *Ecological Applications*, 17(4), 1004-1018.
- Gunther, K. A., Biel, M. J., & Robison, H. L. (1998). Factors influencing the frequency of road-killed wildlife in Yellowstone National Park. Pages. 32-42 in Evink, G. L., Zeigler, D., & Berry, J. (eds). *Proceedings of the International*

Conference on Wildlife Ecology & Transportation. FL-ER-69-98, Florida Department of Transportation, Tallahassee, Florida.

Gunther, K. A., Haroldson, M. A., Frey, K., Cain, S. L., Copeland, J., & Schwartz, C. C. (2004). Grizzly bear–human conflicts in the Greater Yellowstone ecosystem, 1992–2000. *Ursus*, 15(1), 10-22.

Gunther, K. A., & Wyman, T. (2008). Human habituated bears: The next challenge in bear management in Yellowstone National Park. *Yellowstone Science*, 16(2), 35-41.

Gunther, K. A., Wilmot, K. R., Cain, S. L., Wyman, T. C., Reinertson, E. G., & Bramblett, A. M. (2018). Managing human-habituated bears to enhance survival, habitat effectiveness, and public viewing. *Human–Wildlife Interactions*, 12(3), 373-386.

Gurthrie, J. M. (2012). Modelling movement behavior and road crossing in the black bear of south central Florida. M.S. Thesis, Forestry & Natural Resources, University of Kentucky, Kentucky.

Ha, H. (2022). Identifying potential wildlife–vehicle collision locations for black bear (*Ursus americanus*) in Florida under different environmental and human population factors. *Papers in Applied Geography*, 8(2), 185-199.

Haag, P. (2016). *The gunning of America: Business and making of American gun culture*. Basic Books, New York, New York.

Hale, R., & Swearer, S. E. (2016). Ecological traps: Current evidence and future directions. *Proceedings of the Royal Society B: Biological Sciences*, 283(1824), 20152647.

Hallowell, A. I. (1926). Bear Ceremonialism in the Northern Hemisphere. *American Anthropologist*, 28(1), 1-175.

Hamer, D., & Herrero, S. (1987a). Grizzly bear food and habitat in the front ranges of Banff National Park, Alberta. *International Conference on Bear Research & Management*, 7, 199-213.

Hamer, D., & Herrero, S. (1987b). Wildfire's influence on grizzly bear feeding ecology in Banff National Park, Alberta. *International Conference on Bear Research & Management*, 7, 179-186.

Hamer, D. (1996). Buffaloberry [*Shepherdia canadensis* (L.) Nutt.] fruit production in fire-successional bear feeding sites. *Rangeland Ecology & Management*, 49(6), 520-529.

Hamer, D. (1999). Forest fire's influence on yellow hedsarum habitat and its use by grizzly bears in Banff National Park, Alberta. *Canadian Journal of Zoology*, 77(10), 1513-1520.

Hansen, J. E. (2023). The effects of social, familial, and anthropogenic factors on dispersal-related space use and movement behavior in Scandinavian brown bear (*Ursus arctos*). Ph.D. Dissertation, University of South-Eastern Norway, Bø, Telemark, Norway.

Harding, L., & Nagy, J. A. (1980). Responses of grizzly bears to hydrocarbon exploration on Richards Island, Northwest Territories, Canada. *International Conference on Bear Research & Management*, 4, 277-280.

Hardy, A. R., Fuller, J., Huijser, M. P., Kociolek, A. V., & Evans, M. (2006). Evaluation of wildlife crossing structures and fencing on US Highway 93 Evaro to Polson Phase I: Preconstruction data collection and finalization of evaluation plan. Contract No. FHWA/MT-06-008/1744-1, Western Transportation Institute, Bozeman, Montana.

Haroldson, M. A., Schwartz, C. C., Cherry, S., & Moody, D. S. (2004). Possible effects of elk harvest on fall distribution of grizzly bears in the Greater Yellowstone Ecosystem. *Journal of Wildlife Management*, 68(1), 129-137.

Harting, A. L. (1985). Relationships between activity patterns and foraging strategies of Yellowstone grizzly bears. M.S. Thesis, Montana State University, Bozeman, Montana.

Havlick, D. (2002). No place distant: Roads and motorized recreation on America's public lands. Island Press, Washington, D.C.

He, K., Dai, Q., Gu, X., Zhang, Z., Zhou, J., Qi, D., ... & Yang, Z. (2019). Effects of roads on giant panda distribution: a mountain range scale evaluation. *Scientific Reports*, 9(1), Article 1110.

Hendee, J. C., & Mattson, D. J. (2009). Wildlife in wilderness: A North American and international perspective. Pages 309-334 in Dawson, C. P., & Hendee, J. C. (eds). *Wilderness management: Stewardship and protection of resources and values*. 4th Edition. Fulcrum Publishing, Boulder, Colorado.

Hernando, M. De G., Karamanlidis, A. A., Grivas, K., Krambokoukis, L., Papakostas, G., & Beecham, J. (2021). Habitat use and selection patterns inform habitat conservation priorities of an endangered large carnivore in southern Europe. *Endangered Species Research*, 44, 203-215.

Herrero, S. (2018). *Bear attacks: their causes and avoidance*. Rowman & Littlefield, Lanham, Maryland.

Hertel, A. G., Swenson, J. E., & Bischof, R. (2017). A case for considering individual variation in diel activity patterns. *Behavioral Ecology*, 28(6), 1524-1531.

Hill, J. E., DeVault, T. L., Wang, G., & Belant, J. L. (2020). Anthropogenic mortality in mammals increases with the human footprint. *Frontiers in Ecology & the Environment*, 18(1), 13-18.

Hilderbrand, G. V., Schwartz, C. C., Robbins, C. T., Jacoby, M. E., Hanley, T. A., Arthur, S. M., & Servheen, C. (1999). The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology*, 77(1), 132-138.

Hiller, T. L., Belant, J. L., Beringer, J., & Tyre, A. J. (2015). Resource selection by recolonizing American black bears in a fragmented forest landscape. *Ursus*, 26(2), 116-128.

Hipólito, D., Reljić, S., Rosalino, L. M., Wilson, S. M., Fonseca, C., & Huber, D. (2020). Brown bear damage: Patterns and hotspots in Croatia. *Oryx*, 54(4), 511-519.

Hobson, K. A., McLellan, B. N., & Woods, J. G. (2000). Using stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes to infer trophic relationships among black and grizzly bears in the upper Columbia River basin, British Columbia. *Canadian Journal of Zoology*, 78(8), 1332-1339.

Højberg, P. L., Nielsen, M. R., & Jacobsen, J. B. (2017). Fear, economic consequences, hunting competition, and distrust of authorities determine preferences for illegal lethal actions against gray wolves (*Canis lupus*): A choice experiment among landowners in Jutland, Denmark. *Crime, Law & Social Change*, 67, 461-480.

Hooghe, M., & Dassonneville, R. (2018). Explaining the Trump vote: The effect of racist resentment and anti-immigrant sentiments. *Political Science & Politics*, 51(3), 528-534.

Hooker, M. J. (2017). Movement, genetic structure, and space use of central Georgia black bears (*Ursus americanus*) influenced by a highway corridor. Ph.D. Dissertation, University of Georgia, Athens, Georgia.

Hooker, M. J., Clark, J. D., Bond, B. T., & Chamberlain, M. J. (2021). Evaluation of connectivity among American black bear populations in Georgia. *Journal of Wildlife Management*, 85(5), 979-988.

Hornocker, M. G. (1962). Population characteristics and social and reproductive behavior of the grizzly bear in Yellowstone National Park. M.S. Thesis, University of Montana, Missoula, Montana.

Hostetler, J. A., McCown, J. W., Garrison, E. P., Neils, A. M., Barrett, M. A., Sunkist, M. E., ... & Oli, M. K. (2009). Demographic consequences of anthropogenic influences: Florida black bears in north-central Florida. *Biological Conservation*, 142(11), 2456-2463.

- Hout, M. (2012). Social and economic returns to college education in the United States. *Annual Review of Sociology*, 38, 379-400.
- Hovey, F. W., & McLellan, B. N. (1996). Estimating population growth of grizzly bears from the Flathead River drainage using computer simulations of reproduction and survival rates. *Canadian Journal of Zoology*, 74(8), 1409-1416.
- Huber, D., Kusak, J., & Frkovic, A. (1998). Traffic kills of brown bears in Gorski Kotar, Croatia. *Ursus*, 10, 167-171.
- Huijser, M. P., Camel, W., Fairbank, E. R., Purdum, J., Allem, T. D., Hardy, A. R., ... & Becker, D. (2016a). US 93 North post-construction wildlife-vehicle collision and wildlife crossing monitoring on the Flathead Indian Reservation between Evaro and Polson, Montana. Contract No. FHWA/MT-16-009/8208, Western Transportation Institute, Bozeman, Montana.
- Huijser, M. P., Fairbank, E. R., Camel-Means, W., Graham, J., Watson, V., Basting, P., & Becker, D. (2016b). Effectiveness of short sections of wildlife fencing and crossing structures along highways in reducing wildlife-vehicle collisions and providing safe crossing opportunities for large mammals. *Biological Conservation*, 197, 61-68.
- Ibisch, P. L., Hoffmann, M. T., Kreft, S., Pe'er, G., Kati, V., Biber-Freudenberger, L., ... & Selva, N. (2016). A global map of roadless areas and their conservation status. *Science*, 354(6318), 1423-1427.
- International Union for the Conservation of Nature (2018). Brown bear (*Ursus arctos*) isolated subpopulations. The IUCN Red List of Threatened Species, Cambridge, United Kingdom.
<https://www.iucnredlist.org/species/pdf/121229971/attachment>
- Israel, N. M. D. (2018). Roads and gene flow: a meta-analysis of the response of invertebrates and vertebrates to an anthropogenic barrier. Unpublished Manuscript, Auburn University, Auburn, Alabama.
- Jacobsen, K. S., & Linnell, J. D. (2016). Perceptions of environmental justice and the conflict surrounding large carnivore management in Norway—Implications for conflict management. *Biological Conservation*, 203, 197-206.
- Jacobson, S. L., Bliss-Ketchum, L. L., de Rivera, C. E., & Smith, W. P. (2016). A behavior-based framework for assessing barrier effects to wildlife from vehicle traffic volume. *Ecosphere*, 7(4), e01345.
- Jacoby, M. E., Hilderbrand, G. V., Servheen, C., Schwartz, C. C., Arthur, S. M., Hanley, T. A., ... & Michener, R. (1999). Trophic relations of brown and black bears in several western North American ecosystems. *Journal of Wildlife Management*, 921-929.
- Johansson, M., & Karlsson, J. (2011). Subjective experience of fear and the cognitive interpretation of large carnivores. *Human Dimensions of Wildlife*, 16(1), 15-29.
- Johansson, M., Karlsson, J., Pedersen, E., & Flykt, A. (2012). Factors governing human fear of brown bear and wolf. *Human Dimensions of Wildlife*, 17(1), 58-74.
- Johnson, C. J., Boyce, M. S., Schwartz, C. C., & Haroldson, M. A. (2004). Modeling survival: application of the Andersen—Gill model to Yellowstone Grizzly bears. *Journal of Wildlife Management*, 68(4), 966-978.
- Johnson, H. E., Breck, S. W., Baruch-Mordo, S., Lewis, D. L., Lackey, C. W., Wilson, K. R., ... & Beckmann, J. P. (2015). Shifting perceptions of risk and reward: Dynamic selection for human development by black bears in the western United States. *Biological Conservation*, 187, 164-172.
- Johnson, H. E., Lewis, D. L., & Breck, S. W. (2020). Individual and population fitness consequences associated with large carnivore use of residential development. *Ecosphere*, 11(5), e03098.

- Jones, M. D., Berl, J. L., Tri, A. N., Edwards, J. W., & Spiker, H. (2015). Predicting harvest vulnerability for a recovering population of American black bears in western Maryland. *Ursus*, 26(2), 97-106.
- Kaczensky, P. (1999). Large carnivore depredation on livestock in Europe. *Ursus*, 11, 59-71.
- Kaczensky, P., Knauer, F., Krze, B., Jonozovic, M., Adamic, M., & Gossow, H. (2003). The impact of high speed, high volume traffic axes on brown bears in Slovenia. *Biological Conservation*, 111(2), 191-204.
- Kaczensky, P., Huber, D., Knauer, F., Roth, H., Wagner, A., & Kusak, J. (2006). Activity patterns of brown bears (*Ursus arctos*) in Slovenia and Croatia. *Journal of Zoology*, 269(4), 474-485.
- Kaltenborn, B. P., & Bjerke, T. (2002). The relationship of general life values to attitudes toward large carnivores. *Human Ecology Review*, 9(1), 55-61.
- Kaltenborn, B. P., Andersen, O., & Linnell, J. D. (2013). Predators, stewards, or sportsmen—how do Norwegian hunters perceive their role in carnivore management?. *International Journal of Biodiversity Science, Ecosystem Services & Management*, 9(3), 239-248.
- Kaltenborn, B. P., & Brainerd, S. M. (2016). Can poaching inadvertently contribute to increased public acceptance of wolves in Scandinavia?. *European Journal of Wildlife Research*, 62, 179-188.
- Kaphegyi, T. A., Dees, M., Zlatanova, D., Ueffing, C., Dutsov, A., & Kaphegyi, U. (2013). Rapid assessment of linear transport infrastructure in relation to the impact on landscape continuity for large ranging mammals. *Biodiversity & Conservation*, 22, 153-168.
- Karamanlidis, A. A., Straka, M., Drosopoulou, E., de Gabriel Hernando, M., Kocijan, I., Paule, L., & Scouras, Z. (2012). Genetic diversity, structure, and size of an endangered brown bear population threatened by highway construction in the Pindos Mountains, Greece. *European Journal of Wildlife Research*, 58, 511-522.
- Kasworm, W. F., & Manley, T. L. (1990). Road and trail influences on grizzly bears and black bears in northwest Montana. *International Conference on Bear Research & Management*, 8, 79-84.
- Kasworm, W. F., Radandt, T. G., Teisberg, J. E., Vent, T., Welander, A., Proctor, M., Cooley, H., & Fortin-Noreus, J. K. (2021a). Cabinet-Yaak grizzly bear recovery area 2020 research and monitoring progress report. U.S. Fish & Wildlife Service, Missoula, Montana.
- Kasworm, W. F., Radandt, T. G., Teisberg, J. E., Welander, A., Proctor, M., Cooley, H., & Fortin-Noreus, J. K. (2021b). Selkirk Mountains grizzly bear recovery area 2020 research and monitoring progress report. U.S. Fish & Wildlife Service, Missoula, Montana.
- Katzner, T. E., & Arlettaz, R. (2020). Evaluating contributions of recent tracking-based animal movement ecology to conservation management. *Frontiers in Ecology & Evolution*, 7, Article 519.
- Kautz, T. M., Fowler, N. L., Petroelje, T. R., Beyer, D. E., Svoboda, N. J., & Belant, J. L. (2021). Large carnivore response to human road use suggests a landscape of coexistence. *Global Ecology & Conservation*, 30, e01772.
- Kearney, S. P., Coops, N. C., Stenhouse, G. B., Nielsen, S. E., Hermosilla, T., White, J. C., & Wulder, M. A. (2019). Grizzly bear selection of recently harvested forests is dependent on forest recovery rate and landscape composition. *Forest Ecology & Management*, 449, 117459.
- Kendall, K. C., Stetz, J. B., Boulanger, J., Macleod, A. C., Paetkau, D., & White, G. C. (2009). Demography and genetic structure of a recovering grizzly bear population. *Journal of Wildlife Management*, 73(1), 3-16.

- Kendall, K. C., Macleod, A. C., Boyd, K. L., Boulanger, J., Royle, J. A., Kasworm, W. F., ... & Graves, T. A. (2016). Density, distribution, and genetic structure of grizzly bears in the Cabinet-Yaak ecosystem. *Journal of Wildlife Management*, 80(2), 314-331.
- Kendall, K. C., Graves, T. A., Royle, J. A., Macleod, A. C., McKelvey, K. S., Boulanger, J., & Waller, J. S. (2019). Using bear rub data and spatial capture-recapture models to estimate trend in a brown bear population. *Scientific Reports*, 9(1), 16804.
- Kervellec, M., Milleret, C., Vanpé, C., Quenette, P. Y., Sentilles, J., Palazón, S., ... & Gimenez, O. (2023). Integrating opportunistic and structured non-invasive surveys with spatial capture-recapture models to map connectivity of the Pyrenean brown bear population. *Biological Conservation*, 278, 109875.
- Khosravi, R., Wan, H. Y., Sadeghi, M. R., & Cushman, S. A. (2023). Identifying human–brown bear conflict hotspots for prioritizing critical habitat and corridor conservation in southwestern Iran. *Animal Conservation*, 26(1), 31-45.
- Kinder, D. R., & Kiewiet, D. R. (1979). Economic discontent and political behavior: The role of personal grievances and collective economic judgments in congressional voting. *American Journal of Political Science*, 495-527.
- Kite, R., Nelson, T., Stenhouse, G., & Darimont, C. (2016). A movement-driven approach to quantifying grizzly bear (*Ursus arctos*) near-road movement patterns in west-central Alberta, Canada. *Biological Conservation*, 195, 24-32.
- Klees van Bommel, J., Sun, C., Ford, A. T., Todd, M., & Burton, A. C. (2022). Coexistence or conflict: Black bear habitat use along an urban-wildland gradient. *Plos One*, 17(11), e0276448.
- Knight, R. R., & Eberhardt, L. L. (1985). Population dynamics of Yellowstone grizzly bears. *Ecology*, 66(2), 323-334.
- Knight, R. R., Blanchard, B. M., & Eberhardt, L. L. (1988). Mortality patterns and population sinks for Yellowstone grizzly bears, 1973-1985. *Wildlife Society Bulletin*, 16(2), 121-125.
- Kobler, A., & Adamic, M. (2000). Identifying brown bear habitat by a combined GIS and machine learning method. *Ecological Modelling*, 135(2-3), 291-300.
- Kootenai National Forest (2011). Occupancy and use restrictions: Food storage and sanitation special order. F-14-083-L-11. U.S. Forest Service, Kootenai National Forest, Libby, Montana.
- Kovach, S. D., Collins, G. H., Hinkes, M. T., & Denton, J. W. (2006). Reproduction and survival of brown bears in southwest Alaska, USA. *Ursus*, 17(1), 16-29.
- Kristan, III, W. B. (2003). The role of habitat selection behavior in population dynamics: source–sink systems and ecological traps. *Oikos*, 103(3), 457-468.
- Krofel, M., Jonozovič, M., & Jerina, K. (2012). Demography and mortality patterns of removed brown bears in a heavily exploited population. *Ursus*, 23(1), 91-103.
- Kudrenko, S., Ordiz, A., Barysheva, S. L., Baskin, L., & Swenson, J. E. (2020). Human injuries and fatalities caused by brown bears in Russia, 1932–2017. *Wildlife Biology*, 2020(1), 1-10.
- Kusak, J., Huber, D., Gomercic, T., Schwaderer, G., & Gužvica, G. (2009). The permeability of highway in Gorski kotar (Croatia) for large mammals. *European Journal of Wildlife Research*, 55, 7-21.
- Ladle, A., Steenweg, R., Shepherd, B., & Boyce, M. S. (2018). The role of human outdoor recreation in shaping patterns of grizzly bear-black bear co-occurrence. *PLoS One*, 13(2), e0191730.
- Ladle, A., Avgar, T., Wheatley, M., Stenhouse, G. B., Nielsen, S. E., & Boyce, M. S. (2019). Grizzly bear response to spatio-temporal variability in human recreational activity. *Journal of Applied Ecology*, 56(2), 375-386.

- Lamb, C. T., Mowat, G., McLellan, B. N., Nielsen, S. E., & Boutin, S. (2017a). Forbidden fruit: Human settlement and abundant fruit create an ecological trap for an apex omnivore. *Journal of Animal Ecology*, 86(1), 55-65.
- Lamb, C. T., Mowat, G., Reid, A., Smit, L., Proctor, M., McLellan, B. N., ... & Boutin, S. (2017b). Effects of habitat quality and access management on the density of a recovering grizzly bear population. *Journal of Applied Ecology*, 55(3), 1406-1417.
- Lamb, C. T., Ford, A. T., Proctor, M. F., Royle, J. A., Mowat, G., & Boutin, S. (2019). Genetic tagging in the Anthropocene: Scaling ecology from alleles to ecosystems. *Ecological Applications*, 29(4), e01876.
- Lamb, C. T., Ford, A. T., McLellan, B. N., Proctor, M. F., Mowat, G., Ciarniello, L., ... & Boutin, S. (2020). The ecology of human–carnivore coexistence. *Proceedings of the National Academy of Sciences*, 117(30), 17876-17883.
- Lamb, C. T., Smit, L., Mowat, G., McLellan, B., & Proctor, M. (2023). Unsecured attractants, collisions, and high mortality strain coexistence between grizzly bears and people in the Elk Valley, southeast British Columbia. *Conservation Science & Practice*, 5(10), e13012.
- Lebel, F., Dussault, C., Massé, A., & Côté, S. D. (2012). Influence of habitat features and hunter behavior on white-tailed deer harvest. *Journal of Wildlife Management*, 76(7), 1431-1440.
- Lebreton, J. D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs*, 62(1), 67–118.
- Lee, T. S., Creech, T. G., Martinson, A., Nielsen, S. E., Jakes, A. F., Jones, P. F., ... & Ford, A. T. (2021). Prioritizing human safety and multispecies connectivity across a regional road network. *Conservation Science & Practice*, 3(2), e327.
- Lee, T. S., Jordan-McLachlan, S., & Sanderson, K. (2024). Linking landscapes across Highway 3: Wildlife and road mitigation assessment. Miistakis Institute, Calgary, Alberta.
- Leopold, A. S. (1959). *Wildlife of Mexico: The game birds and mammals*. University of California Press, Berkeley, California.
- Leu, M., Hanser, S. E., & Knick, S. T. (2008). The human footprint in the west: a large-scale analysis of anthropogenic impacts. *Ecological Applications*, 18(5), 1119-1139.
- Lewis, J. S., Rachlow, J. L., Horne, J. S., Garton, E. O., Wakkinen, W. L., Hayden, J., & Zager, P. (2011). Identifying habitat characteristics to predict highway crossing areas for black bears within a human-modified landscape. *Landscape & Urban Planning*, 101(2), 99-107.
- Linke, J., McDermid, G. J., Fortin, M. J., & Stenhouse, G. B. (2013). Relationships between grizzly bears and human disturbances in a rapidly changing multi-use forest landscape. *Biological Conservation*, 166, 54-63.
- Lode, T. (2000). Effect of a motorway on mortality and isolation of wildlife populations. *AMBIO*, 29(3), 163-166.
- Logan, K. A., & Runge, J. P. (2021). Effects of hunting on a puma population in Colorado. *Wildlife Monographs*, 209(1), 1-35.
- Lüchtrath, A., & Schraml, U. (2015). The missing lynx—Understanding hunters' opposition to large carnivores. *Wildlife Biology*, 21(2), 110-119.
- Lute, M. L., & Gore, M. L. (2014). Knowledge and power in wildlife management. *Journal of Wildlife Management*, 78(6), 1060-1068.

- Lute, M. L., Bump, A., & Gore, M. L. (2014). Identity-driven differences in stakeholder concerns about hunting wolves. *PLoS One*, 9(12), e114460.
- Mace, R.D., Waller, J.S., Manley, T.L., Lyon, L.J., & Zuuring, H. (1996) Relationships among grizzly bears, roads and habitat in the Swan Mountains, Montana. *Journal of Applied Ecology*, 33, 1395–1404.
- Mace, R. D., & Waller, J. S. (1997). Spatial and temporal interaction of male and female grizzly bears in northwestern Montana. *Journal of Wildlife Management*, 39-52.
- Mace, R. D., Waller, J. S., Manley, T. L., Ake, K., & Wittinger, W. T. (1999). Landscape evaluation of grizzly bear habitat in western Montana. *Conservation Biology*, 13(2), 367-377.
- Mace, R., & Chilton, T. (2009). Northern Continental Divide Ecosystem grizzly bear monitoring team annual report - 2008. Montana Fish, Wildlife & Parks, Kalispell, Montana.
- Mace, R., Phillips, L., Meier, T., & Owen, P. (2011). Habitat use and movement patterns of grizzly bears in Denali National Park relative to the Denali Park Road. Natural Resources Technical Report NPS/XXXX/NRTR-2011/XXX.
- Mace, R., & Roberts, L. (2011). Northern Continental Divide Ecosystem grizzly bear monitoring team annual report, 2009-2010. Montana Fish, Wildlife & Parks, Kalispell, Montana.
- Mace, R., & Roberts, L. (2012a). Northern Continental Divide Ecosystem grizzly bear monitoring team annual report, 2011. Montana Fish, Wildlife & Parks, Kalispell, Montana.
- Mace, R., & Roberts, L. (2012b). Northern Continental Divide Ecosystem grizzly bear monitoring team annual report, 2012. Montana Fish, Wildlife & Parks, Kalispell, Montana.
- Mace, R. D., Carney, D. W., Chilton-Radandt, T., Courville, S. A., Haroldson, M. A., Harris, R. B., ... & Schwartz, C. C. (2012). Grizzly bear population vital rates and trend in the Northern Continental Divide Ecosystem, Montana. *Journal of Wildlife Management*, 76(1), 119-128.
- Mace, R., & Roberts, L. (2013). Northern Continental Divide Ecosystem grizzly bear monitoring team annual report, 2013. Montana Fish, Wildlife & Parks, Kalispell, Montana.
- Mace, R., & Roberts, L. (2014). Northern Continental Divide Ecosystem grizzly bear monitoring team annual report, 2014. Montana Fish, Wildlife & Parks, Kalispell, Montana.
- Mace, R., & Roberts, L. (2015). Northern Continental Divide Ecosystem grizzly bear monitoring team annual report, 2015. Montana Fish, Wildlife & Parks, Kalispell, Montana.
- Macfarlane, W. W., Logan, J. A., & Kern, W. R. (2013). An innovative aerial assessment of Greater Yellowstone Ecosystem mountain pine beetle-caused whitebark pine mortality. *Ecological Applications*, 23(2), 421-437.
- MacHutchon, A. G., Himmer, S., Davis, H., & Gallagher, M. (1998). Temporal and spatial activity patterns among coastal bear populations. *Ursus*, 10, 539-546.
- Mansfield, S. A., Rogers, L. L., Robison, S., & Powell, R. A. (2022). Bed site selection by female North American black bears (*Ursus americanus*). *Journal of Mammalogy*, 103(2), 361-372.
- Marion, S., Curveira Santos, G., Herdman, E., Hubbs, A., Kearney, S. P., & Burton, A. C. (2024). Mammal responses to human recreation depend on landscape context. *PloS one*, 19(7), e0300870.
- Martin, J., Basille, M., Van Moorter, B., Kindberg, J., Allaine, D., & Swenson, J. E. (2010). Coping with human disturbance: Spatial and temporal tactics of the brown bear (*Ursus arctos*). *Canadian Journal of Zoology*, 88(9), 875-883.

- Mateo-Sánchez, M. C., Cushman, S. A., & Saura, S. (2014). Connecting endangered brown bear subpopulations in the Cantabrian Range (north-western Spain). *Animal Conservation*, 17(5), 430-440.
- Mattson, D. J., & Despain, G. G. (1985). Grizzly bear component mapping handbook for the Yellowstone Ecosystem. U.S. National Park Service & U.S. Forest Service, Bozeman, Montana.
<http://dx.doi.org/10.13140/RG.2.2.30107.03363>
- Mattson, D. J., Knight, R. R., & Blanchard, B. M., (1986). Derivation of habitat component values for the Yellowstone grizzly bear. Pages 222-229 in Evans, K., Lindzey, F., Servheen, C., Winn, D., & Zager, P. (eds). *Proceedings-Grizzly Bear Habitat Symposium*. U.S. Forest Service, General Technical Report INT-207.
- Mattson, D. J., Knight, R. R., & Blanchard, B. M. (1987). The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. *International Conference on Bear Research & Management*, 7, 259-273.
- Mattson, D. J. (1990). Human impacts on bear habitat use. *International Conference on Bear Research & Management*, 8, 33-56.
- Mattson, D. J., Blanchard, B. M., & Knight, R. R. (1992). Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. *Journal of Wildlife Management*, 56(3), 432-442.
- Mattson, D. J. (1993). Background and proposed standards for managing grizzly bear habitat security in the Yellowstone Ecosystem. Cooperative Park Studies Unit, University of Idaho, Moscow, Idaho.
<http://dx.doi.org/10.13140/RG.2.2.16317.10728>
- Mattson, D. J., Reinhart, D. P., & Blanchard, B. M. (1994). Variation in production and bear use of whitebark pine seeds in the Yellowstone area. Pages 205-220 in Despain, D. G. (ed). *Plants and their environments: Proceedings of the first biennial scientific conference on the Greater Yellowstone Ecosystem*. US National Park Service Technical Report NPS/NRYELL/NRTR-93.
- Mattson, D. J., Herrero, S., Wright, R. G., & Pease, C. M. (1996a). Designing and managing protected areas for grizzly bears: How much is enough?. Pages 133-164 in Wright, R. G., & Lemons, J. (eds). *National parks and protected areas: Their role in environmental protection*. Blackwell Science, Cambridge, Massachusetts.
- Mattson, D. J., Herrero, S., Wright, R. G., & Pease, C. M. (1996b). Science and management of Rocky Mountain grizzly bears. *Conservation Biology*, 10(4), 1013-1025.
- Mattson, D. (1997a). Wilderness-dependent wildlife. *International Journal of Wilderness*, 3, 34-38.
- Mattson, D. J. (1997b). Use of ungulates by Yellowstone grizzly bears *Ursus arctos*. *Biological Conservation*, 81(1-2), 161-177.
- Mattson, D. J., & Reinhart, D. P. (1997). Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. *Journal of Applied Ecology*, 34(4), 926-940.
- Mattson, D. J. (1998). Changes in mortality of Yellowstone's grizzly bears. *Ursus*, 10, 129-138.
- Mattson, D. J., & Merrill, T. (2002). Extirpations of grizzly bears in the contiguous United States, 1850–2000. *Conservation Biology*, 16(4), 1123-1136.
- Mattson, D. J. (2004). Living with fierce creatures? An overview and models of mammalian carnivore conservation. Pages 151-176 in Fascione, N., Delach, A., & Smith, M. (eds). *People and predators: From conflict to coexistence*. Island Press, Washington, D.C.

Mattson, D. J., & Merrill, T. (2004). A model-based appraisal of habitat conditions for grizzly bears in the Cabinet–Yaak region of Montana and Idaho. *Ursus*, 15(1), 76-89.

Mattson, D. J., Barber, K., Maw, R., & Renkin, R. (2004). Coefficients of productivity for Yellowstone’s grizzly bear habitat. USGS Biological Resources Discipline. Biological Science Report USGS/BRD/BSR—2002-0007.

Mattson, D. J., Kendall, K. C., & Reinhart, D. P. (2005). Whitebark pine, grizzly bears, and red squirrels. Pages 121-136 in Tomback, D. F., Arno, S. F., & Keane, R. E. (eds). *Whitebark pine communities: Ecology and restoration*. Island Press, Washington, D.C.

Mattson, D. J., Byrd, K. L., Rutherford, M. B., Brown, S. R., & Clark, T. W. (2006). Finding common ground in large carnivore conservation: Mapping contending perspectives. *Environmental Science & Policy*, 9(4), 392-405.

Mattson, D. J., & Ruther, E. J. (2012). Explaining reported puma-related behaviors and behavioral intentions among northern Arizona residents. *Human Dimensions of Wildlife*, 17(2), 91-111.

Mattson, D. J. (2019a). Effects of trains and railways on grizzly bears: An evaluation of the effects of increased train traffic on the Burlington Northern Santa Fe & Montana Rail-Link railways, Montana-Idaho. Grizzly Bear Recovery Project Report, GBRP-2019-1. <http://dx.doi.org/10.13140/RG.2.2.12559.02723>

Mattson, D. J. (2019b). Effects of pedestrians on grizzly bears: An evaluation of the effects of hikers, hunters, photographers, campers, and watchers. Grizzly Bear Recovery Project Report, GBRP-2019-3. <http://dx.doi.org/10.13140/RG.2.2.36103.96161>

Mattson, D. J. (2019c). Heart of the Grizzly Bear Nation: An evaluation of the status of Northern Continental Divide grizzly bears. Grizzly Bear Recovery Project Report, GBRP-2019-2. <http://dx.doi.org/10.13140/RG.2.2.34369.40809>

Mattson, D. J. (2020). Efficacies and effects of sport hunting grizzly bears: An evaluation of prospective demographic and social effects of sport hunting grizzly bears in the contiguous U.S. Grizzly Bear Recovery Project Report, GBRP-2020-1. <http://dx.doi.org/10.13140/RG.2.2.29611.67365>

Mattson, D. J. (2021a). Teaching bears: Complexities and contingencies of deterrence and aversive conditioning. Grizzly Bear Recovery Project Report, GBRP-2021-3. <http://dx.doi.org/10.13140/RG.2.2.21718.42560>

Mattson, D. J. (2021b). Estimating densities, distributions, and total population sizes of extirpated grizzly bear in the contiguous United States. Grizzly Bear Recovery Project Technical Paper, GBRP-TP-2021-1. <http://dx.doi.org/10.13140/RG.2.2.35140.19841>

Mattson, D. J. (2021c). The grizzly bear promised land: Past, present, and future of grizzly bears in the Bitterroot, Clearwater, Salmon and Selway country. Grizzly Bear Recovery Project Report, GBRP-2021-1. <http://dx.doi.org/10.13140/RG.2.2.19083.87848>

Mattson, D. (2022a). A will to dominate: Problems and pathologies of state wildlife management. Grizzly Times Essays, 2-5. https://www.grizzlytimes.org/_files/ugd/d2beb3_a4aff4d546d941b08341d6f7d27e66ad.pdf

Mattson, D. J. (2022b) Grizzly bears for the Southwest: History and prospects for grizzly bears in Arizona, New Mexico and Colorado. Grizzly Bear Recovery Project Report, GBRP-2022-1.

Mattson, D. J. (2023). Flawed science: A critique of science practices and products by the Interagency Grizzly Bear Study Team, 2006-2023. Grizzly Bear Recovery Project Report, GBRP-2023-1.

Matosiuk, M., Smietana, W., Czajkowska, M., Paule, L., Štofik, J., Krajmerová, D., ... & Ratkiewicz, M. (2019). Genetic differentiation and asymmetric gene flow among Carpathian brown bear (*Ursus arctos*) populations—Implications for conservation of transboundary populations. *Ecology & Evolution*, 9(3), 1501-1511.

- Mayer, A. L., & Cameron, G. N. (2003). Consideration of grain and extent in landscape studies of terrestrial vertebrate ecology. *Landscape & Urban Planning*, 65(4), 201-217.
- McCann, R. K. (1991). Activity measures of free-ranging grizzly bears (*Ursus arctos*) in the Flathead drainage. M.S. Thesis, University of British Columbia, Vancouver, British Columbia.
- McCown, J. W., Kubilis, P., Eason, T. H., & Scheick, B. K. (2009). Effect of traffic volume on American black bears in central Florida, USA. *Ursus*, 20(1), 39-46.
- McDonough, T. J., & Christ, A. M. (2012). Geographic variation in size, growth, and sexual dimorphism of Alaska brown bears, *Ursus arctos*. *Journal of Mammalogy*, 93(3), 686-697.
- McLellan, B. A. (2023). Linking large scale monitoring and spatially explicit capture-recapture models to identify factors shaping large carnivore densities: Case study of the American black bear in Ontario, Canada. M.S. Thesis, Trent University, Oshawa, Ontario.
- McLellan, B.N., & Shackleton, D.M. (1988) Grizzly bears and resource-extraction industries: effects of roads on behavior, habitat use and demography. *Journal of Applied Ecology*, 25, 451–460.
- McLellan, B. N., Hovey, F. W., Mace, R. D., Woods, J. G., Carney, D. W., Gibeau, M. L., ... & Kasworm, W. F. (1999). Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. *Journal of Wildlife Management*, 63(3), 911-920.
- McLellan, B. N., & Hovey, F. W. (2001). Habitats selected by grizzly bears in a multiple use landscape. *Journal of Wildlife Management*, 65, 92-99.
- McLellan, B. N. (2015). Some mechanisms underlying variation in vital rates of grizzly bears on a multiple use landscape. *Journal of Wildlife Management*, 79(5), 749-765.
- McLellan, B. N., Proctor, M. F., Huber, D. & Michel, S. (2017). *Ursus arctos*. The IUCN Red List of Threatened Species 2017: e.T41688A121229971.
- McLellan, M. L., & McLellan, B. N. (2015). Effect of season and high ambient temperature on activity levels and patterns of grizzly bears (*Ursus arctos*). *PLoS One*, 10(2), e0117734.
- McLellan, M. (2020). Identifying mechanisms of population change in two threatened grizzly bear populations. Ph.D. Dissertation, Victoria University of Wellington, Wellington, New Zealand.
- McLoughlin, P. D., Taylor, M. K., Cluff, H. D., Gau, R. J., Mulders, R., Case, R. L., & Messier, F. (2003). Population viability of barren-ground grizzly bears in Nunavut and the Northwest Territories. *Arctic*, 56(2), 185-190.
- Merkle, J. A., Robinson, H. S., Krausman, P. R., & Alaback, P. (2013). Food availability and foraging near human developments by black bears. *Journal of Mammalogy*, 94(2), 378-385.
- Merrill, T., Mattson, D. J., Wright, R. G., & Quigley, H. B. (1999). Defining landscapes suitable for restoration of grizzly bears *Ursus arctos* in Idaho. *Biological Conservation*, 87(2), 231-248.
- Merrill, T., & Mattson, D. (2003). The extent and location of habitat biophysically suitable for grizzly bears in the Yellowstone region. *Ursus*, 14, 171-187.
- Mietz, S. N. (1994). Linkage zone identification and evaluation of management options for grizzly bears in the Evaro Hill area. M.S. Thesis, University of Montana, Missoula, Montana.

- Mikle, N., Graves, T. A., Kovach, R., Kendall, K. C., & Macleod, A. C. (2016). Demographic mechanisms underpinning genetic assimilation of remnant groups of a large carnivore. *Proceedings of the Royal Society B: Biological Sciences*, 283(1839), 20161467.
- Miller, C. R., & Waits, L. P. (2003). The history of effective population size and genetic diversity in the Yellowstone grizzly (*Ursus arctos*): Implications for conservation. *Proceedings of the National Academy of Sciences*, 100(7), 4334-4339.
- Miller, S. D. (1997). Impacts of heavy hunting pressure and the density and demographics of brown bear populations on southcentral Alaska. Federal Aid in Wildlife Restoration, Research Final Report, Study 4.26, Alaska Department of Game & Fish, Juneau, Alaska.
- Moe, T. F., Kindberg, J., Jansson, I., & Swenson, J. E. (2007). Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (*Ursus arctos*). *Canadian Journal of Zoology*, 85(4), 518-525.
- Mohammadi, A., Almasieh, K., Nayeri, D., Ataei, F., Khani, A., López-Bao, J. V., ... & Cushman, S. A. (2021). Identifying priority core habitats and corridors for effective conservation of brown bears in Iran. *Scientific Reports*, 11(1), 1-13.
- Moore, L. J., Petrovan, S. O., Bates, A. J., Hicks, H. L., Baker, P. J., Perkins, S. E., & Yarnell, R. W. (2023). Demographic effects of road mortality on mammalian populations: A systematic review. *Biological Reviews*, 98(4), 1033-1050.
- Morales-González, A., Ruiz-Villar, H., Ordiz, A., & Penteriani, V. (2020). Large carnivores living alongside humans: Brown bears in human-modified landscapes. *Global Ecology & Conservation*, 22, e00937.
- Morehouse, A. T., & Boyce, M. S. (2016). Grizzly bears without borders: Spatially explicit capture–recapture in southwestern Alberta. *Journal of Wildlife Management*, 80(7), 1152-1166.
- Morgan, D., Proctor, M., Mowat, G., McLellan, B., Hamilton, T., & Turney, L. (2019). Conservation ranking of grizzly bear population units – 2019. Ministry of Environment & Climate Change Strategy, Victoria, British Columbia.
- Morgan, S. L., & Lee, J. (2018). Trump voters and the white working class. *Sociological Science*, 5, 234-245.
- Mote, F. W. (2003). *Imperial China, 900–1800*. Harvard University Press, Cambridge, Massachusetts.
- Mowat, G., Heard, D. C., & Schwarz, C. J. (2013). Predicting grizzly bear density in western North America. *PloS One*, 8(12), e82757.
- Mueller, C., Herrero, S., & Gibeau, M. L. (2004). Distribution of subadult grizzly bears in relation to human development in the Bow River Watershed, Alberta. *Ursus*, 15(1), 35-47.
- Muth, R. M., & Bowe Jr, J. F. (1998). Illegal harvest of renewable natural resources in North America: Toward a typology of the motivations for poaching. *Society & Natural Resources*, 11(1), 9-24.
- Mychajliw, A. M., Adams, A. J., Brown, K. C., Campbell, B. T., Hardesty-Moore, M., Welch, Z. S., ... & Alagona, P. S. (2024). Coupled social and ecological change drove the historical extinction of the California grizzly bear (*Ursus arctos californicus*). *Proceedings of the Royal Society B*, 291(2014), 20230921.
- Mysterud, I. (1983). Characteristics of summer beds of European brown bears in Norway. *International Conference on Bear Research & Management*, 5, 208-222.
- Nagy, J.A. & Gunson, J.R. (1990). Management plan for grizzly bears in Alberta. Wildlife Management Planning Series, No. 2. Alberta Forestry, Lands, and Wildlife, Fish & Wildlife Division, Edmonton, Alberta.

Naughton-Treves, L. I. S. A., Grossberg, R., & Treves, A. (2003). Paying for tolerance: rural citizens' attitudes toward wolf depredation and compensation. *Conservation Biology*, 17(6), 1500-1511.

Naves, J., Wiegand, T., Revilla, E., & Delibes, M. (2003). Endangered species constrained by natural and human factors: the case of brown bears in northern Spain. *Conservation Biology*, 17(5), 1276-1289.

Nellemann C., Støen O.G., Kindberg J., Swenson J.E., Vistnes I., Ericsson G., Katajisto J., Kaltenborn B.P., Martin J. & Ordiz A. (2007). Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biological Conservation*, 138 (1-2), 157–165.

Neumann, W., Ericsson, G., Dettki, H., Bunnefeld, N., Keuler, N. S., Helmers, D. P., & Radeloff, V. C. (2012). Difference in spatiotemporal patterns of wildlife road-crossings and wildlife-vehicle collisions. *Biological Conservation*, 145(1), 70-78.

Nie, M. (2008). *The governance of western public lands: Mapping its present and future*. University of Kansas Press, Lawrence, Kansas.

Nie, M. A. (2003). *Beyond wolves: The politics of wolf recovery and management*. University of Minnesota Press, Minneapolis, Minnesota.

Nielsen, S. E., Herrero, S., Boyce, M. S., Mace, R. D., Benn, B., Gibeau, M. L., & Jevons, S. (2004a). Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. *Biological Conservation*, 120(1), 101-113.

Nielsen, S. E., Boyce, M. S., & Stenhouse, G. B. (2004b). Grizzly bears and forestry: I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. *Forest Ecology & Management*, 199(1), 51-65.

Nielsen, S. E., Munro, R. H. M., Bainbridge, E. L., Stenhouse, G. B., & Boyce, M. S. (2004c). Grizzly bears and forestry: II. Distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada. *Forest Ecology & Management*, 199(1), 67-82.

Nielsen, S. E., Stenhouse, G. B., & Boyce, M. S. (2006). A habitat-based framework for grizzly bear conservation in Alberta. *Biological conservation*, 130(2), 217-229.

Nielsen, S. E., Stenhouse, G. B., Beyer, H. L., Huettmann, F., & Boyce, M. S. (2008). Can natural disturbance-based forestry rescue a declining population of grizzly bears?. *Biological Conservation*, 141(9), 2193-2207.

Nielsen, S. E., McDermid, G., Stenhouse, G. B., & Boyce, M. S. (2010). Dynamic wildlife habitat models: Seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. *Biological Conservation*, 143(7), 1623-1634.

Nisi, A. C., Suraci, J. P., Ranc, N., Frank, L. G., Oriol-Cotterill, A., Ekwanga, S., ... & Wilmers, C. C. (2022). Temporal scale of habitat selection for large carnivores: Balancing energetics, risk and finding prey. *Journal of Animal Ecology*, 91(1), 182-195.

Northern Continental Divide Ecosystem Flathead, Lewis and Clark, and Helena National Forests (2000). *Food Storage Special Order LC00-18*. U.S. Forest Service, Region 1, Missoula, Montana.

Northern Continental Divide Ecosystem Grizzly Bear Subcommittee (2019). *Conservation Strategy for the grizzly bear in the Northern Continental Divide Ecosystem*. Interagency Grizzly Bear Committee, U.S. Fish & Wildlife Service, Missoula, Montana.

Northrup, J. M., Pitt, J., Muhly, T. B., Stenhouse, G. B., Musiani, M., & Boyce, M. S. (2012a). Vehicle traffic shapes grizzly bear behaviour on a multiple use landscape. *Journal of Applied Ecology*, 49(5), 1159-1167.

- Northrup, J. M., Stenhouse, G. B., & Boyce, M. S. (2012b). Agricultural lands as ecological traps for grizzly bears. *Animal Conservation*, 15(4), 369-377.
- Oberosler, V., Tenan, S., & Rovero, F. (2020). Spatial and temporal patterns of human avoidance by brown bears in a reintroduced population. *Hystrix*, 31(2), 148-153.
- Olson, T. L., Squibb, R. C., & Gilbert, B. K. (1998). Brown bear diurnal activity and human use: a comparison of two salmon streams. *Ursus*, 10, 547-555.
- Ordiz, A., Støen, O. G., Delibes, M., & Swenson, J. E. (2011). Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia*, 166, 59-67.
- Ordiz, A., Kindberg, J., Sæbø, S., Swenson, J. E., & Støen, O. G. (2014). Brown bear circadian behavior reveals human environmental encroachment. *Biological Conservation*, 173, 1-9.
- Ordiz, A., Sæbø, S., Kindberg, J., Swenson, J. E., & Støen, O. G. (2017). Seasonality and human disturbance alter brown bear activity patterns: implications for circumpolar carnivore conservation?. *Animal Conservation*, 20(1), 51-60.
- Otis, D. L., & White, G. C. (1999). Autocorrelation of location estimates and the analysis of radiotracking data. *Journal of Wildlife Management*, 63, 1039-1044.
- Pacifici, M., Santini, L., Di Marco, M., Baisero, D., Francucci, L., Marasini, G. G., ... & Rondinini, C. (2013). Generation length for mammals. *Nature Conservation*, 5, 89-94.
- Palm, E. C., Landguth, E. L., Holden, Z. A., Day, C. C., Lamb, C. T., Frame, P. F., Morehouse, A. T., Mowat, G., Proctor, M. F., Sawaya, M. A., Stenhouse, G., Whittington, J., & Zeller, K. A. (2023). Corridor-based approach with spatial cross-validation reveals scale-dependent effects of geographic distance, human footprint and canopy cover on grizzly bear genetic connectivity. *Molecular Ecology*, 32, 5211–5227.
- Parsons, B. M., Coops, N. C., Stenhouse, G. B., Burton, A. C., & Nelson, T. A. (2020). Building a perceptual zone of influence for wildlife: delineating the effects of roads on grizzly bear movement. *European Journal of Wildlife Research*, 66, 1-16.
- Parsons, B. M., Coops, N. C., Kearney, S. P., Burton, A. C., Nelson, T. A., & Stenhouse, G. B. (2021). Road visibility influences habitat selection by grizzly bears (*Ursus arctos horribilis*). *Canadian Journal of Zoology*, 99(3), 161-171.
- Parsons, B., Wilson, A. E., Graham, K., & Stenhouse, G. B. (2022). Grizzly bear (*Ursus arctos*) movements and habitat use predict human-caused mortality across temporal scales. *Canadian Journal of Zoology*, 101, 81-94.
- Pastoureau, M. (2011). *The bear: A history of a fallen king*. Cambridge University Press, Cambridge, United Kingdom.
- Pease, C. M., & Mattson, D. J. (1999). Demography of the Yellowstone grizzly bears. *Ecology*, 80(3), 957-975.
- Peel, J. (2005). *The precautionary principle in practice: Environmental decision-making and scientific uncertainty*. The Federation Press, Leichhardt, New South Wales.
- Penteriani, V., Delgado, M. D. M., Pinchera, F., Naves, J., Fernández-Gil, A., Kojola, I., ... & López-Bao, J. V. (2016). Human behaviour can trigger large carnivore attacks in developed countries. *Scientific Reports*, 6(1), 20552.
- Penteriani, V., Delgado, M. D. M., Krofel, M., Jerina, K., Ordiz, A., Dalerum, F., ... & Bombieri, G. (2018). Evolutionary and ecological traps for brown bears *Ursus arctos* in human modified landscapes. *Mammal Review*, 48(3), 180-193.

- Percy, M. P. (2004). Spatio-temporal movement and road crossing patterns of wolves, black bears and grizzly bears in the bow river valley of Banff National Park. M.S. Thesis, University of Alberta, Edmonton, Alberta.
- Peters, W., Hebblewhite, M., Cavedon, M., Pedrotti, L., Mustoni, A., Zibordi, F., ... & Cagnacci, F. (2015). Resource selection and connectivity reveal conservation challenges for reintroduced brown bears in the Italian Alps. *Biological Conservation*, 186, 123-133.
- Petersen, D. (2014). *Ghost grizzlies: Does the great bear still haunt Colorado?*. Booktango. Bloomington, Indiana.
- Peterson, M. N., von Essen, E., Hansen, H. P., & Peterson, T. R. (2019). Shoot shovel and sanction yourself: Self-policing as a response to wolf poaching among Swedish hunters. *Ambio*, 48, 230-239.
- Picton, H. D. (1978). Climate and reproduction of grizzly bears in Yellowstone National Park. *Nature*, 274(5674), 888-889.
- Piédalou, B., Quenette, P. Y., Bombillon, N., Gastineau, A., Miquel, C., & Gimenez, O. (2019). Determinants and patterns of habitat use by the brown bear *Ursus arctos* in the French Pyrenees revealed by occupancy modelling. *Oryx*, 53(2), 334-343.
- Pohja-Mykrä, M., & Kurki, S. (2014). Strong community support for illegal killing challenges wolf management. *European Journal of Wildlife Research*, 60, 759-770.
- Pohja-Mykrä, M. (2016). Felony or act of justice?—Illegal killing of large carnivores as defiance of authorities. *Journal of Rural Studies*, 44, 46-54.
- Posillico, M., Meriggi, A., Pagnin, E., Lovari, S., & Russo, L. (2004). A habitat model for brown bear conservation and land use planning in the central Apennines. *Biological Conservation*, 118(2), 141-150.
- Pritchard, P. (2014). *Environmental risk management*. Taylor & Francis, London, United Kingdom.
- Primm, S. (2000). Real bears, symbol bears, and problem solving. *Northern Rockies Conservation Cooperative News*, 13, 6-8.
- Procko, M., Naidoo, R., LeMay, V., & Burton, A. C. (2023). Human presence and infrastructure impact wildlife nocturnality differently across an assemblage of mammalian species. *Plos One*, 18(5), e0286131.
- Proctor, M. F., McLellan, B. N., & Strobeck, C. (2002). Population fragmentation of grizzly bears in southeastern British Columbia, Canada. *Ursus*, 13, 153-160.
- Proctor, M. F., McLellan, B. N., Strobeck, C., & Barclay, R. M. (2004). Gender-specific dispersal distances of grizzly bears estimated by genetic analysis. *Canadian Journal of Zoology*, 82(7), 1108-1118.
- Proctor, M. F., McLellan, B. N., Strobeck, C., & Barclay, R. M. (2005). Genetic analysis reveals demographic fragmentation of grizzly bears yielding vulnerably small populations. *Proceedings of the Royal Society B: Biological Sciences*, 272(1579), 2409-2416.
- Proctor, M. F., Paetkau, D., McLellan, B. N., Stenhouse, G. B., Kendall, K. C., Mace, R. D., ... & Strobeck, C. (2012). Population fragmentation and inter ecosystem movements of grizzly bears in western Canada and the northern United States. *Wildlife Monographs*, 180(1), 1-46.
- Proctor, M. F., Nielsen, S. E., Kasworm, W. F., Servheen, C., Radandt, T. G., Machutchon, A. G., & Boyce, M. S. (2015). Grizzly bear connectivity mapping in the Canada–United States trans border region. *Journal of Wildlife Management*, 79(4), 544-558.

- Proctor, M. F., Lamb, C. T., & MacHutchon, A. G. (2017). The grizzly dance between berries and bullets: relationships among bottom-up food resources and top-down mortality risk on grizzly bear populations in southeast British Columbia. Trans-border Grizzly Bear Project, Kaslo, British Columbia.
- Proctor, M. F., McLellan, B. N., Stenhouse, G. B., Mowat, G., Lamb, C. T., & Boyce, M. S. (2020). Effects of roads and motorized human access on grizzly bear populations in British Columbia and Alberta, Canada. *Ursus*, 2019(30e2), 16-39.
- Proctor, M. F., Lamb, C. T., Boulanger, J., MacHutchon, A. G., Kasworm, W. F., Paetkau, D., ... & Servheen, C. (2023). Berries and bullets: Influence of food and mortality risk on grizzly bears in British Columbia. *Wildlife Monographs*, 213(1), e1078.
- Psaralexi, M., Lazarina, M., Mertzanis, Y., Michaelidou, D. E., & Sgardelis, S. (2022). Exploring 15 years of brown bear (*Ursus arctos*)-vehicle collisions in northwestern Greece. *Nature Conservation*, 47, 105-119.
- Quiles, P., & Barrientos, R. (2024). Interspecific interactions disrupted by roads. *Biological Reviews*, 99(3), 1121-1139.
- Recio, M. R., Knauer, F., Molinari-Jobin, A., Huber, D., Filacorda, S., & Jerina, K. (2021). Context-dependent behaviour and connectivity of recolonizing brown bear populations identify transboundary conservation challenges in Central Europe. *Animal Conservation*, 24(1), 73-83.
- Rega-Brodsky, C. C., Weiss, K. C., Green, A. M., Iannarilli, F., Tleimat, J., Fritts, S., ... & Allen, M. L. (2023). Mammalian functional diversity and trait responses to anthropogenic and environmental factors across the contiguous USA. *Urban Ecosystems*, 26(2), 309-322.
- Reinhart, D. P., & Mattson, D. J. (1990). Bear use of cutthroat trout spawning streams in Yellowstone National Park. *International Conference on Bear Research & Management*, 8, 343-350.
- Riitters, K. H., & Wickham, J. D. (2003). How far to the nearest road?. *Frontiers in Ecology & The Environment*, 1(3), 125-129.
- Roberts, J. (1977). *The amazing adventures of Lord Gore: A true saga from the Old West*. Sundance Publishing, Silverton, Colorado.
- Robertson, B. A., Rehage, J. S., & Sih, A. (2013). Ecological novelty and the emergence of evolutionary traps. *Trends in Ecology & Evolution*, 28(9), 552-560.
- Robinson, C., Duinker, P. N., & Beazley, K. F. (2010). A conceptual framework for understanding, assessing, and mitigating ecological effects of forest roads. *Environmental Reviews*, 18, 61-86.
- Robinson, M. J. (2005). *Predatory bureaucracy: The extermination of wolves and the transformation of the West*. University Press of Colorado, Boulder, Colorado.
- Roesch, M. J. (2010). Identifying wildlife crossing zones for the prioritization of highway mitigation measures along US Highway 2: West Glacier, MT to Milepost 193. Professional Paper, University of Montana, Missoula, Montana.
- Roever, C. L., Boyce, M. S., & Stenhouse, G. B. (2008a). Grizzly bears and forestry: II: grizzly bear habitat selection and conflicts with road placement. *Forest Ecology & Management*, 256(6), 1262-1269.
- Roever, C. L., Boyce, M. S., & Stenhouse, G. B. (2008b). Grizzly bears and forestry: I: Road vegetation and placement as an attractant to grizzly bears. *Forest Ecology & Management*, 256(6), 1253-1261.
- Roever, C.L., Boyce, M.S. & Stenhouse, G.B. (2010). Grizzly bear movements relative to roads: application of step selection functions. *Ecography*, 33, 1113–1122.

- Rowland, M. M., Nielson, R. M., Wisdom, M. J., Johnson, B. K., Findholt, S., Clark, D., ... & Naylor, B. J. (2021). Influence of landscape characteristics on hunter space use and success. *Journal of Wildlife Management*, 85(7), 1394-1409.
- Rutherford, A., Ellis, C., McGowan, P., McClure, M., Ament, R., & Grebenc, J. (2014). Highway mitigation for wildlife in Northwest Montana: Estimating the impacts of exurban growth and traffic demand on grizzly bears and other key wildlife species. Sonoran Institute, Western Transportation Institute, Center for Large Landscape Conservation, and Future West, Bozeman, Montana.
- Rytterstedt, E. (2016). 'I don't see myself as a criminal': Motivation and neutralization of illegal hunting by Swedish Norrland hunters. Pages 217-239 in Potter, G. R., Nurse, A. & Hall, M. (eds). *The geography of environmental crime*. Palgrave Macmillon, Basingstoke, United Kingdom.
- Rytwinski, T., & Fahrig, L. (2011). Reproductive rate and body size predict road impacts on mammal abundance. *Ecological Applications*, 21(2), 589-600.
- Rytwinski, T., & Fahrig, L. (2012). Do species life history traits explain population responses to roads? A meta-analysis. *Biological Conservation*, 147(1), 87-98.
- Rytwinski, T., & Fahrig, L. (2015). The impacts of roads and traffic on terrestrial animal populations. Pages 237-246 in Van der Ree, R., Smith, D. J., & Grilo, C. (eds). *Handbook of road ecology*. John Wiley & Sons, New York, New York.
- Rytwinski, T., Soanes, K., Jaeger, J. A., Fahrig, L., Findlay, C. S., Houlahan, J., ... & van der Grift, E. A. (2016). How effective is road mitigation at reducing road-kill? A meta-analysis. *PLoS One*, 11(11), e0166941.
- Sagør, J. T., Swenson, J. E., & Røskoft, E. (1997). Compatibility of brown bear *Ursus arctos* and free-ranging sheep in Norway. *Biological Conservation*, 81(1-2), 91-95.
- Sandstrom, P. L. (1996). Identification of potential linkage zones for grizzly bears in the Swan-Clearwater Valley using GIS. M.S. Thesis, University of Montana, Missoula, Montana.
- Sawaya, M. A., Clevenger, A. P., & Kalinowski, S. T. (2013). Demographic connectivity for ursid populations at wildlife crossing structures in Banff National Park. *Conservation Biology*, 27(4), 721-730.
- Sawaya, M. A., Kalinowski, S. T., & Clevenger, A. P. (2014). Genetic connectivity for two bear species at wildlife crossing structures in Banff National Park. *Proceedings of the Royal Society B: Biological Sciences*, 281(1780), 20131705.
- Schlaepfer, M. A., Runge, M. C., & Sherman, P. W. (2002). Ecological and evolutionary traps. *Trends in Ecology & Evolution*, 17(10), 474-480.
- Schlesinger, L. A., & Heskett, J. L. (1991). Breaking the cycle of failure in services. *MIT Sloan Management Review*, 32(3), 17-28.
- Schleyer, B. O. (1983). Activity patterns of grizzly bears in the Yellowstone ecosystem and their reproductive behavior, predation, and use of carrion. M.S. These, Montana State University, Bozeman, Montana.
- Shrader-Frechette, K. S., & McCoy, E. D. (1994). *Method in ecology: Strategies for conservation*. Cambridge University Press, Cambridge, United Kingdom.
- Schroeder, S. A., Fulton, D. C., Cornicelli, L., & Bruskotter, J. T. (2018). How Minnesota wolf hunter and trapper attitudes and risk-and benefit-based beliefs predict wolf management preferences. *Human Dimensions of Wildlife*, 23(6), 552-568.

- Schroeder, S. A., Landon, A. C., Fulton, D. C., & McInenly, L. E. (2022). On the multiple identities of stakeholders in wolf management in Minnesota, United States. *Frontiers in Ecology & Evolution*, 10, 798795.
- Schullery, P. (1986). *The bears of Yellowstone*. Second edition. Roberts Rhinehart, Boulder, Colorado.
- Schwartz, C. C., Haroldson, M. A., White, G. C., Harris, R. B., Cherry, S., Keating, K. A., ... & Servheen, C. (2006). Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs*, 161(1), 1-68.
- Schwartz, C. C., Haroldson, M. A., & White, G. C. (2010a). Hazards affecting grizzly bear survival in the Greater Yellowstone Ecosystem. *The Journal of Wildlife Management*, 74(4), 654-667.
- Schwartz, C. C., Cain, S. L., Podrutzny, S., Cherry, S., & Frattaroli, L. (2010b). Contrasting activity patterns of sympatric and allopatric black and grizzly bears. *Journal of Wildlife Management*, 74(8), 1628-1638.
- Schwartz, C. C., Gude, P. H., Landenburger, L., Haroldson, M. A., & Podrutzny, S. (2012). Impacts of rural development on Yellowstone wildlife: linking grizzly bear *Ursus arctos* demographics with projected residential growth. *Wildlife Biology*, 18(3), 246-257.
- Schwartz, C. C., Fortin, J. K., Teisberg, J. E., Haroldson, M. A., Servheen, C., Robbins, C. T., & Van Manen, F. T. (2014). Body and diet composition of sympatric black and grizzly bears in the Greater Yellowstone Ecosystem. *Journal of Wildlife Management*, 78(1), 68-78.
- Sellers, R. A., Richard, R., Miller, S., & Smith, T. (1999). Population dynamics of a naturally regulated brown bear population on the coast of Katmai National Park and Preserve. National Park Service, Alaska Region, Alaska Department of Fish & Game, Final Resource Report NPS/AR/NRTR-99/36.
- Sells, S. N., Costello, C. M., Lukacs, P. M., Roberts, L. L., & Vinks, M. A. (2022). Grizzly bear habitat selection across the Northern Continental Divide Ecosystem. *Biological Conservation*, 276, 109813.
- Sells, S. N., Costello, C. M., Lukacs, P. M., Roberts, L. L., & Vinks, M. A. (2023). Predicted connectivity pathways between grizzly bear ecosystems in Western Montana. *Biological Conservation*, 284, 110199.
- Serenari, C., & Peterson, M. N. (2016). A sociopolitical perspective on the illegal take of wildlife in the southeastern, USA. *International Journal of Rural Criminology*, 3(1), 29-49.
- Serrouya, R., Kellner, A., Pavan, G., Lewis, D. W., DeMars, C. A., & McLellan, B. N. (2017). Time vs. distance: Alternate metrics of animal resource selection provide opposing inference. *Ecosphere*, 8(3), e01730.
- Servheen, C., Waller, J. S., & Sandstrom, P. (2001). Identification and management of linkage zones for grizzly bears between the large blocks of public land in the northern Rocky Mountains. Pages 161-170 in Irwin, C. L., Garrett, P., & McDermott, K. P. (eds). *Proceedings of the 2001 International Conference on Ecology and Transportation*. North Carolina State University, Raleigh, North Carolina.
- Seryodkin, I. V., Kostyria, A. V., Goodrich, J. M., & Miquelle, D. G. (2013). Daily activity patterns of brown bear (*Ursus arctos*) of the Sikhote-Alin mountain range (Primorskiy Krai, Russia). *Russian Journal of Ecology*, 44, 50-55.
- Shennan, S., Downey, S. S., Timpson, A., Edinborough, K., Colledge, S., Kerig, T., ... & Thomas, M. G. (2013). Regional population collapse followed initial agriculture booms in mid-Holocene Europe. *Nature Communications*, 4(1), 2486.
- Shepard, E. L., Wilson, R. P., Quintana, F., Laich, A. G., Liebsch, N., Albareda, D. A., ... & Macdonald, D. W. (2008). Identification of animal movement patterns using tri-axial accelerometry. *Endangered Species Research*, 10, 47-60.

- Shimozuru, M., Shirane, Y., Yamanaka, M., Nakanishi, M., Ishinazaka, T., Kasai, S., ... & Tsubota, T. (2020). Maternal human habituation enhances sons' risk of human-caused mortality in a large carnivore, brown bears. *Scientific Reports*, 10(1), 16498.
- Short Bull, R. A., Cushman, S. A., Mace, R., Chilton, T., Kendall, K. C., Landguth, E. L., ... & Luikart, G. (2011). Why replication is important in landscape genetics: American black bear in the Rocky Mountains. *Molecular Ecology*, 20(6), 1092-1107.
- Sidorovich, A., Novitsky, R., & Solovej, I. (2020). Road mortality of carnivores (Mammalia, Carnivora) in Belarus. *Zoodyversity*, 54(3), 211-220.
- Singer, F. J., & Beattie, J. B. (1986). The controlled traffic system and associated wildlife responses in Denali National Park. *Arctic*, 53(2), 195-203.
- Singleton, P. H., Gaines, W. L., & Lehmkuhl, J. F. (2004). Landscape permeability for grizzly bear movements in Washington and southwestern British Columbia. *Ursus*, 15(1), 90-103.
- Situnayake, M. N. (2018). Space-use strategies of brown bears (*Ursus arctos*) to avoid the human hunter. M.S. Thesis, Wageningen University, Wageningen, The Netherlands.
- Skogen, K., & Krange, O. (2020). The Political dimensions of illegal wolf hunting: Anti-elitism, lack of trust in institutions and acceptance of illegal wolf killing among Norwegian hunters. *Sociologia Ruralis*, 60(3), 551-573.
- Skuban, M., Findo, S., Kajba, M., Koren, M., Chamera, J., & Antal, V. (2017). Effects of roads on brown bear movements and mortality in Slovakia. *European Journal of Wildlife Research*, 63(5), 82.
- Skuban, M., Find'o, S., & Kajba, M. (2018). Bears napping nearby: daybed selection by brown bears (*Ursus arctos*) in a human-dominated landscape. *Canadian Journal of Zoology*, 96(1), 1-11.
- Slagle, K. M., Bruskotter, J. T., & Wilson, R. S. (2012). The role of affect in public support and opposition to wolf management. *Human Dimensions of Wildlife*, 17(1), 44-57.
- Slotkin, R. (1998a). *Gunfighter nation: The myth of the frontier in twentieth-century America*. University of Oklahoma Press, Norman, Oklahoma.
- Slotkin, R. (1998b). *The fatal environment: The myth of the frontier in the age of industrialization, 1800-1890*. University of Oklahoma Press, Norman, Oklahoma.
- Slotkin, R. (2000). *Regeneration through violence: The mythology of the American frontier, 1600-1860*. University of Oklahoma Press, Norman, Oklahoma.
- Smith, D. N., & Hanley, E. (2018). The anger games: Who voted for Donald Trump in the 2016 election, and why?. *Critical Sociology*, 44(2), 195-212.
- Smith, T. S., Herrero, S., & DeBruyn, T. D. (2005). Alaskan brown bears, humans, and habituation. *Ursus*, 16(1), 1-10.
- Soanes, K., Rytwinski, T., Fahrig, L., Huijser, M. P., Jaeger, J. A., Teixeira, F. Z., ... & van Der Grift, E. A. (2024). Do wildlife crossing structures mitigate the barrier effect of roads on animal movement? A global assessment. *Journal of Applied Ecology*, 61(3), 417-430.
- Sorensen, A. A., Stenhouse, G. B., Bourbonnais, M. L., & Nelson, T. A. (2015). Effects of habitat quality and anthropogenic disturbance on grizzly bear (*Ursus arctos horribilis*) home-range fidelity. *Canadian Journal of Zoology*, 93(11), 857-865.

- Sorensen, A., Denny, C., McKay, T., & Stenhouse, G. (2021). Response of grizzly bears (*Ursus arctos*) to pipelines in Alberta. *Environmental Management*, 67(6), 1158-1170.
- Souliere, C. M., Coogan, S. C., Stenhouse, G. B., & Nielsen, S. E. (2020). Harvested forests as a surrogate to wildfires in relation to grizzly bear food-supply in west-central Alberta. *Forest Ecology & Management*, 456, 117685.
- Stewart, B. P., Nelson, T. A., Wulder, M. A., Nielsen, S. E., & Stenhouse, G. (2012). Impact of disturbance characteristics and age on grizzly bear habitat selection. *Applied Geography*, 34, 614-625.
- Steyaert, S. M., Endrestøl, A., Hacklaender, K., Swenson, J. E., & Zedrosser, A. (2012). The mating system of the brown bear *Ursus arctos*. *Mammal Review*, 42(1), 12-34.
- Steyaert, S. M., Zedrosser, A., Elfström, M., Ordiz, A., Leclerc, M., Frank, S. C., ... & Swenson, J. E. (2016a). Ecological implications from spatial patterns in human-caused brown bear mortality. *Wildlife Biology*, 22(4), 144-152.
- Steyaert, S. M. J. G., Leclerc, M., Pelletier, F., Kindberg, J., Brunberg, S., Swenson, J. E., & Zedrosser, A. (2016b). Human shields mediate sexual conflict in a top predator. *Proceedings of the Royal Society B: Biological Sciences*, 283(1833), 20160906.
- Stillfried, M., Belant, J. L., Svoboda, N. J., Beyer, D. E., & Kramer-Schadt, S. (2015). When top predators become prey: black bears alter movement behaviour in response to hunting pressure. *Behavioural Processes*, 120, 30-39.
- Stirling, I., & Derocher, A. E. (1990). Factors affecting the evolution and behavioral ecology of the modern bears. *International Conference on Bear Research & Management*, 8, 189-204.
- Støen, O. G., Ordiz, A., Evans, A. L., Laske, T. G., Kindberg, J., Frøbert, O., ... & Arnemo, J. M. (2015). Physiological evidence for a human-induced landscape of fear in brown bears (*Ursus arctos*). *Physiology & Behavior*, 152, 244-248.
- Storer, T. I., & Tevis, L. P., Jr. (1996). *California grizzly*. University of California Press, Berkeley, California.
- Straka, M., Paule, L., Ionescu, O., Štofik, J., & Adamec, M. (2012). Microsatellite diversity and structure of Carpathian brown bears (*Ursus arctos*): Consequences of human caused fragmentation. *Conservation Genetics*, 13, 153-164.
- Stedman, R., Diefenbach, D. R., Swope, C. B., Finley, J. C., Luloff, A. E., Zinn, H. C., ... & Wang, G. A. (2004). Integrating wildlife and human-dimensions research methods to study hunters. *Journal of Wildlife Management*, 68(4), 762-773.
- Stringham, S. F. (1986). Effects of climate, dump closure, and other factors on Yellowstone grizzly bear litter size. *International Conference on Bear Research & Management*, 6, 33-39.
- Stringham, S. F., & Rogers, L. L. (2017). Fear of humans by bears and other animals (Anthropophobia): how much is natural. *Journal of Behavior*, 2, 1009.
- Stringham, S. F., & Rogers, L. L. (2023a). Are brown bears less aggressive in Europe than in North America?. *Wildlife Research Institute, Research Report, Autumn 2023*, 1.
- Stringham, S. F., Rogers, L. L., & Bryant, A. (2023b). Have black and grizzly bears become more aggressive? Human-bear fatality trends 1900-2019. *Wildlife Research Institute, Research Report, Autumn 2023*, 2.
- Suring, L. H., & Del Frate, G. (2002). Spatial analysis of locations of brown bears killed in defense of life or property on the Kenai Peninsula, Alaska, USA. *Ursus*, 13, 237-245.

- Suring, L. H., Farley, S. D., Hilderbrand, G. V., Goldstein, M. I., Howlin, S., & Erickson, W. P. (2006). Patterns of landscape use by female brown bears on the Kenai Peninsula, Alaska. *Journal of Wildlife Management*, 70(6), 1580-1587.
- Suzuki, M., & Saito, M. U. (2023). Forest road use by mammals revealed by camera traps: A case study in northeastern Japan. *Landscape & Ecological Engineering*, 19(2), 289-296.
- Suzuki, M., & Saito, M. U. (2024). Seasonal changes in forest road use by mammals in a heavy snowfall area, north-eastern Japan: effects of management intensities. *Journal of Vertebrate Biology*, 73(24001), 24001-1.
- Swenson, J. E., Sandegren, F., Soderberg, A., Heim, M., Sørensen, O. J., Bjarvall, A., ... & Wabakken, P. (1999). Interactions between brown bears and humans in Scandinavia. *Biosphere Conservation*, 2(1), 1-9.
- Swenson, J. E., Sandegren, F., Brunberg, S., Segerström, P., & Segerström, P. (2001). Factors associated with loss of brown bear cubs in Sweden. *Ursus*, 12, 69-80.
- Swihart, R. K., & Slade, N. A. (1985). Testing for independence of observations in animal movements. *Ecology*, 66(4), 1176-1184.
- Teng, S. N., Xu, C., Teng, L., & Svenning, J. C. (2020). Long-term effects of cultural filtering on megafauna species distributions across China. *Proceedings of the National Academy of Sciences*, 117(1), 486-493.
- Teixeira, F. Z., Rytwinski, T., & Fahrig, L. (2020). Inference in road ecology research: what we know versus what we think we know. *Biology Letters*, 16(7), 20200140.
- Thomas, J. W., Gill, J. D., Pack, J. C., Healy, W. M., & Sanderson, H. R. (1976). Influence of forestland characteristics on spatial distribution of hunters. *Journal of Wildlife Management*, 500-506.
- Titus, K., & Beier, L. (1992). Population and habitat ecology of brown bears on Admiralty and Chichagof Islands. Federal Aid in Restoration Research Project Report, W-23-4. Alaska Department of Fish & Game, Juneau, Alaska.
- Tomkiewicz, S. M., Fuller, M. R., Kie, J. G., & Bates, K. K. (2010). Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1550), 2163-2176.
- Törnros, J. (1995). Effect of driving speed on reaction time during motorway driving. *Accident Analysis & Prevention*, 27(4), 435-442.
- Tracy, D. M. (1977). Reactions of wildlife to human activity along Mount McKinley National Park road. M.S. thesis, University of Alaska Fairbanks, Fairbanks, Alaska.
- Tri, A. N., Edwards, J. W., Ryan, C. W., Carpenter, C. P., Carr, P. C., Ternent, M. A., ... & Petty, J. T. (2017). Harvest rates and cause-specific mortality of American black bears in the wildland–urban interface of the Mid-Atlantic region, USA. *Ursus*, 28(2), 195-207.
- Troyer, W. A., & Hensel, R. J. (1964). Structure and distribution of a Kodiak bear population. *The Journal of Wildlife Management*, 28, 769-772.
- Tucker, M. A., Schipper, A. M., Adams, T. S., Attias, N., Avgar, T., Babic, N. L., ... & Stacy-Dawes, J. (2023). Behavioral responses of terrestrial mammals to COVID-19 lockdowns. *Science*, 380(6649), 1059-1064.
- Turvey, S. T., Crees, J. J., Li, Z., Bielby, J., & Yuan, J. (2017). Long-term archives reveal shifting extinction selectivity in China's postglacial mammal fauna. *Proceedings of the Royal Society B: Biological Sciences*, 284(1867), 20171979.

U.S. Fish & Wildlife Service (2007). Recovery Plan Supplement: Habitat-based recovery criteria for the Yellowstone Ecosystem. U.S. Fish & Wildlife Service, Missoula, Montana.

U.S. Fish & Wildlife Service (2021). Grizzly bear in the lower-48 states (*Ursus arctos horribilis*): 5-year status review. U.S. Fish & Wildlife Service, Upper Colorado Region, Denver, Colorado.

U.S. Forest Service (2006). Record of Decision: Forest Plan Amendment for grizzly bear habitat conservation in the Greater Yellowstone Area National Forests. U.S. Forest Service, Washington, D.C.

U.S. Forest Service (2011). Record of Decision: Forest Plan Amendments for motorized access management within the Selkirk and Cabinet-Yaak Grizzly Bear Recovery Zones. U.S. Forest Service, Kootenai, Lolo, & Idaho Panhandle National Forests.

<https://igbconline.org/committees/selkirk/#:~:text=Roles%20of%20the%20Selkirk%2FCabinet,the%20Grizzly%20Bear%20Recovery%20Plan>.

Vaeokhaw, S., Ngoprasert, D., Swatdipong, A., Gale, G. A., Klinsawat, W., & Vichitsoonthonkul, T. (2020). Effects of a highway on the genetic diversity of Asiatic black bears. *Ursus*, 31(3), 1-15.

Van de Walle, J., Pelletier, F., Zedrosser, A., Swenson, J. E., Jenouvrier, S., & Bischof, R. (2021). The interplay between hunting rate, hunting selectivity, and reproductive strategies shapes population dynamics of a large carnivore. *Evolutionary Applications*, 14(10), 2414-2432.

Van de Walle, J., Leclerc, M., Steyaert, S. M., Zedrosser, A., Swenson, J. E., & Pelletier, F. (2019). Proximity to humans is associated with longer maternal care in brown bears. *Behavioral Ecology & Sociobiology*, 73, 1-11.

Van der Grift, E. A., van der Ree, R., Fahrig, L., Findlay, S., Houlahan, J., Jaeger, J. A., ... & Olson, L. (2013). Evaluating the effectiveness of road mitigation measures. *Biodiversity & Conservation*, 22, 425-448.

Van der Marel, R. C., Holroyd, P. C., & Duinker, P. N. (2020). Managing human footprint to achieve large-landscape conservation outcomes: Establishing density limits on motorized route-user networks in Alberta's Eastern Slopes. *Global Ecology & Conservation*, 22, e00901.

Van der Ree, R., Jaeger, J. A., van der Grift, E. A., & Clevenger, A. P. (2011). Effects of roads and traffic on wildlife populations and landscape function: Road ecology is moving toward larger scales. *Ecology and society*, 16(1).

Van der Ree, R., Smith, D. J., & Grilo, C. (eds) (2015). *Handbook of road ecology*. John Wiley & Sons, New York, New York.

Van Manen, F. T., McCollister, M. F., Nicholson, J. M., Thompson, L. M., Kindall, J. L., & Jones, M. D. (2012). Short-Term Impacts of a 4-Lane Highway on American Black Bears in Eastern North Carolina. *Wildlife Monograph* 181, 1-35.

Van Manen, F. T., Haroldson, M. A., Bjornlie, D. D., Ebinger, M. R., Thompson, D. J., Costello, C. M., & White, G. C. (2016). Density dependence, whitebark pine, and vital rates of grizzly bears. *Journal of Wildlife Management*, 80(2), 300-313.

Van Manen, F. T., Haroldson, M. A., & Karabensh, B. E. (2019). Yellowstone grizzly bear investigations: Annual report of the Interagency Grizzly Bear Study Team 2018. U.S. Geological Survey, Bozeman, Montana.

Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., ... & Watson, J. E. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications*, 7(1), Article 12558.

- Visintin, C., Van Der Ree, R., & McCarthy, M. A. (2016). A simple framework for a complex problem? Predicting wildlife–vehicle collisions. *Ecology & Evolution*, 6(17), 6409-6421.
- Von Essen, E., Hansen, H. P., Källström, H. N., Peterson, M. N., & Peterson, T. R. (2015). The radicalisation of rural resistance: How hunting counterpublics in the Nordic countries contribute to illegal hunting. *Journal of Rural Studies*, 39, 199-209.
- Von Essen, E., Hansen, H. P., Peterson, M. N., & Peterson, T. R. (2018). Discourses on illegal hunting in Sweden: the meaning of silence and resistance. *Environmental Sociology*, 4(3), 370-380.
- Waits, L. P. (1999). Molecular genetic applications for bear research. *Ursus*, 11, 253-260.
- Wakkinen, W. L., Kasworm, W. F. (1997). Grizzly bear and road density relationships in the Selkirk and Cabinet-Yaak Recovery Zones. Idaho Department of Fish & Game, Bonners Ferry, Idaho and U.S. Fish & Wildlife Service, Libby, Montana.
- Wakkinen, W. L., & Kasworm, W. F. (2004). Demographics and population trends of grizzly bears in the Cabinet–Yaak and Selkirk Ecosystems of British Columbia, Idaho, Montana, and Washington. *Ursus*, 15(1), 65-75.
- Walker, R., & Craighead, L. (1997). Analyzing wildlife movement corridors in Montana using GIS. Pages 1-18 in *Proceedings of the 1997 ESRI user conference*. San Diego, California.
- Waller, J. & Servheen, C. (2005). Effects of transportation infrastructure on grizzly bears in northwestern Montana. *Journal of Wildlife Management*, 69, 985–1000.
- Waller, J. S., Servheen, C., & Patterson, D. A. (2005). Probabilistic measure of road lethality. Pages 503-508 in Irwin, C. L., Garrett, P., & McDermott, K. P. (eds). *International Conference on Ecology & Transportation*. Center for Transportation & the Environment, North Carolina State University, Raleigh, North Carolina.
- Waller, J. S., & Miller, C. S. (2015). Decadal Growth of Traffic Volume on US Highway 2 in Northwestern Montana. *Intermountain Journal of Sciences*, 21(1-4), 29-37.
- Wang, C., Quddus, M. A., & Ison, S. G. (2013). The effect of traffic and road characteristics on road safety: A review and future research direction. *Safety science*, 57, 264-275.
- Wang, Y. (2022). *The rise and fall of imperial China: The social origins of state development*. Princeton University Press, Princeton, New Jersey.
- Ware, J. V., Nelson, O. L., Robbins, C. T., & Jansen, H. T. (2012). Temporal organization of activity in the brown bear (*Ursus arctos*): Roles of circadian rhythms, light, and food entrainment. *American Journal of Physiology-Regulatory, Integrative & Comparative Physiology*, 303(9), R890-R902.
- Watabe, R., & Saito, M. U. (2021). Effects of vehicle-passing frequency on forest roads on the activity patterns of carnivores. *Landscape & Ecological Engineering*, 17, 225-231.
- WCS (Wildlife Conservation Society) & CIESIN (Center for International Earth Science Information Network), Columbia University (2005). Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Influence Index (HII) Dataset (Geographic). NASA Socioeconomic Data and Applications Center (SEDAC). <https://doi.org/10.7927/H4BP00QC>.
- Weaver, J., Escano, R., Mattson, D., Puchlerz, T., & Despain, D. (1986). A cumulative effects model for grizzly bear management in the Yellowstone Ecosystem. Pages 234-246 in Evans, K., Lindzey, F., Servheen, C., Winn, D., & Zager, P. (eds). *Proceedings-Grizzly Bear Habitat Symposium*. U.S. Forest Service, General Technical Report INT-207.

- Wells, S. L., McNew, L. B., Tyers, D. B., Van Manen, F. T., & Thompson, D. J. (2019). Grizzly bear depredation on grazing allotments in the Yellowstone Ecosystem. *Journal of Wildlife Management*, 83(3), 556-566.
- Wheat, R. E., & Wilmers, C. C. (2016). Habituation reverses fear-based ecological effects in brown bears (*Ursus arctos*). *Ecosphere*, 7(7), e01408.
- Wheatley, M., & Johnson, C. (2009). Factors limiting our understanding of ecological scale. *Ecological Complexity*, 6(2), 150-159.
- Wheatley, M. (2010). Domains of scale in forest-landscape metrics: implications for species-habitat modeling. *Acta Oecologica*, 36(2), 259-267.
- White, P. J., Gunther, K. A., & Van Manen, F. T. (2017). Yellowstone grizzly bears: Ecology and conservation of an icon of wildness. Yellowstone National Park, Yellowstone Forever and U.S. Geological Survey, Northern Rocky Mountain Science Center, Bozeman, Montana.
- Whittington, J., Low, P., & Hunt, B. (2019). Temporal road closures improve habitat quality for wildlife. *Scientific Reports*, 9(1), 3772.
- Whittington, J., Hebblewhite, M., Baron, R. W., Ford, A. T., & Paczkowski, J. (2022). Towns and trails drive carnivore movement behaviour, resource selection, and connectivity. *Movement Ecology*, 10(1), Article 17.
- Wiegand, T., Naves, J., Stephan, T., & Fernandez, A. (1998). Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Cordillera Cantabrica, Spain. *Ecological Monographs*, 68(4), 539-570.
- Wiegand, T., Moloney, K. A., Naves, J., & Knauer, F. (1999). Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. *The American Naturalist*, 154(6), 605-627.
- Wielgus, R. B., Bunnell, F. L., Wakkinen, W. L., & Zager, P. E. (1994). Population dynamics of Selkirk Mountain grizzly bears. *Journal of Wildlife Management*, 58(2), 266-272.
- Wielgus R.B., Vernier P.R. & Schivatcheva T. (2002). Grizzly bear use of open, closed, and restricted forestry roads. *Canadian Journal of Forest Research*, 32, 1597–1606.
- Wilson, S. M., Madel, M. J., Mattson, D. J., Graham, J. M., Burchfield, J. A., & Belsky, J. M. (2005). Natural landscape features, human-related attractants, and conflict hotspots: a spatial analysis of human–grizzly bear conflicts. *Ursus*, 16(1), 117-129.
- Wilson, S. M., Madel, M. J., Mattson, D. J., Graham, J. M., & Merrill, T. (2006). Landscape conditions predisposing grizzly bears to conflicts on private agricultural lands in the western USA. *Biological Conservation*, 130(1), 47-59.
- Wise, M. D. (2016). Producing predators: Wolves, work, and conquest in the Northern Rockies. University of Nebraska Press, Lincoln, Nebraska.
- Yost, A. C., & Wright, R. G. (2001). Moose, caribou, and grizzly bear distribution in relation to road traffic in Denali National Park, Alaska. *Arctic*, 54(1), 41-48.
- Yri, I. M. (2006). Seasonal and diel variation in road avoidance behavior of female Scandinavian brown bears. M.S. Thesis, Norwegian University of Life Sciences, Ås, Norway.
- Zager, P., Jonkel, C., & Habeck, J. (1983). Logging and wildfire influence on grizzly bear habitat in northwestern Montana. *International Conference on Bear Research & Management*, 5, 124-132.
- Zager, P. E., & Jonkel, C. J. (1983). Managing grizzly bear habitat in the northern Rocky Mountains. *Journal of Forestry*, 81(8), 524-536.

Zajac, R. M., Bruskotter, J. T., Wilson, R. S., & Prange, S. (2012). Learning to live with black bears: A psychological model of acceptance. *Journal of Wildlife Management*, 76(7), 1331-1340.

Zarco-González, Z., Carrera-Treviño, R., & Monroy-Vilchis, O. (2023). Conservation of black bear (*Ursus americanus*) in Mexico through GPS tracking: Crossing and roadkill sites. *Wildlife Research*, 51(1), Article WR22121.

Zeller, K. A., Wattles, D. W., Conlee, L., & DeStefano, S. (2019). Black bears alter movements in response to anthropogenic features with time of day and season. *Movement Ecology*, 7, 1-14.

Zeller, K. A., Wattles, D. W., & Destefano, S. (2020). Evaluating methods for identifying large mammal road crossing locations: Black bears as a case study. *Landscape Ecology*, 35, 1799-1808.

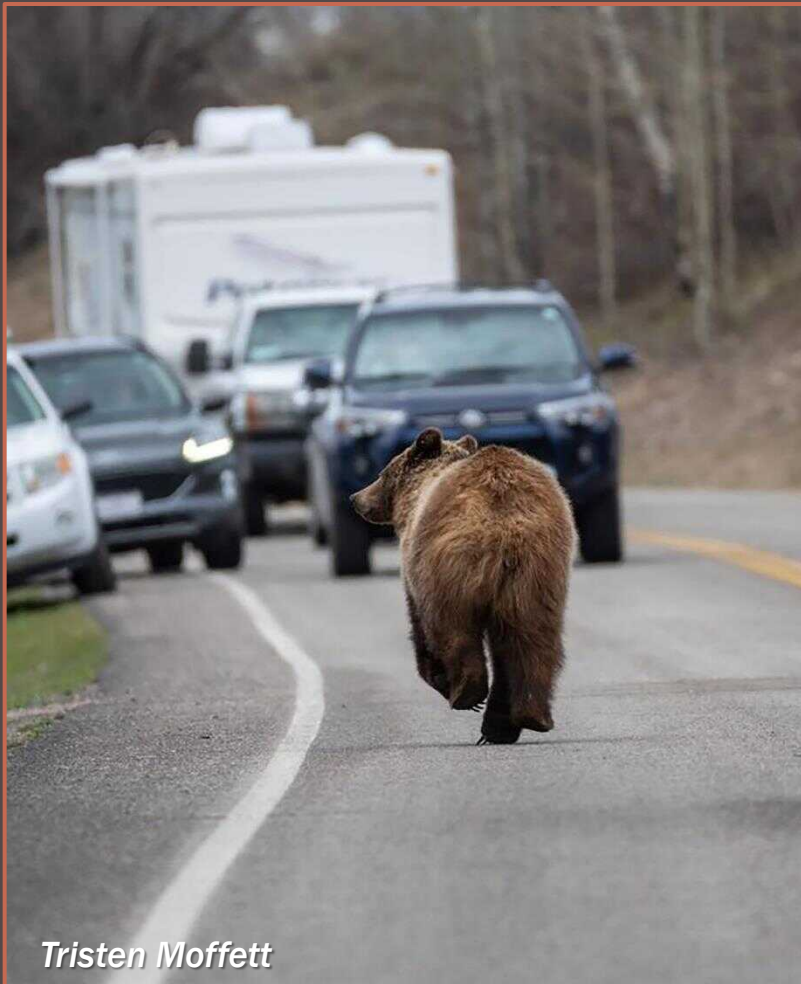
Zeller, K. A., Wattles, D. W., Conlee, L., & Destefano, S. (2021). Response of female black bears to a high-density road network and identification of long-term road mitigation sites. *Animal Conservation*, 24(2), 167-180.

Zheng, H., Qin, Y., Guo, F., Xiong, J., Xu, B., & Chen, Y. (2018). Speed and reaction behavior in different highway landscapes: A driving simulator study. *Traffic Injury Prevention*, 19(8), 880-884.

Ziółkowska, E., Ostapowicz, K., Radeloff, V. C., Kuemmerle, T., Sergiel, A., Zwijacz-Kozica, T., ... & Selva, N. (2016). Assessing differences in connectivity based on habitat versus movement models for brown bears in the Carpathians. *Landscape Ecology*, 31, 1863-1882.

Zuniga-Palacios, J., Zuria, I., Castellanos, I., Lara, C., & Sanchez-Rojas, G. (2021). What do we know (and need to know) about the role of urban habitats as ecological traps? Systematic review and meta-analysis. *Science of the Total Environment*, 780, 146559.

Zunino, F., & Herrero, S. (1972). The status of the brown bear in Abruzzo National Park, Italy, 1971. *Biological Conservation*, 4, 263-272.



Tristen Moffett



Roads, Residences, and grizzly bears

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