FLAWED SCIENCE

A Critique of Science Practices and Products by the Interagency Grizzly Bear Study Team 2006-2023

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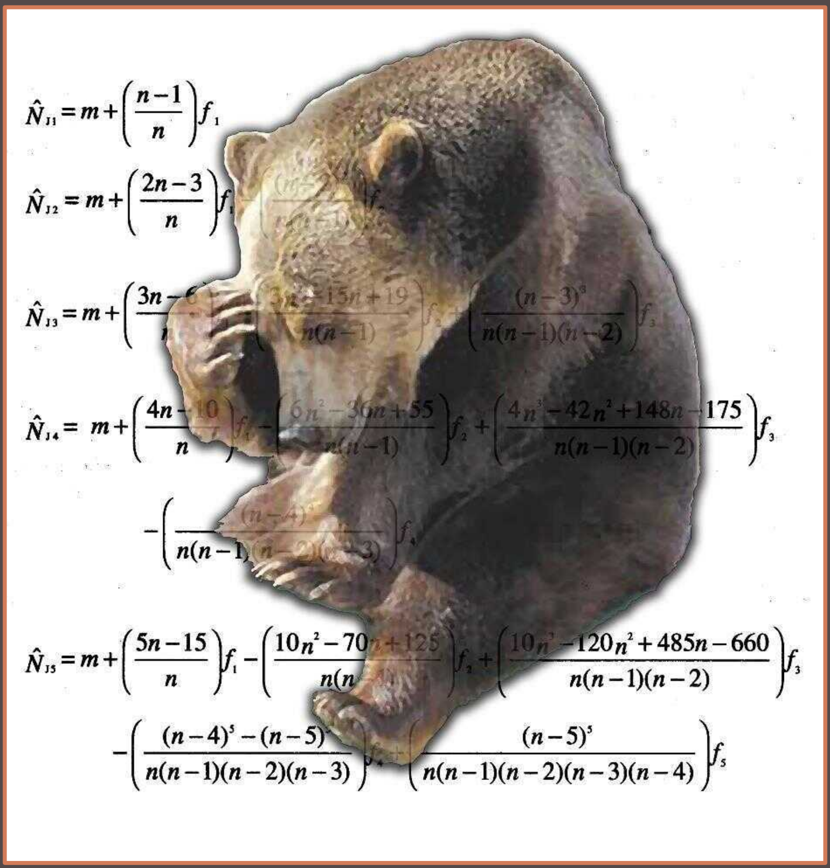

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The Grizzly Bear Recovery Project

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Livingston,
Montana

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Summary

- ***A History Rooted in Litigation***—The history surrounding two successive efforts by the U.S. Fish & Wildlife Service (USFWS) to remove ESA protections for Greater Yellowstone Ecosystem (GYE) grizzly bears in 2007 and 2017 has had a major configuring effect on research practices and products by the Interagency Grizzly Bear Study Team (IGBST) during the past 20+ years (**Section 2**).

- ***Scientific Failings of Delisting Rules***—Both efforts by the USFWS to remove ESA protections for GYE grizzly were stopped by federal district and appellate court judges who determined that the USFWS misused or selectively misrepresented scientific information in its deliberations. Judges during the first, 2007-2010, round of litigation found that the agency had been negligent in accounting for the effects of whitebark pine (*Pinus albicaulis*) seed consumption on demography of GYE grizzly bears and had misrepresented the magnitude of whitebark pine mortality during the previous ten years. Judges during the second, 2017-2020, round of litigation similarly found that the USFWS had misrepresented research regarding genetic health of the GYE population and not provided an adequate mechanism for managing grizzly bear mortality (**Section 2**).

- ***A "Straw Man" Research Agenda***—This history of legal losses triggered the deep involvement of USFWS personnel in design and execution of IGBST research, with the explicit goal of rebutting judicial rulings. This politicized research agenda featured a highly rarefied "strawman" contest that focused almost exclusively on a battle between the statistical effects of whitebark pine losses and putatively increased bears densities on demography and behavior of GYE grizzly bears. This constrained and politicized design was flawed from the onset by neglecting numerous additional factors that prospectively affected grizzly bear demography and by relying on dubious or flawed measures of both bear density and whitebark pine abundance (**Section 2**).

- ***Misrepresented Abundance of Whitebark Pine***—IGBST researchers mismeasured or misrepresented the temporal availability of whitebark pine seeds to GYE bears in all their key analyses primarily by conflating abundance of edible seeds, as such, with numbers of live whitebark pine trees during a period of widespread mortality caused by a mountain pine beetle (*Dendroctonus ponderosae*) outbreak. Mortality of mature trees was offset during the early part of this outbreak by a near doubling of cone production on surviving trees, resulting in essentially no temporal correlation between annual cone crops and numbers of live trees. Because IGBST researchers erroneously relied on the latter as a proxy for the former in most analyses, their representations of pine seed availability had little or no relationship to reality (**Sections 3.2**).

- ***Mismapped Whitebark Pine***—The IGBST also substantially underestimated the spatial extent of cone-producing whitebark pine by relying on a map derived from remote sensing that was contaminated by substantial errors of omission. Most locations where field crews verified that grizzly bears had consumed

whitebark pine seeds were located *outside* the IGBST's mapped distribution – a level of error that delegitimized statements by IGBST researchers claiming that a substantial portion of GYE bears historically lacked access to mature cone-producing whitebark pine. These substantial errors of omission also called into question the results of IGBST analyses purporting to address the behavioral responses of bears to losses of whitebark pine during and after the mountain pine beetle outbreak (**Section 3.3**).

- ***Neglect of Manifold Environmental Change***—IGBST researchers also routinely failed to account for numerous other factors that likely affected demography of GYE grizzly bears, including increased consumption of army cutworm moths (*Euxoa auxilliaris*) by grizzly bears in the Absaroka Mountains; functional extirpation of cutthroat trout (*Oncorhynchus clarkii*) as a bear food in southcentral portions of the ecosystem; declines in numbers of elk (*Cervus canadensis*) ecosystem wide; declines in numbers of bison (*Bison bison*) in central portions of Yellowstone National Park; synchronous exponential increases in numbers of bison in northern portions of the park; an epic drought that lasted from 2000 to 2009; and systematic increases in summer temperatures (**Sections 3.4-3.5**).

- ***Disregard for Changes in Key Natural Foods***—A substantial amount of research offers *prima facie* evidence that all these environmental changes likely affected demography, behavior, and distribution of GYE grizzly bears during 1990-present. Loss of cutthroat trout eliminated an important bear food in one of the most secure portions of the ecosystem. Increased exploitation of army cutworm moths attracted bears to some of the most remote and secure parts of the Absaroka Mountains. Meat from elk and bison was and continues to be one of the most important sources of energy and nutrients for GYE bears, but with regionally varied importance. Drought has continued to have numerous but annually varied ecosystem-wide effects on availability of vegetal foods, including excavated roots and grazed foliage. Importantly, IGBST researchers did not explicitly account for any of these prospectively weighty environmental effects in most of their reported analyses (**Sections 3.6-3.8**).

- ***Neglected Compensatory Consumption of Meat***—There is indisputable evidence that GYE grizzly bears compensated for losses of whitebark pine, cutthroat trout, and native ungulates by not only more heavily consuming army cutworm moths, but also by more intensively exploiting anthropogenic meat – notably livestock on public land grazing allotments and remains of kills made by elk hunters. As with prospective effects attributable to losses of native foods, IGBST researchers failed to account for demographic effects that likely arose from bears exploiting hazardous anthropogenic foods – as well as hazards to cubs arising from exploitation of meat from any source by their mothers (**Section 3.9**).

- ***Neglected Hazards of Consuming Anthropogenic Meat***—The consequences of losing native foods located in secure environments and related compensatory increases in exploitation of anthropogenic meat were manifest in a quadrupling of known or likely grizzly bear mortalities. This sharp increase in bear deaths closely followed terminal losses of whitebark pine trees to a mountain pine beetles outbreak and was typified by a near doubling of the proportion of deaths caused by conflicts with elk hunters or retaliations for depredation on livestock. Mortalities simultaneously doubled as a fraction of total estimated population size, suggesting a commensurate increase in grizzly bear mortality rates. Even more consequential, the fraction of female versus male bears killed because of depredation conflicts also more than doubled (**Sections 3.10-3.12**).

- ***Obfuscating Artifacts of Changing Methods***—At the same time that these dramatic environmental changes and related effects on diets, behavior, and demography of grizzly bears were unfolding, methods for estimating size and trend of the GYE bear population remained in flux and beset by bias. Presumed instantaneous increases in population size amounting to sometimes 100s of bears were largely and at times even entirely an artifact of changing methods (**Section 4.1**).

- ***Biased Methods for Estimating Population Size & Trend***—Even with presumed improvements in models, the metric that drove most methods and results during 2007-2023 remained counts of unduplicated females with cubs-of-the-year (COY). These counts and derivative estimates of population size and trend could be explained almost entirely by increasing efforts on the part of researchers to detect unduplicated females with COY during aerial surveys, as well as by increases in sightability of bears arising from dietary shifts that led bears to more heavily exploit non-forest habitats – notably increased consumption of meat from ungulates and cutworm moths on alpine aggregation sites (**Section 4.2**).

- ***Risky Management of Mortality***—*Prima facie* problems with estimating population size and trend in the GYE continue to be aggravated by methods used to derive a proxy estimate of annual mortality that GYE managers rely on for annual deliberations. This proxy measure is little more than the ratio of estimated total dead and live bears (numerator and denominator, respectively) estimated for the GYE each year. Even though managers and researchers both assume that this proxy accurately represents true mortality rates there, is fact, no known relationship between the two. Even more problematic, the proxy measure of annual mortality rates used for management purposes is reckoned against benchmarks that were derived from simulation models employing estimates of mortality rates based on *known fates of radio-marked bears* – again with no well-established or otherwise known relationship between the proxy measure and a fundamentally different set of methods and data (**Section 4.3**).

- ***Biased Estimates of Bear Mortality***—Problems arising from the absence of any direct or verifiable relationship between methods used to calculate proxies for real-time management of bear mortality and methods used by researchers to estimate population mortality benchmarks have been aggravated by employment of biased methods for field estimates of total annual mortality. These methods developed by the IGBST for estimating numbers of unreported and undetected in addition to known and probably probable deaths almost certainly underestimate the true numbers dying (**Section 4.4**).

- ***Implausible Estimates of Death Rates***—Other evidence suggests that death rates calculated by managers from field data and by the IGBST from radio-marked bears have been increasingly underestimated over time. *Field rates* have been biased low simply because total numbers of bears dying during a given year have been increasingly underestimated. Other evidence calls into question estimates of mortality rates calculated by the IGBST from *radio-marked bears*, including a *doubling* in numbers of bears known to die relative to total estimated population size (a proxy for mortality rate), synchronous with dietary shifts arising from losses of whitebark pine seeds. The annual churn in numbers of bears captured and subsequently monitored similarly nearly doubled during this same period, suggesting that captured bears were increasingly dying at a rate faster than they could be captured (**Section 4.5**).

- ***Doubtful Estimates of Population Growth Rate***—The IGBST used a trend metric that was biased by search effort and bear sightabilities (i.e., unduplicated females with COY) together with implausibly low estimates of bear death rates to derive estimates of population size and trajectory for GYE grizzly bears. The resulting dubious estimates were likely inflated, with this bias compounded by failure of IGBST researchers to account for reduced reproductive output of older female bears (i.e., senescence). This concatenation of problems calls into question all estimates of population size and trend produced by the IGBST during the past 20 years (**Section 4.6**).

- ***A Dubious Measure of Bear Density***—Returning to the contest between effects of conspecific density and whitebark pine losses on GYE grizzly bears, it turns out that the metric used by the IGBST for spatial and temporal representations of bears densities was likely biased by increasing efforts to capture and radio-track bears, which further called into question analyses compromised by mismeasurements of whitebark pine seed availability and inattention to other environmental effects. When adjusted for an expanding distribution, population-averaged bear densities did not appreciably change during 1990-2022 and were in fact lowest at a time that conflicted with when the IGBST claimed densities were highest (**Section 4.7**).

- ***Naïve Conceptions of Carrying Capacity & Density Dependence***—Mismeasurement of key environmental and demographic variables by the IGBST were compounded by the invocation of simplistic and misleading conceptions of carrying capacity and density-dependent effects. IGSBT researchers assumed a static capacity of the environment to support bears, comparable to a sardine can, and effects of bears on each other comparable to those of randomly moving ping-pong balls, with all effects equal. But carrying capacity self-evidently fluctuates annually and over time. The spatial organization of bears is also dynamic, as evident in changing diets and habitat selection. Different diets entail different hazards, especially from encounters of subordinate bears with adult males, sufficient to explain all changes in survival of cub and yearling bears independent of any variation in bear densities. When these behavioral changes are considered in concert with changing habitats and foods, the static reckonings of carrying capacity and "density-dependent effects" by the IGBST are basically meaningless (**Sections 4.7-4.8**).

- ***Disregard for Long-Term Population Viability***—The IGBST and USFWS basically ignored the best available science regarding requisites of long-term population viability, defensible time frames for judging risk, and relationships between genetically effective and total population size, resulting in unsubstantiated claims that a census population of 500 grizzly bears would ensure long-term genetic health. The current scientific consensus as well as plausible models of long-term population viability suggest that populations of grizzly bears should number 3,000-4,000 animals to ensure genetic health and adaptive evolutionary potential over periods of 40 bear generations – roughly 400 years (**Section 5.1**).

- ***Implausible Estimates of Genetically Effective Population Size (N_e)***—The IGBST produced estimates of N_e (numbers of bears making genetic contributions to subsequent generations) that were an implausibly high fraction of estimated total numbers of bears – in the range of 40-60% – as well as inconsistent with direct approximations from demographic data. Moreover, trends in the ratio of effective to census population size increased substantially over time. These problematic patterns call into question estimates of N_e made by the IGBST, especially given the highly complex and contingent nature of models used to estimate this elusive quantity (**Section 5.2**).

- ***Overlooked Logistics of Trucking Bears***—The USFWS, IGBST, and state wildlife management agencies are making plans to translocate 2-4 bears per decade from the Northern Continental Divide (NCDE) to Greater Yellowstone populations to alleviate concerns about long-term genetic health. These plans are unrealistic and otherwise dubious for several reasons including evidence suggesting that 10-20 successfully translocated bears may be needed each decade (i.e., bear generation) to mitigate loss of alleles and genetic heterozygosity, and that this number may increase to 75-150 if rates of successful breeding by transplanted bears are comparable to observations from other ecosystems (i.e., 13%). Nor do these plans consider the possibility of *outbreeding* *depression* resulting from the loss of locally adaptive genes with the long-distance transport of bears from dissimilar environments of the NCDE (**Section 5.3**).

- ***Poorly Framed Models & Hypotheses***—The multiple failings of IGBST research described in Sections 3-5 of this report evince an approach to science that neglects numerous consequential environmental drivers of grizzly bear behavior and demography, selectively attends to a handful of factors chosen largely for political reasons, mismeasures or misrepresents the few factors that are attended to, and deploys methods that produce dubious results at odds with straight-forward evidence. In more arcane terms, these failings are manifest in under-specified hypotheses and models and prejudiced interpretations of research results constructed with the apparent *a priori* intent of dismissing effects attributable to environmental change while ascribing all demographic changes to effects of conspecific densities (**Section 6.1**).

- ***Social, Psychological, and Institutional Distortions***—The politicized history spawned by failed attempts to remove ESA protections predictably interacted with social-psychological dynamics to amplify corruptive effects on scientific practices of IGBST researchers. Key elements of these dynamics included in-group loyalties, financial dependencies, and perverse institutional incentives created by the USFWS, state wildlife management agencies, and the U.S. Geological Survey (USGS) – parent organization of the IGBST (**Section 6.2**).

- ***Corruptive Financial and Political Influences***—Research agendas of IGBST scientists were fundamentally shaped by personal and monetary influences exerted by the USFWS and exacerbated by financial dependencies created by a parent agency operating under a business model of research production. IGBST researchers existed, moreover, in a politically over-heated authoritative environment dominated by regional elected officials and appointed agency leaders who used a biased selection of unreliable information to promote removal of ESA protections for GYE grizzly bears (Section 6.2).

- ***Perpetuation of a Data Monopoly***—The production of reliable science requires transparency and opportunities for multiple independent researchers to test and potentially replicate research results. This especially holds true for topics that spawn controversy, as does grizzly bear management. There is only one GYE grizzly bear population as well as a single data set collected at public expense by government employees. Under such circumstances, there is no justification for IGBST researchers aggressively perpetuating a data monopoly, as they have done for the past 30+ years. This monopoly has debarred any opportunity for correctives offered by ideals of scientific practice and ample scope to produce the flawed science described in this report (**Section 6.3**).

- ***Invocation of Fallible Peer Review***—Finally, IGSBT researchers claim to correct all the problematic practices and products described here through the presumed cleansing process of peer review. The IGBST and USFWS have routinely justified this presumption with inflated claims for the efficacies of peer review, and with disregard for evidence showing that peer review is fallible and no substitute for corrections arising from the often-contentious dialectic of multiple independent scientists investigating topics of shared interest in an open arena (**Section 6.4**).

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1. Introduction

Publications produced by the Interagency Grizzly Bear Study Team (IGBST) between 2006 and 2023 are frequently invoked by the U.S. Fish & Wildlife Service, U.S. Forest Service, and various state wildlife management agencies in official decision-making processes in the Greater Yellowstone Ecosystem (GYE) and elsewhere. A consistent coordinated theme of these invocations includes assertions that grizzly bears are omnivores unaffected by available foods and resulting differences in diets. Because of this, managers further claim that bears in the GYE have been unaffected by major environmental changes that have unfolded during the last three decades. As a corollary, proponents of this narrative assert that essentially all observed changes in behavior and demography are thus attributable to increasing bear densities, resulting in a surfeit of expendable bears in a population reaching carrying capacity.

These themes and the invoked body of supporting IGBST science have been prominently featured by those supporting removal of Endangered Species Act protections for Yellowstone's grizzly bear population during two efforts spanning 2007-2011 and 2017-2020 as well as by agency decision-makers who routinely justify actions or *status quo* arrangements that are likely to harm grizzly bears (Section 1). There are unequivocal causal links between the corpus of IGBST science purporting to show a population at carrying capacity, limited only by internal dynamic driven by densities of conspecifics, and arguments made by agency managers ostensibly justifying deleterious actions – all premised on claims of unending increases in size of the bear population, expendable surpluses of bears, and an unlimited ability of bears to adapt to changing environments[1].

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[1] There are numerous examples of this phenomenon evident in references made to IGBST science in official decisions by managers of grizzly bear populations and habitat. Declarations and comments documenting this pattern in decision-making processes can be found at: https://www.grizzlytimes.org/comments-on-government-plans and https://www.grizzlytimes.org/declarations-testimony

However, none of these assertions withstands critical scrutiny, largely because nearly all the publications invoked to justify them are flawed by bias as well as compromised by methodological, conceptual, and mensurational problems. This suite of problems applies to Bjornlie et al. (2014a), Costello et al. (2014), Gunther et al. (2014), Van Manen et al. (2016), and Corriadini et al. (2023), which together comprise the primary body of research referenced by agency decision-makers. In what follows I describe numerous critical failings in the research reported in these publications, concluding with problems embedded in the political and operational environment of the Interagency Grizzly Bear Study Team that fatally compromise the scientific enterprise of IGBST scientists and their collaborators. Each issue is addressed in a different section, but with one building on the other to form a coherent critique. I conclude in Sections 16-18 with a provisional explanation of how the scientific undertakings I focus on here were politicized and tainted.

As a prelude, Section 2 offers a brief history providing necessary context for the genesis of IGBST research results that are one focus of this critique. Sections 3.1-4.12 offer more insights into how this history tainted scientific practices and products by the Study Team during 1998-2023 and allowed for numerous failings to be cumulatively neglected, overlooked, uncorrected, or even willfully embraced during the process of scientific inquiry and publication. There are several plausible explanations for these corrosive dynamics, including the politicized environment within which the IGSBT operated (Section 2), especially the extent to which litigation, funding, and other outside influences shaped IGBST science during the past 25 years. Perhaps even more important, history interacted with institutional incentives and social-psychological human impulses to create a dynamic that conspired to corrupt most IGBST science of relevance to deliberations over the future of Yellowstone grizzly bears.

2. The Historical Roots of Politicized Science: An Introduction

Scientific information about the Yellowstone grizzly bear population has long been contested, politicized, and fraught with subjectivity (e.g., Schullery 1986, Mattson & Craighead 1994, Craighead et al. 1995, Mattson 1996, Wilkinson 1998, Heeren et al. 2017, Ketchum 2019). However, these politicizing dynamics were amplified after 1993 and the initiation of concerted efforts by grizzly bear managers and IGBST researchers to create a corpus of science that could be used to justify removal of ESA protections for Yellowstone's grizzly bear population, notably the rule issued by the U.S. Fish & Wildlife Service (USFWS) in 2007 shortly after publication of a monograph by Schwartz et al. (2006a) claiming to show that demography of the population was increasingly governed by density-dependent phenomena triggered by a population near carrying capacity (but see Section 14).

The 2007 rule was the first of two that temporarily removed long-standing Endangered Species Act (ESA) protections for grizzly bears in the GYE (U.S. Fish & Wildlife Service 2007). By chance, this first rule was promulgated during a major episode of whitebark pine (*Pinus albicaulis*) mortality caused by an outbreak of mountain pine beetles (*Dendroctonus ponderosae*) unleashed by drought and climate warming in the tree's normally frigid high-elevation haunts (Section 3; Logan et al. 2010, Macfarlane et al. 2013). Cutthroat trout (*Oncorrhychus clarkii*) populations that spawned in streams tributary to Yellowstone Lake were also undergoing a catastrophic decline caused by predation from non-native Lake trout (*Salvelinus namaycush*) and deteriorating hydrologic conditions. Prior to 2000, both foods had been one of four main sources of energy and nutrients for Yellowstone grizzly bears (Section 2). Whitebark pine seeds were an especially important food for female bears. On average, females ate twice as many pine seeds as did adult males, and benefited by having larger litters of cubs when they consumed more seeds during a bumper cone crop (Mattson 2000, Felicetti et al. 2003). Of greater consequence, there were substantial increases in human-caused mortality particularly among adolescents and human-tolerant bears during years when pine seeds were scarce (Mattson et al. 1992a, Mattson 1998, Pease & Mattson 1999, Schwartz et al. 2006a).

The lengthy rule issued by the USFWS in 2007 contained numerous assertions regarding the status of the bear population as well as bear foods and habitats. Among these were claims that whitebark pine seeds were of little importance to Yellowstone grizzly bears, that on-going losses of whitebark pine to bark beetles were minor (e.g., 15-20% overall mortality), and that effects of this mortality would have little impact on the bear population. The rule also contained related claims asserting that grizzly bears were adaptable omnivores unaffected by changes in habitat or foods, including not only whitebark pine, but also cutthroat trout, elk (*Cervus canadensis*), and bison (*Bison bison*).

The USFWS Rule was contested by litigation in federal court during 2007-2011, in part based on claims that the USFWS and the USFWS Recovery Coordinator at the time had misrepresented not only losses of whitebark pine, but also importance of pine seeds to behavior and demography of the grizzly bear population. The USFWS lost in federal district as well as federal appellate courts, partly based on determinations by involved judges that the USFWS had misrepresented science regarding the importance of whitebark pine seeds to Yellowstone grizzly bears, as well as on-going losses of whitebark pine to the mountain pine beetle outbreak (e.g., U.S. Court of Appeals for the Ninth Circuit 2011) –

losses that ended up amounting to heavy to moderate mortality in an astounding 80% of watershed catchments with whitebark pine in the ecosystem (Macfarlane et al. 2013, 2023). This was an unusual instance where judges dropped deference to agency expertise on technical matters and determined that relevant science had been treated in “an arbitrary and capricious manner.”

These legal losses by the USFWS in federal district and appellate courts led the agency to become deeply engaged in configuring science undertaken by IGBST researchers during the next decade, largely through involvement of the USFWS Recovery Coordinator in designing the research program as well as through enticements created by generous funding from the USFWS (see *Supplement Information* [*SI*] for this Report, including 36-37, 42-43). The Recovery Coordinator and involved IGBST researchers framed scientific inquiry as a literal “straw man” contest between the effects of whitebark pine loss and more opaque density-dependent phenomena arising from a population that had presumably reached carrying capacity (*SI*: 31-32, 62); see Sections 15-16). Little consideration was given to other complex environmental dynamics unfolding in the GYE before and after 2010 (Sections 5-11). Curiously, early in the process of designing a IGBST research agenda, 18 out of 19 attendees at a 2012 workshop focused on investigating demography of the GYA population believed there was no credible way to disentangle the effects of whitebark pine loss and bear density (GYA Demographics Workshop, February 1, 2012:14; *SI*: 55-59), which would debar statistically defensible conclusions regarding a dominant effect of either factor on grizzly bear demography.

The timeline of USFWS and IGBST deliberations regarding a path forward and adoption of the “straw man” agenda for producing science to rebut the court ruling is telling. Within days of the Appellate Court’s 2011 ruling USFWS leadership deliberated over three options: (1) give up on removing ESA protections for GYE grizzly bears; (2) create a new body of science to refute the Court’s opinion, and then issue a new delisting rule; or (3) reissue the exact same rule again and roll the dice on a new round of litigation (*SI*: 17-30). Agency leadership chose the second option and within a month the IGBST and USFWS Recovery Coordinator has formulated the “straw man” science agenda targeting effects of whitebark pine (*SI*: 31).

A close reading of correspondence and planning documents from this period (*Supplemental Information*) reveals a fixed focus on addressing adverse legal rulings that arose from the 2007-2011 litigation. Not surprisingly, this period of suspect scientific inquiry by the IGBST produced Bjornlie et al. (2014a), Costello et al. (2014), Gunther et al. (2014), and Van Manen et al. (2016). The urgency with which the USFWS and its Recovery Coordinator wanted to translate this body of research into a basis for issuing another rule to remove ESA protections from Yellowstone grizzly bears is evident in release of a summary report prior to publication of any of the research in scientific journals (Van Manen et al. 2013). Shortly after its release, the report was referenced by managers on the Interagency Grizzly Bear Committee (IGBC) as their primary basis for endorsing another effort to remove ESA protections for Yellowstone grizzly bears (Yellowstone Ecosystem Subcommittee 2014).

The next lengthy rule removing protections for GYE grizzly bears was issued by the USFWS in 2017 (U.S. Fish & Wildlife Service 2017), shortly after publication of Van Manen et al. (2016). This rule drew almost exclusively on IGBST science funded by the USFWS and shaped by the USFWS Recovery Coordinator during 2011-2016. Once again, the USFWS claimed that loss of whitebark pine had been inconsequential for Yellowstone grizzly bears (Bjornlie et al. 2014a, Costello et al. 2014, Van Manen et al. 2016); that bears in this population were infinitely adaptable (Gunther et al. 2014); that the population was genetically healthy (Kamath et al. 2015); and that density-dependent phenomena triggered by a population at carrying capacity were driving vital rates (Van Manen et al. 2016). This rule, like the first, was contested in court during 2017-2020; and the USFWS was yet again unable to defend its decision in federal district and appellate courts largely because of how scientific and technical matters were treated (U.S. Court of Appeals for the Ninth Circuit 2020). Tellingly, intervenors on behalf of the USFWS included not only the states of Wyoming, Montana, and Idaho, but also the National Rifle Association (NRA) and Safari Club. The three states would have been vested with authority over management of Yellowstone grizzly bears had the rule been upheld. Wyoming had already issued 23 permits for a grizzly bear trophy hunt planned to start immediately following a favorable Appellate Court ruling (Wyoming Game & Fish Commission 2018) – a move with obvious appeal to the NRA and Safari Club.

This second round of legal losses seemingly further entrenched an IGBST and USFWS narrative holding that changes in bear foods have had little impact on the GYE grizzly bear population and that demography of the population has long been configured primarily by “density-dependent” effects triggered by the population encountering a fixed carrying capacity (see Sections 4.7-4.8). This narrative continues to be routinely augmented by claims about the resilience of adaptable omnivorous bears. As has been the case since at least 2006, this thematic ensemble of claims continues to yield problematic research designs and often indefensible interpretations of research results, exemplified more recently by the Wells et al. (2019) analysis of grizzly bear cattle depredation and the Corradini et al. (2023) analysis of grizzly bear body composition (Sections 3.5, 3.11, and 3.12). The following Sections more explicitly delve into how this contentious political history configured IGBST research and plausibly produced the numerous scientific failings detailed below.

3. The Complexity of Environment Changes

The following Sections (3.1-3.12) describe not only numerous environmental changes in the Greater Yellowstone Ecosystem (GYE) that demonstrably affected behaviors, diets, and demography of grizzly bears, but also systematic inattention to key aspects of these dynamics in analyses undertaken by the IGBST during 2004-2023. This disregard by the IGBST for plausibly important drivers of change in grizzly bear life histories fatally compromised most of the Study Team's analyses – a failing compounded by mismeasurement and misrepresentation of the few environmental factors that were considered and by dubious inferences reached using suspect logic. The implications of these shortcomings are far-reaching because conclusions from this flawed research are currently the primary basis for management of grizzly bears in the GYE.

3.1. Omnivory vs Indifference to Food Quality and Quantity

Gunther et al. (2014) state that Yellowstone's grizzly bears eat over "260 species of foods…representing 4 of the 5 kingdoms of life." In various places, the authors thereafter imply that foods are dietarily equivalent—this despite acknowledging that energy concentration and nutrient content does vary among foods. Nonetheless, those who have subsequently referenced this paper typically use it as a basis for asserting that Yellowstone's grizzly bears are well able to substitute one food for another with little resulting effect on bear behavior or demography (e.g., Fortin et al. 2013). This claim undergirds many related claims made in Bjornlie et al. (2014a), Costello et al. (2014), Van Manen et al. (2016), and Corriadini et al. (2023).

A Grounding in Nutritional Research

Treatment of the nutritional ecology of grizzly bears by IGSBT researchers and GYE managers misconstrues or altogether overlooks a considerable body of relevant science. More specifically, nutritional quality of foods available to grizzly bears in the Yellowstone ecosystem varies by an order of magnitude (Mattson et al. 2004). Not all foods offer equal digestible protein and energy. Moreover, and perhaps more importantly, bear foods differ substantially in concentrations of dietary fat. Fat is perhaps the most important of all nutrients to bears (Erlenbach et al. 2014) and is uniquely abundant in army cutworm moths (*Euxoa auxiliaris*), whitebark pine seeds, and ungulates such as elk and bison during the fall and late summer (Mattson et al. 2004, Erlenbach et al. 2014).

The density, architecture, and comparative nutrient content of foods furthermore have major effects on foraging efficiencies, efficiencies of weight gain, and accretion of fat versus lean body mass among bears, with subsequent effects on mass dynamics during and after hibernation (e.g., Farley & Robbins 1995; Atkinson et al. 1996; Welch et al. 1997; Hilderbrand et al. 1999a, 1999b; Rode & Robbins 2000; Rode et al. 2001; Felicetti et al. 2003a; Robbins et al. 2007; McLellan 2011; Robbins et al. 2012; Erlenbach et al. 2014). As a rule, smaller bears fare better than larger bears on fleshy fruits and grazed foliage, whereas larger bears disproportionately benefit from eating meat. Even so, all bears are beset by a need to balance the energy and protein concentrations of their diet to maintain lean body mass and accrue fat. On top of this, the energetic costs of extracting and handling various foods differ substantially, to the extent that extraction costs can largely negate the digestible energy available in most root foods (Holcroft & Herrero 1984, Mattson 1997a, Mattson et al. 2004). More to the point, the size, sex, and overall diet of different bears dictates the relative benefits they obtain from different foods. Not all foods are equal, nor are all foods equal to different bears.

Parenthetically, bears are not Latin taxonomists. They do not key out their foods in *Flora of the Pacific Northwest* attempting, for example, to differentiate one bluegrass from another, or bluegrasses from wheatgrasses. Taxonomic distinctions that matter to people, as they do to Gunther et al. (2014), have little or no relevance to grizzly bears. Differences that matter to bears predictably arise from characteristic densities and architectures of foods at foraging sites, the energetic expenses of extraction, and per gram densities of energy and nutrients—along with how all these characteristics vary seasonally and annually. In other words, the fact that Yellowstone's grizzly bears eat "260 species of foods…representing 4 of the 5 kingdoms of life" is largely irrelevant to bears and bear foraging.

Specifics of Greater Yellowstone

With this as grounding, any assessment of how environmental change has affected Yellowstone's grizzly bears during the past 20 years needs to account for where bears obtained energy and nutrients between 1977 and 2003. More specifically, the available evidence suggests that most came from ungulate meat, cutthroat trout, whitebark pine seeds, and army cutworm moths during this period – with the strongest evidence coming from estimates based on analyzed scat contents corrected for detection, digestibility, and prevalence (Mattson et al. 2004:26-28; López-Alfaro et al. 2013). A major contribution of ungulate meat to Yellowstone's grizzly bear diet is also substantiated by other independent estimates based on feeding site examinations (Mattson 1997b) and analysis of isotopes in tissues collected from captured or killed bears (Jacoby et al. 1999; Schwartz et al. 2014).

Insofar as army cutworm moths are concerned, the evidence for a major dietary contribution is more circumstantial, but nonetheless compelling. When the composition of feces collected on or near alpine moth aggregation sites is corrected for differential passage through the digestive tract, moths comprise 80-90% of the total (Mattson et al. 1991a; Section 3.7). Moths have thus plausibly constituted an important bear food since especially the mid-1980s when steadily increasing numbers of bears were observed on moth sites during July-September, with bears at these sites currently accounting for hundreds of sightings and roughly 15-45% of all initial sightings of unduplicated females with cubs-of-the-year (Van Manen et al. 2023a; Section 4.2).

Given the historical reliance of Yellowstone's grizzly bears on essentially four foods (lumping elk and bison together as ungulates), major losses of any one of these foods would almost certainly have had major impacts – which came to pass. Cutthroat trout underwent catastrophic declines beginning in mid-1990s (Section 3.8) followed by declines of whitebark pine beginning in the early 2000s (Section 3.2). Moreover, as I point out in Section 3.9, elk populations substantially declined during the late-1990s, leaving only army cutworm moths and some bison herds to represent the euphemistic "Big 4". This begs the question of whether plausible alternative foods have been (and will be) of sufficient quality from a nutritional perspective to compensate for losses of key foods during the past 20+ years.

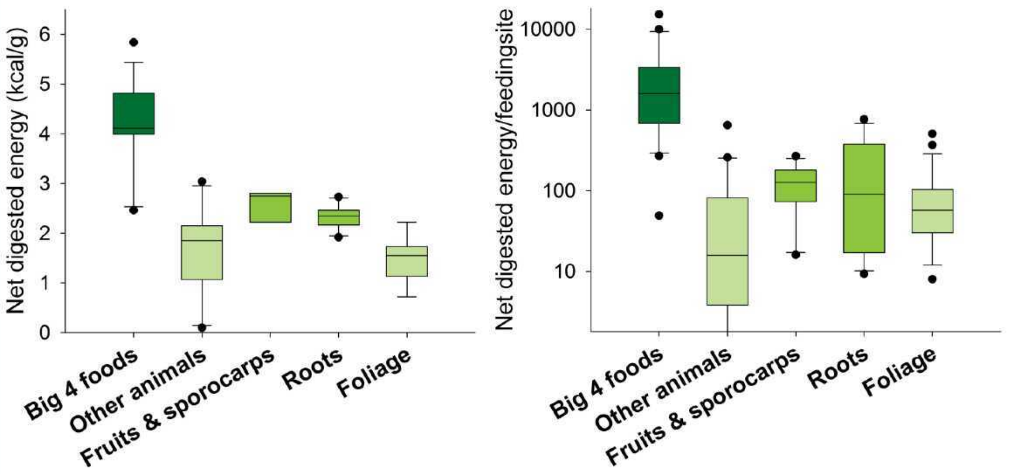


Figure 1. These box and whisker diagrams summarize the net digested energy obtained by Yellowstone grizzly bears from five different groups of foods on a per gram basis and from a given feeding bout (or feeding site). These data come from (Mattson et al. 2004) and differentiate the 'big 4" (ungulates, cutthroat trout, whitebark pine seeds, and army cutworm moths) from other categories including foods that could be consumed in compensation for losses of current dietary mainstays. None of the dietary alternatives are of comparable quality to the "Big 4," where reckoned on a per gram basis or on the basis of energetic benefits derived from a a typically foraging site.

Even accounting for outlier items, the Big 4 are energetically superior to any other foods that might have been consumed by bears during the past two decades to compensate for historical losses (Figure 1; Mattson et al. 2004), including other animal foods (e.g., rodents and ants) and fruits and fungi (i.e., sporocarps). Even so, the implications of per gram nutritional difference are complicated by potential effects arising from changes in bear distributions and landscape-level abundance of foods, and the extent to which replacement foods have occurred at sites favoring efficient use. None of this is known, other than well-documented increases in grizzly bear activity on moth sites (Section 3.8) and depredations on livestock (Section 3.11).

There is a final important point belying claims by Gunther et al. (2014) and others that grizzly bears can accommodate changes in food abundance simply because they are omnivorous and resilient. This point relates to continent-wide differences in grizzly bear densities and the extent to which these densities reflect differences in habitat productivity. Mowat et al. (2013) unequivocally show that grizzly bear densities systematically vary by an order of magnitude as a direct function of habitat productivity. The most obvious difference is between coastal areas with spawning salmon and interior areas without. But, even in interior areas, densities can vary substantially as a direct function of various proxies for overall environmental productivity.

Implications

As a premise, GYE grizzly bears have been and will prospectively continue to be affected by changes in foods and habitats – with potentially substantial effects on behavior, distribution, and demography. This prefatory conclusion is unambiguously better supported by the weight of evidence than the alternative conclusion that has shaped research interpretations and management applications for the past 20 years.

3.2. Whitebark Pine Trees vs Whitebark Pine Seeds

Given the extent to which a contest between effects of whitebark pine seed abundance and bear density featured in post-2011 research undertaken by the IGBST (Section 2), there was an imperative to accurately represent spatial and temporal dimensions of both variables. As I address in Section 4.7, the measure of bear densities was (and continues to be) suspect. Here and in the following section (Section 3.3) I describe serious errors that compromised how whitebark pine seed abundance was represented, with implications for the validity of essentially all inferences reported in Bjornlie et al. (2014a), Costello et al. (2014), and Van Manen et al. (2016) regarding effects of whitebark pine losses during 2000-2009. As I elaborate in this section, the IGBST made a systematic and consequential error that arose from conflating the extent of whitebark pine forests with abundance of seeds annually available to bears.

As a prefatory point, grizzly bears do not eat whitebark pine trees but rather the seeds contained in whitebark pinecones, most of which they obtain from larders made by red squirrels (e.g., Mattson & Reinhart 1997). As a result, any multi-annual representation of whitebark pine seeds available to Yellowstone's grizzly bears needs to reflect landscape-level cone or seed production, not solely numbers of cone-producing trees, as such, or even the aerial extent of forests containing mature whitebark pine. However, during 2012-2016 Interagency Grizzly Bear Study Team (IGBST) researchers consistently and erroneously equated temporal trends in abundance of mature trees with seed production in their analyses of how grizzly bear demography was affected by abundance of whitebark pine (e.g., Van Manen et al 2016).

Issues

This conflation matters because during and after extensive mortality of mature whitebark pine trees caused by an outbreak of mountain pine beetles (*Dendroctonus ponderosae*) during 2000-2009 (Macfarlane et al. 2013), median annual cone production increased by as much as 2.5-fold on surviving trees. Figure 2 shows per annum counts of cones on whitebark pine trees monitored on fixed transects by the IGBST, averaged for all monitored trees. The running three-year average of annual values is shown as a yellow-green line, which is relevant because of the somatic and behavioral averaging that occurs in concert with the three-year reproductive cycle of Yellowstone's female grizzly bears. In addition, annually averaged cone production is shown as dashed horizontal lines for three time periods that correspond with breaks in long-term trends. Notably, median cone production for 2006-2014 was roughly 2.5-times greater than median cone production for either 1982-1995 or 1997-2004. In other words, concurrent with mortality of most cone-producing trees in the ecosystem, cone production on remaining trees increased by over 2-fold.

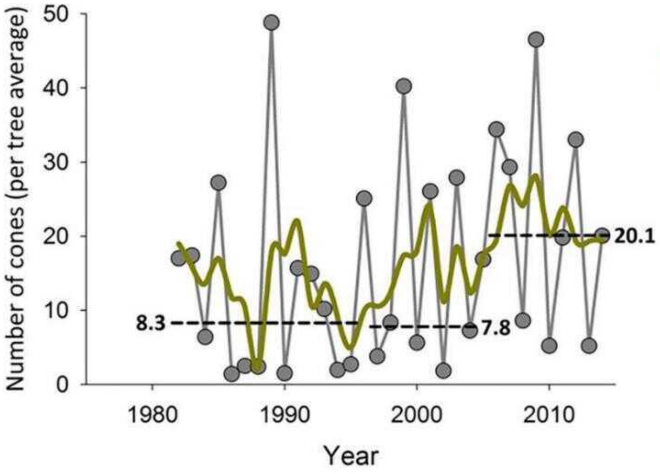


Figure 2. This graphic shows average number of cones counted on whitebark pine trees at fixed transects by the IGBST between 1982 and 2014 (gray dots) along with a 3-yr moving average of these values (yellow-green line) and medians calculated for annual values for three different time periods (dashed lines).

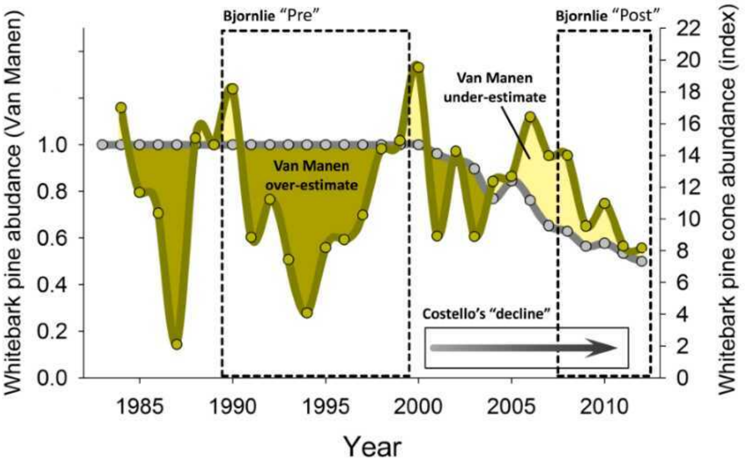


Figure 3. The IGBST index of mature whitebark pine is shown in this figure by the dotted gray line; the index of landscape-level cone availability accounting for losses of trees to bark beetles and the 1988 wildfires is shown by the dotted green line; and time periods relevant to errors in three key IGBST research publications are denoted by the first author's name and, in the case of Bjornlie et al. (2014a), by dashed boxes, in the case of Costello et al. (2014), by an arrow, and, in the case of Van Manen et al. (2016), by the extent of erroneous over- and under-estimations.

The IGBST represented annual availability of pine seeds to grizzly bears in Bjornlie et al. (2014a) and Van Manen et al. (2016: Figure 2) using estimates derived from remote sensing of live mature whitebark pine trees, but without accounting for the 2-fold increase in per tree cone production. A logical corrective for this error entails incorporating information about the size of cone crops on surviving trees with the estimated extent of whitebark pine forests by multiplying annual estimates of whitebark pine cover (from Van Manen et al. [2016]) by numbers of cones counted on live trees, as in Figure 3. This logically produces an index of total landscape-level abundance of seed-containing cones available for Yellowstone's grizzly bears to consume during a given year, which is requisite for any meaningful analyses of how temporal availability of whitebark pine seeds might have affected grizzly bear demography or movements.

Van Manen et al. (2016) made one additional error in representing the aerial extent of whitebark pine forests. They failed to account for the considerable losses of whitebark pine that occurred during the extensive wildfires of 1988. The constant abundance that Van Manen et al. (2016: Figure 2) show between 1983 and 2000 does not capture the approximate 17% decrease in whitebark pine forest cover between 1988 and 1989 (3-50%, depending on the precise area; Mattson 2000). This omission further compounds problems arising from the IGBST's systematic failure to account for effects of annual variation in cone crop size.

The index of cone abundance in Figure 3 shows a dramatically different inter-annual pattern compared to that depicted solely by systematically declining aerial extent of whitebark pine trees, which is critical to assessing the veracity of claims in Bjornlie et al. (2014a), Costello et al. (2014) and Van Manen et al. (2016). More specifically, pine seeds were *least* abundant during two early periods that the IGBST represented as having the *greatest* abundance. This discrepancy is attributable to the large increase in average sizes of cone crops on surviving trees during the early 2000s that mitigated mortality from mountain pine beetles. It was only after 2006 that losses of trees to beetles began to swamp the effects of larger cone crops, resulting in the onset of a terminal decline.

Figure 3 provides details regarding the implications of this problem for two key IGBST publications. The analysis of home ranges by Bjornlie et al. (2014a) was based on the premise that the period 1988-1999 was a period of pine seed abundance, and the period 2007-2012 a period of pine seed dearth. Pine seeds were, in fact, more abundant during the later period compared to the earlier period. Bjornlie et al. (2014a) got patterns of pine seed availability backwards. Likewise, the analysis of demography by Van Manen et al. (2016) substantially overestimated pine seed abundance during 1983-1999 and underestimated pine seed abundance during 2005-2010, which turned their assumptions upside down.

Implications

These errors invalidate the analyses and conclusions reported by Bjornlie et al. (2014a) and Van Manen et al. (2016). Both papers have been central to many claims made by government agencies in decision-making processes governing management of Yellowstone's grizzly bear population and habitat. The IGBST under-represented availability of pine seeds during the early 2000s and over-represented availability during the 1990s by relying solely on an index of tree abundance. The presumed patterns of whitebark pinecone availability that undergird IGBST analyses published between 2012 and 2016 were the antithesis of reality – barring the terminal decline in whitebark pine that began in 2006.

Parenthetically, losses of mature whitebark pine trees are real and on-going (e.g., Buotte et al. 2016, Shanahan et al. 2016, Macfarlane et al. 2023). Looking to the future, even though losses were largely masked by increases in per tree cone production during the early 2000s, natural mitigations such as these have run the course, with negative net consequences for Yellowstone grizzly bears. These consequences are evident in the dramatic increase in grizzly bear mortality after 2010 and related compensatory increases in consumption of meat by bears from anthropogenic sources (Sections 3.10, 3.11 and 4.5).

3.3. Whitebark Pine Distribution

The IGBST used a map of whitebark pine distribution derived from remotely sensed imagery for its spatial representation of whitebark pine forests (Landenburger et al. 2008). This map was used for analyses of grizzly bear demography, home ranges, diet, and habitat selection (Costello et al. 2014, Bjornlie et al. 2014a, Gunther et al. 2014, Van Manen et al. 2016), and was the basis for IGBST claims that roughly 23-33% of all bear ranges during 1977-2012 contained <1% whitebark pine forest.

Issues

The map of whitebark pine distribution used by the IGBST was problematic largely because it was contaminated by significant errors of omission, resulting in large areas being shown as without mature whitebark pine when, in fact, these areas did contain significant enclaves of mature cone-producing trees. These omissions are largely the basis for claims made by Bjornlie et al. (2014a), Costello et al. (2014), Gunther et al. (2014) and later by the U.S. Fish & Wildlife Service that a significant percentage of grizzly bears lacked access to cones produced by mature whitebark pine trees, putatively adding weight to claims that whitebark pine was unimportant to the population.

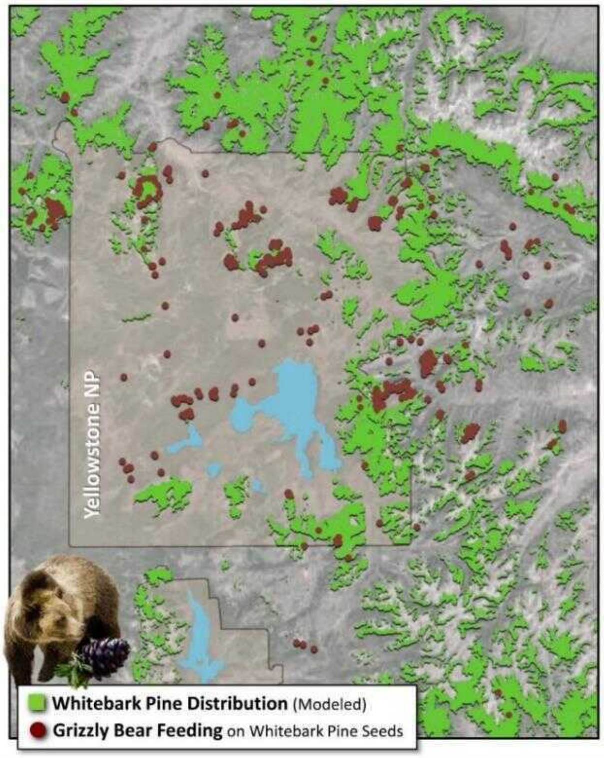


Figure 4. This map shows the distribution of known locations where grizzly bears fed on pine seeds 1977-1996 as dark brown dots superimposed on, in green, the remotely-sensed distribution of whitebark pine used in analyses reported by Gunther et al. (2014), Bjornlie et al. (2014a), Costello et al. (2014), and Van Manen et al. (2016). The mapped distribution contains only 42% of all instances where grizzly bears were known to feed on pine seeds. Even if field crews had a systematic tendency to erroneously locate feeding sites as much as 200 m outside the mapped distribution of whitebark pine, the level of inclusion increases to only 63%. Fully 25% of feeding sites are located >650 m away from the nearest whitebark pine detected by remote sensing. Importantly, almost all the erroneously overlooked sites where bears fed on pine seeds were located at lower elevations, and of those missed by the farthest distance, almost all were on the central plateaus of Yellowstone National Park where Bjornlie et al. (2014a), Costello et al. (2014), and Gunther et al. (2014) claimed that grizzly bear home ranges contained little or no mature whitebark pine.

Figure 4 shows the distribution map used by the IGBST as well as locations of sites where grizzly bears were documented by the IGBST during 1977-1996 to feed on whitebark pine seeds. Feeding on whitebark pine seeds was confirmed by field crews during investigations that involved people on the ground looking at the remains of whitebark pinecones exploited by grizzly bears, and then verifying the almost invariable presence of nearby mature whitebark pine trees (e.g., Mattson 2000, Mattson et al.

2004). Compared to remotely sensed maps, these ground observations are thus a much more reliable reckoning of not only the presence of cone-producing whitebark pine but also the presence of these trees in sufficient numbers to support grizzly bear consumption of pine seeds.

Known locations where grizzly bears fed on pine seeds are shown in Figure 4 as dark brown dots superimposed on a map showing, in green, the estimated distribution of whitebark pine used in analyses reported by Gunther et al. (2014), Bjornlie et al. (2014a), Costello et al. (2014), and Van Manen et al. (2016). This mapped distribution contains only 42% of all instances where grizzly bears were known to feed on pine seeds. Even if field crews had a systematic tendency to erroneously locate feeding sites as much as 200 m outside the mapped distribution of whitebark pine, the level of inclusion increases to only 63%. Fully 25% of feeding sites were located >650 m away from the nearest whitebark pine detected by remote sensing. Importantly, almost all the erroneously overlooked sites where bears fed on pine seeds were located at lower elevations, and of those missed by the farthest distance, almost all were on the central plateaus of Yellowstone National Park where Bjornlie et al. (2014a), Costello et al. (2014), and Gunther et al. (2014) claimed that grizzly bear home ranges contained little or no mature whitebark pine.

Implications

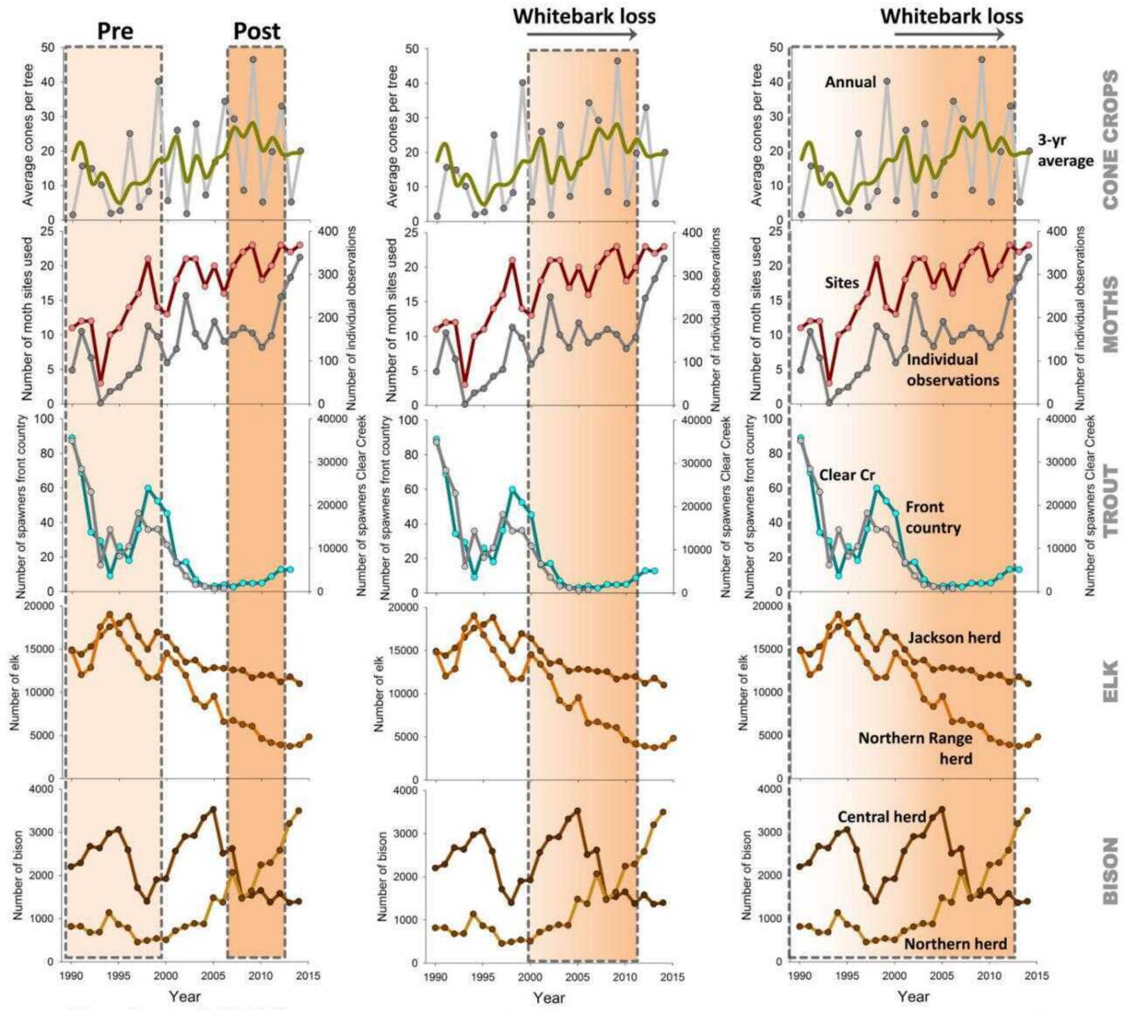
IGBST researchers had no defensible basis for claiming that 23-33% of historic grizzly bear ranges in the Greater Yellowstone Ecosystem contained little or no whitebark pine, and further claiming that whitebark pine was unimportant to a corresponding percentage of bears. In fact, almost all grizzly bear home ranges likely contained some whitebark pine. The exact percentage of bears without access to whitebark pine is unknown given that home range delineations used by IGBST scientists are not publicly available, but this percentage was almost certainly trivial.

As a bottom line, errors made by IGBST scientists in delineating whitebark pine forests and representing temporal availability of pine seeds (Section 3.2) together invalidate virtually all claims regarding effects of whitebark pine seed abundance on grizzly bear demography, diet, and behavior by Gunther et al. (2014), Bjornlie et al. (2014a), Costello et al. (2014), and Van Manen et al. (2016) – a problem made worse by inattention to numerous other factors shaping the environment of Yellowstone grizzly bears.

3.4. Drought and Abundance of Other Key Foods: An Introduction

In this and following sections I cover additional flaws in analyses reported by the IGBST that arise from inattention to numerous major changes in Yellowstone's grizzly bear habitat. All these ignored factors are *prima facie* important given that they pertain to availability of historically important grizzly bear foods, including elk, bison, cutthroat trout, and army cutworm moths (Section 3.1), along with other foods likely to have been affected by drought.

It is worth emphasizing here that most science produced by the IGBST and invoked by management agencies entails complex models of a complex ecological system. These kinds of models are only valid if stringent standards are met and, even if met, a specific models constitutes only one of numerous possibilities. Model-building is, in fact, one of the most vagarious and bias-prone of scientific undertakings (Boyce et al. 2016; see Section 6.1). Of relevance to this and following sections, credible models of grizzly bear demography and behavior need to include all factors likely to have had significant effects on these outcomes, largely because isolating the effect of any single factor such as bear density or whitebark pine abundance is only possible if all other plausibly important effects are statistically accounted for.



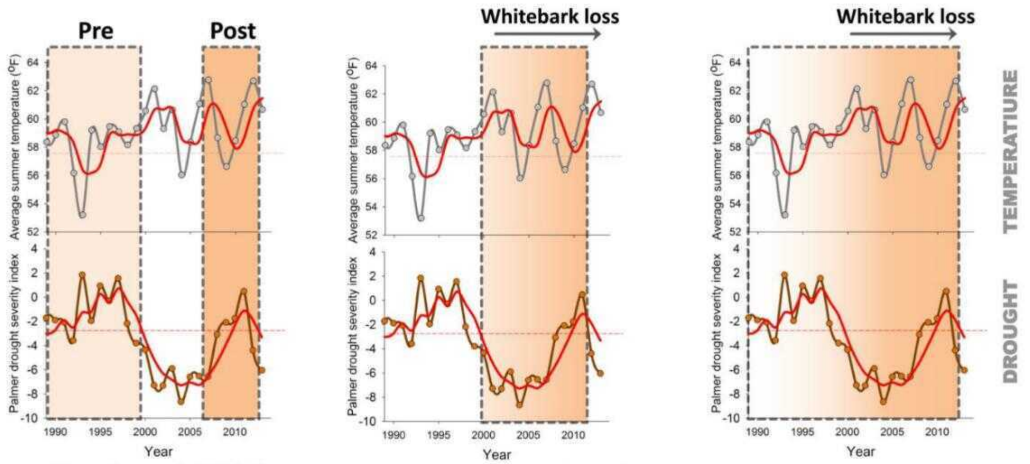
Bjornlie et al. (2014) Costello et al. (2014) Van Manen et al. (2016)

Figure 5. This figure shows trends in abundance for key Yellowstone grizzly bear foods in rows arrayed from top to bottom intersected with rows denoting how three different analyses by the IGBST treated time periods. These treatments are shown as vertical boxes shaded various hues of orange, with progressively darker hues of orange denoting biased estimates of whitebark pine abundance used in IGBST analyses (see Section 1). Cone crops on surviving trees trended upward during 1990-2014 (top row), as did bear consumption of army cutworm moths (second row down), whereas cutthroat trout were functionally eliminated as a bear food (third row) concurrent with major declines in the Northern Range and Jackson elk herds (fourth row). Bison herds showed reverse trends, with major declines in the Central herd and major increases in the Northern herd (bottom).

Issues

Figures 5 and 6 illustrate a sampling of important environmental changes specific to trends in abundance of important grizzly bear foods that were not accounted for in any IGBST analyses between 2005 and 2022. These foods, top to bottom, include indexed size of whitebark pinecone crops (as per Section 3.2), bear use of army cutworm moth aggregation sites (Section 3.7), numbers of spawning cutthroat trout (Section 3.8), numbers of elk in the ecosystem's two largest herds (Section 3.9), and, finally, at bottom, numbers of bison in Yellowstone's Central and Northern herds (Section 3.9).

The vertical bars shaded different colors of orange denote how time periods were treated in three seminal IGBST papers published between 2014-2016. Bjornlie et al. (2014a) framed their analysis in terms of two time periods, one before (pre) and one after (post) major losses of whitebark pine to mountain pine beetles. This framing assumed that relevant changes in the environment of Yellowstone's grizzly bear during these two periods only included bear density and extent of whitebark pine forests. The vertical shading in the graph farthest right shows as ever-darker hues of orange how Van Manen et al. (2016) approximated the decrease in whitebark pine forests — and again, without considering any other environmental trends. Finally, the center graph shows the 2000-2011 period addressed by Costello et al. (2014) as a shaded vertical box, with this research likewise assuming that changes in abundance of whitebark pine were of sole relevance.



Bjornlie et al. (2014) Costello et al. (2014) Van Manen et al. (2016)

Figure 6. The basic configuration in this figure is the same as in Figure 3 but featuring trends in summer temperature (top row) and drought severity (bottom). The red lines are 3-year moving averages and the gray dots, annual values. Drought is indexed by the Palmer Drought Severity Index. All data are publicly available from NOAA. Temperatures trended upward during this period at the same time that the region was plunged into an epic drought during 1999-2006.

The takeaway from Figure 5 is straight-forward. The IGBST failed to account for numerous unfolding major trends in food abundance. Bjornlie et al. (2014a) failed to account for the fact that numbers of elk and cutthroat trout had declined, and that moth site use and whitebark pinecone crop sizes had increased between the 'pre' and 'post' periods. Van Manen et al. (2016) likewise failed to account for these same trends as continuous temporal and spatial phenomena. Finally, Costello et al. (2014) did not account for increasing levels of moth site use, decreasing numbers of elk, and only incompletely accounted for landscape-level abundance of whitebark pine seeds.

Figure 6 makes the added point that these three IGBST analyses also neglected longer-term trends in weather with near-certain effects on numerous vegetal and animal foods (Mattson 2000). More specifically, Bjornlie et al. (2014a) failed to account for higher average summer temperatures during their 'post' period; Van Manen et al. (2016) failed to account for an epic drought as well as a trend towards progressively higher summer temperatures; and Costello et al. (2014) failed to account for gradual recovery from the deep drought of the early 2000s. All these neglected patterns plausibly affected grizzly bear movements, diet, and demography.

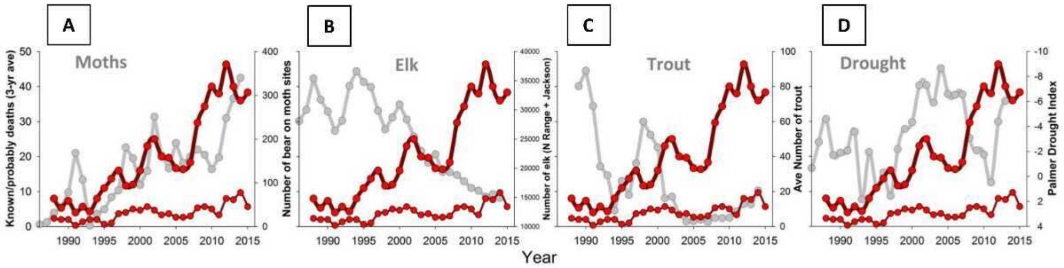


Figure 7. These four panels superimpose trends in total known and probable grizzly bear mortality on trends in abundance of four foods plus drought for the period 1986-2015. Mortality is shown in red as a 3-year running average, with natural mortality (lower red line) differentiated from total mortality (top red line). The gray lines show, left to right, (A) trends in number of bears seen on moth sites; (B) numbers of elk in the Northern Range and Greater Jackson herds; (C) average numbers of trout counted in monitored spawning streams around Yellowstone Lake; and (D) an inverted representation of the Palmer Drought Index for the highest-elevation drainages of the Yellowstone ecosystem (i.e., peaks in the trend line indicate greater drought severity). These trends suggest that grizzly bear mortality increased concurrent with functional extirpation of cutthroat trout as a bear food and initial declines in elk populations, with this trend accelerating during terminal declines of elk and the peak of severe drought. These patterns are in addition to the clearcut increase in grizzly bear mortality after terminal declines of whitebark pine. The only exception to negative correlations between bear deaths and abundance of natural foods is a positive correlation with exploitation of army cutworm moth sites.

Aside from the self-evident problems of misconstruing or overlooking plausibly important environmental effects, there is, in fact, *prima facie* evidence that death rates of Yellowstone's grizzly bears were affected during 1988-2015 by drought and substantial variation in abundance of moths, elk, and trout – concurrent with only a slight positive trend in grizzly bear densities (Figure 21). Figure 7 is illustrative of annually correlated variation between bear deaths and bear foods. A simple multiple regression model containing trends in elk populations (Figure 7b) and availability of whitebark pine seeds explains 74% of total and 76% of human-caused mortality. Abundance of both foods has negative effects, as one would expect. A similar model including elk, trout (Figure 7c; negative), and drought (Figure 7d; positive) explains 70% of human-caused mortality. Yet another model based on latent variables derived from principal components analysis explains 70% of total deaths and 72% of human-caused mortality, with elk, trout, and whitebark pine all loading as negative effects, and moths (anomalously) and drought as positive effects.

These statistical relations do not bespeak a direct causal link between quality and quantity of foods and bear deaths. Bears rarely starve to death, but rather die as a realization of hazards associated with consuming different diets. But, as I describe in Sections 3.10-3.12, loss of native ungulates, cutthroat trout, and pine seeds likely drove bears to exploit hazardous foods such as livestock and gut piles left by elk hunters, resulting in greater numbers of fatal encounters with lethal humans.

Implications

By itself, inattention to substantial trends in availability of important foods compromises the validity of IGBST analyses during the last 20+ years – even without considering failings arising from misrepresentation of spatial and temporal abundance of whitebark pine seeds (Sections 3.2 and 3.3). In what follows, I describe in more detail why the environmental changes overlooked by IGBST researchers likely had important effects not only on grizzly bear demography and behavior, but also models representing these complex phenomena.

3.5. Temporal and Spatial Interactions of Foods and Bear Density

Demography and behavior of GYE grizzly bears were not only likely affected by temporal trends in numerous key foods during the last 20+ years, but also by potentially complex spatial interactions that led to compensatory changes in diet, including some with positive and others with negative effects on bear demography. More to the point, IGBST researchers have not explicitly accounted for any of these temporal-spatial interactions or, when claiming to do so, failed to do a credible job.

This failing is particularly evident in Corradini et al. (2023). The authors of this paper report an analysis of variation in body composition of Yellowstone grizzly bears during 2000-2020, notably changes in fat and lean mass. Unlike earlier IGBST research, Corradini et al. (2023) claim to have accounted for the effects of multiple foods (i.e., abundance of pine seeds, trout, and ungulate populations) by using the periods 2000-2009 and 2010-2020 as *proxies* for a high-calorie diet, with 2010-2020 represented as a period of comparative dearth. For unexplained reasons, well-documented grizzly bear exploitation of army cutworm moths (a high fat-content food; Section 3.7), gut piles, and cattle (high fat and protein content foods; Section 3.9) was not considered in this framing. There was, moreover, no consideration given to spatial differences in food use and abundance, even though spatial variation in bear densities was explicitly considered (but see Section 4.7). This incommensurate treatment of spatial and temporal variation in bear foods and bear densities alone prejudiced the analysis reported by Corradini et al. (2023).

Even so, Corradini et al. (2023) confidently claimed that reductions in average lean body mass of younger females were driven by increases in bear density, and that bears compensated for reduced access to high-quality foods during 2010-2020 by exploiting other unidentified foods of presumably lesser quality and in the process maintaining comparable levels of body fat. Despite the authors' apparent confidence, this conclusion is unsubstantiated because food abundance and quality probably did not decline during the latter period, largely because of compensatory spatially-explicit shifts in bear diets—and furthermore because population-wide bear densities likely did not increase, even taking the density index developed by Bjornlie et al. (2014a) at face value (but see Section 4.7).

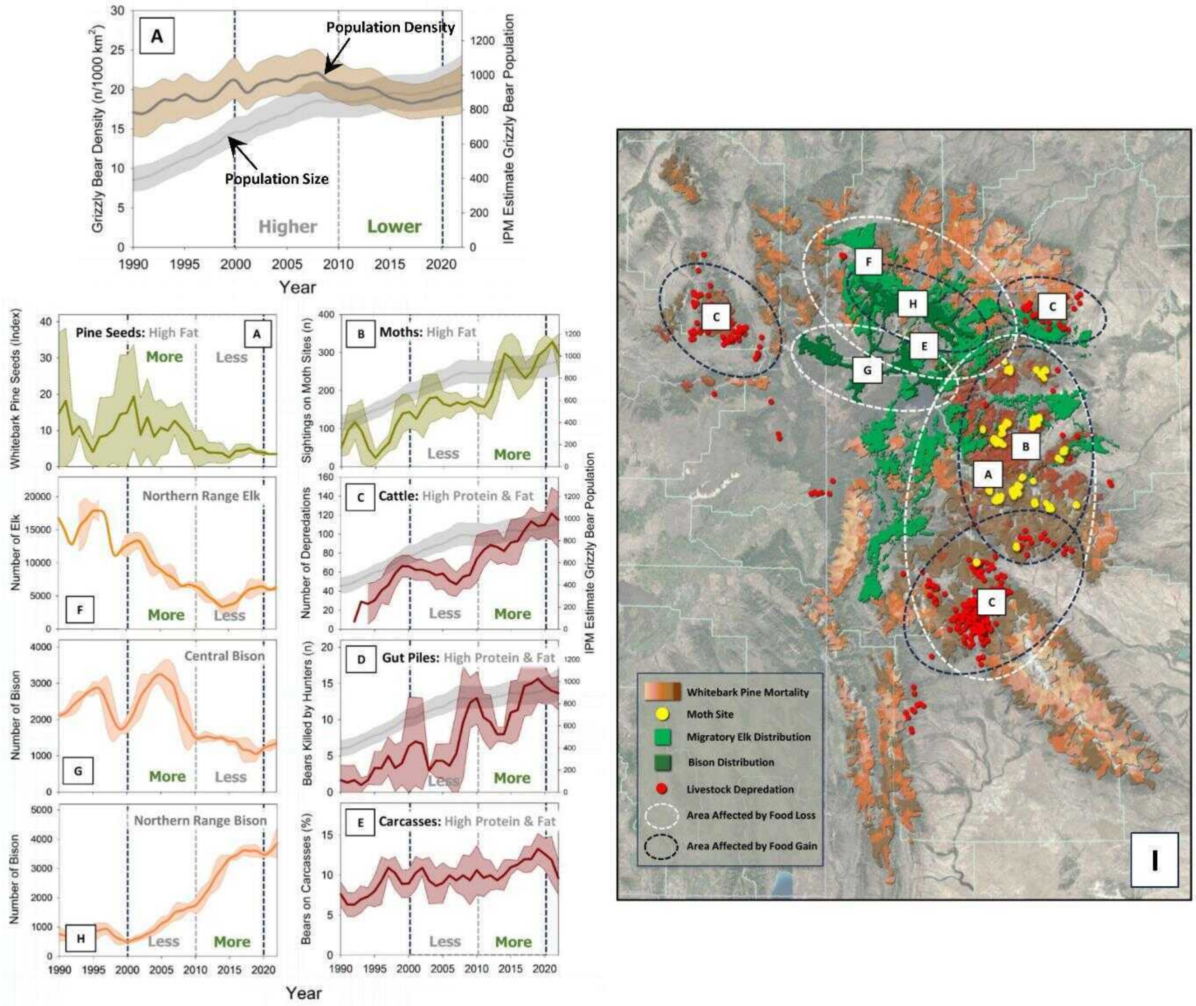


Figure 8. These graphics illustrate some of the complex temporal and geospatial dynamics affecting grizzly bears and their foods in the Greater Yellowstone Ecosystem, emphasizing the problems with how these changes were framed in the analysis by Corradini et al. (2023). The graphics in (A)-(H) show temporal changes in bear foods, bear use of foods, and population size and density. Each of the foods featured in (B)-(H) have a different geographic distribution illustrated in the map at right, with each focal geographic areas denoted by the letters identifying foods in the graphics at left. The graphic in (A) shows estimated size of the grizzly bear population in gray versus changes in bear densities accounting for increases in population distribution within the Demographic Monitoring Area. Although population size increased, density did not and, if anything, peaked during 2000-2009. Whitebark pine seeds (B) and size of the Northern Range elk herd (F) declined dramatically during 2000-2009, whereas consumption of army cutworm moths (B), meat from cattle depredation (C), and gut piles left by elk hunters increased substantially throughout 2000-2020 concurrent with increases in size of the Northern Range bison (H). Exploitation of naturally-occurring carcasses by bears was generally greater during 2010-2020 compared to 2000-2009, whereas abundance of the central Yellowstone bison herd peaked during 2000-2009. The map at right (I) illustrates how heaviest losses of whitebark pine in the ecosystem (A) were offset by increased exploitation of moths (B) and increased depredation on cattle (C). Similarly, losses of elk on the Northern Range (F) and bison in the central herd (G) were likely offset by increases in bison numbers on the Northern Range (H). Exploitation of remains left by hunters (D) and increased depredation on cattle in northwestern and northeastern areas (C) likely compensated for losses of whitebark pine and elk throughout the ecosystem. Overall, grizzly bears were likely eating more proteinaceous and high-fat content foods during 2010-2020 compared to 2000-2009 while bear densities remained relatively static.

Figure 8 more comprehensively illustrates how the framing of food effects by Corradini et al. (2023) failed. Although abundance of whitebark pine seeds declined to low ebb during 2010-2020 (Figure 8a), concurrent with declines in abundance of elk on the Northern Range (Figure 8f) and bison in the central Yellowstone Park herd (Figure 8b), bison on the Northern Range increased substantially (Figure 8h) along with grizzly bear exploitation of army cutworm moths (Figure 8b), cattle (Figure 8c), and gut piles left by elk hunters (Figure 8d). These spatial patterns were, moreover, compensatory. Increases in moth consumption and depredation of cattle occurred in areas that experienced the heaviest whitebark pine mortality (Macfarlane et al. 2013, 2023). Heavy exploitation of carcasses in Yellowstone Park (Figure 8e) was, moreover, likely sustained by increasing numbers of opportunities to scavenge on bison from the Northern Range herd (cf., Green et al. 1997, Mattson 1997b), potentially sufficient to offset declines in numbers of Northern Range elk and central Yellowstone Park bison. Increased predation on elk calves (e.g., Fortin et al. 2013, Middleton et al. 2013) together with greater exploitation of cattle and gut piles (i.e., indicated by lethal encounters with elk hunters) furthermore likely compensated for losses of whitebark pine ecosystem wide. If anything, bears probably consumed comparable or greater amounts of high-fat-content food during 2010-2020 compared to during 2000-2009 (see Mattson et al. 2004).

Perhaps the most significant shortcoming of this research was its disregard for the interplay of risk and benefit arising from exploitation of different foods by grizzly bears, along with the extent to which these risks likely varied among sex and age classes (Section 3.12). Bears were clearly eating more meat from ungulates during 2010-2020 (Section 2.9). However, there is compelling evidence that females and younger bears incur greater risk of interspecific predation by adult males when they exploit this sort of concentrated food (Section 3.12), with young females consistently tending to eat less meat as a presumed consequence (Mattson 1997b, 2000; Jacoby et al. 1999; Hobson et al. 2000; McLellan 2011; Fortin et al. 2013). Given all the limitations of Corradini et al. (2023), a shift to eating more meat rather than any increase in bear densities likely led to the reduced overall sizes of young females during 2010-2020 compared to 2000-2009. Greater exploitation of fat-rich low-protein-content moths by bears likewise probably contributed to a simultaneous population-averaged decrease in lean body mass among young bears concurrent with maintenance of body fat levels comparable to when pine seeds were comparatively more abundant.

Implications

Perhaps more than any other IGBST research, Corradini et al. (2023) illustrates the extent to which this team and its collaborators have tended to build edifices of conclusions on flawed research designs and sometimes non-existent evidence, invariably building towards a case for the dominance of "density-dependent" effects on GYE grizzly bear demography. As I argue here and in Sections 3.11-3.12, demography of this population has more likely been driven by increasing exploitation of high-risk foods rather than increases in bear densities. The following five sections (Sections 3.6-3.11) look at specific bear foods to further elaborate on why this neglect of spatial, temporal, and compositional dynamics of bear foods during a time of dramatic environmental change undercut the ill-founded conclusion in Corradini et al. (2023) that all changes in grizzly bear body composition were caused by changes in bear density (and see Section 4.7).

3.6. Spatial Interactions with Whitebark Pine Mortality

Whitebark pine seeds were not consumed equally in all parts of the Greater Yellowstone Ecosystem prior to the major die-off of whitebark pine trees during 2000-2009. Figure 9a shows how this variation in consumption maps onto the pre-1990 distribution of whitebark pine in the GYE. Consumption was heaviest in an arc to the east and south that tracked the Absaroka Mountains and highlands of the Bridger-Teton National Forest (Figure 9a; Knight et al. 1984, Mattson et al. 2004). Not surprisingly, this arc corresponded with the greatest extent of whitebark pine forests in the GYE occupied by grizzly bears during 1977-1996.

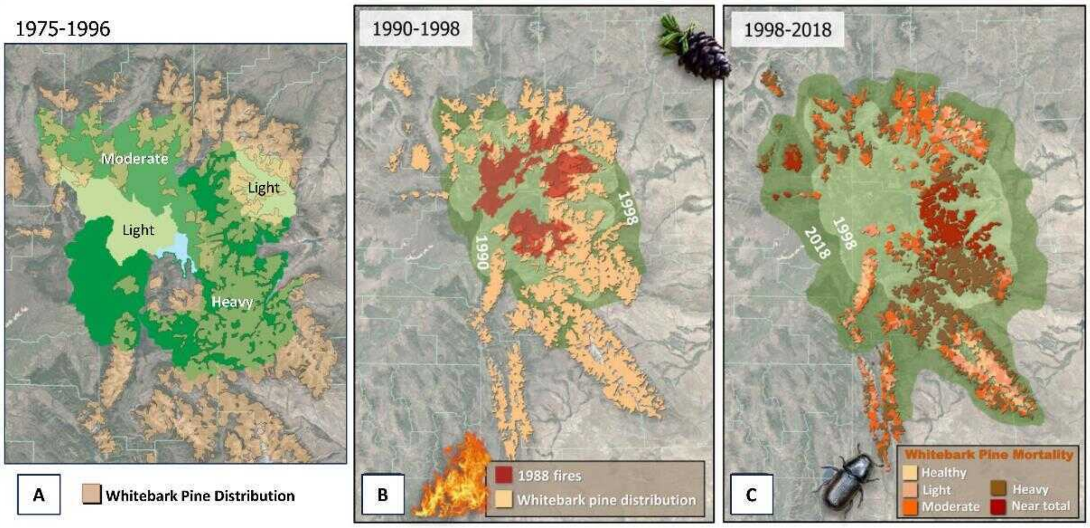


Figure 9. These maps illustrate spatial patterns of mortality among mature whitebark pine trees, trends in distributions of grizzly bears, and historical exploitation of pine seeds by bears in the Greater Yellowstone Ecosystem. The map in (A) shows levels of pine seed exploitation by grizzly bears documented during 1977-1996, prior to widespread whitebark pine mortality, with areas of heaviest exploitation in dark green and lightest exploitation in light green (Knight et al. 1984, Mattson et al. 2004). Map (B) shows the extent of whitebark pine distribution (in beige) prior to a major episode of mortality during 2000-2009, along with the distribution of Yellowstone grizzly bears circa 1990 and 1998 (in shades of green). The extent of wildfires that burned during 1988 are shown in red (Macfarlane et al. 2013, Van Manen et al. 2019). The map in (B) shows the extent and magnitude of mortality among mature whitebark pine caused by an outbreak of mountain pine beetles unleashed by warming temperatures during 2000-2009 (Macfarlane et al. 2013), along with the approximate distribution of Yellowstone grizzly bears circa 1998 and 2018 (Van Manen et al. 2019). A significant portion of whitebark pine was killed by the 1988 wildfires within the 1990 distribution of grizzly bears, plausibly contributing to expansion of the grizzly bear population into healthy whitebark pine during the subsequent 10 years. Whitebark pine experienced especially severe beetle-caused mortality within areas where grizzly bears had mostly heavily exploited this resource, which no doubt catalyzed a rapid of expansion of the Yellowstone grizzly bear population during the subsequent 10 years (Bjornlie et al. 2014b), proportionally well exceeding any population increase (Van Manen et al. 2023).

Different episodes of expansion in distribution of GYE grizzly bears correlated with different episodes of mortality in whitebark pine forests. Figure 9b shows the approximate distribution of GYE grizzly bears before and after wildfires during 1988 burned roughly 5,690 km^2 in the center of the ecosystem (Greater Yellowstone Coordinating Committee 1989), including a substantial amount of whitebark pine (Podruzny et al. 1999, Mattson 2000). Shortly after, distribution of the GYE grizzly bear population expanded into peripheral areas, despite comparatively little or no increase in population density (see Figure 26). The correlation between whitebark pine mortality and increased distribution of GYE's grizzly bears was even more dramatic after 2000-2009 (Figure 9c). Notably, the greatest increases in grizzly bear distribution occurred in areas on southern and southeastern margins of the ecosystem where reliance on pine seeds had been historically greatest, and where alternative native foods such as army cutworm moths (Figure 10) and meat from ungulates (Figure 13) were least abundant, setting the stage for a substantial increase in depredation on livestock in these areas (Sections 3.10-3.11).

Issues

These geographic patterns of whitebark pine mortality, occurrence of important alternate foods, and increases in distribution had obvious implications for diet, behavior, habitat selection, and demography of GYE grizzly bears. Even so, a comprehensive analysis of spatially explicit interactions among all these factors was never undertaken by IGBST scientists. Van Manen et al. (2016) only considered interactions of bear density (but see Section 4.7) and extent of whitebark pine forests, albeit erroneously (see Sections 3.2 and 3.3). Costello et al. (2014) considered the extent of movements and selection for whitebark pine forests within established home ranges, but without accounting for regional variation in consumption of pine seeds and availability of alternate foods (see Sections 3.5 and 3.6). In addition to misrepresenting temporal availability of pine seeds (Section 3.2), Bjornlie et al. (2014a) also failed to account for diets and alternate foods in their analysis of home range sizes, which would have mirrored abundance and losses of whitebark pine. Even more problematic, Corridini et al. (2023) assumed a geospatially homogeneous effect of food availability, including pine seeds, on body composition of bears before and after 2010 in defiance of ample contradictory evidence (Section 3.6).

Implications

The IGBST failed to account for a potential role of progressive whitebark pine losses in catalyzing episodes of expansion in the distribution of GYE grizzly bears and instead reflexively attributed all these increases to putative increases in population size and density (but see Sections 4.7 and 6.2-6.5). Notably, these claims were not based on any direct evidence. Regardless of this weak evidentiary basis, the IGBST's neglect of alternative hypotheses regarding drivers of pulsed increases in distribution of the GYE grizzly bear population, linked to changes in food abundance, is a clear evidence of preconceived conclusions driving a research agenda (Section 2).

3.7. Increasing Exploitation of Cutworm Moths

Army cutworm moths are among the highest quality grizzly bear foods in the Yellowstone ecosystem (Mattson et al. 2004, Erlenbach et al. 2014; Section 3.1). By summer's end, over-summering moths can consist of 50-80% fat (Kevan & Kendall 1997, White et al. 1998). This high concentration of fats predictably accelerates accumulation of adipose reserve by female grizzly bears that eat them (Robbins et al. 2007, Robbins et al. 2012, Erlenbach et al. 2014) and, with that, the odds that these females will attain body fat >20% needed to produce and sustain cubs (Farley & Robbins 1995, Hilderbrand et al. 2000, Robbins et al. 2012).

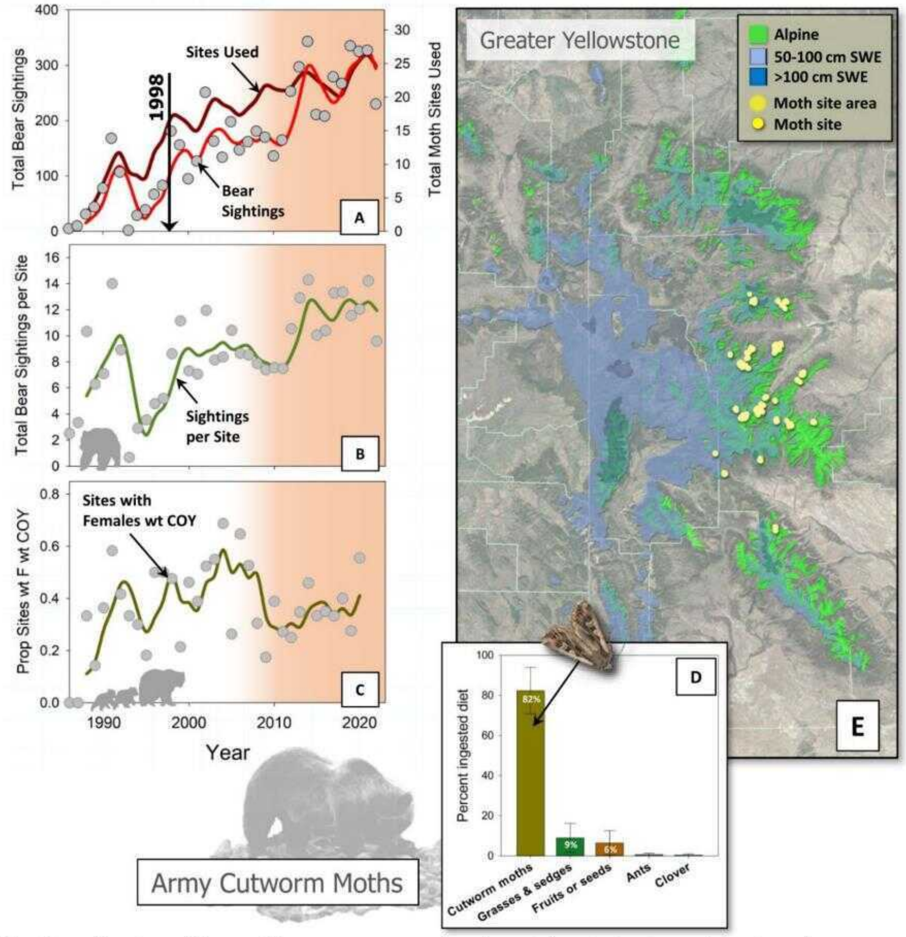


Figure 10. This collection of figures illustrates temporal and spatial variation in exploitation of army cutworm moths by grizzly bears in the Greater Yellowstone Ecosystem (GYE). The trend lines in the panels at left show (A) numbers of sites used by grizzly bears to feed on aggregations of army cutworm moths (burgundy line), along with total numbers of observations of individual bears (light gray dots and red line); (B) the average number of bear sightings per site (from [A]), and (C) the proportion of all observations attributable to females with cubs-of-the-year. The vertical area shaded orange corresponds to the culmination of whitebark pine mortality cause by mountain pine beetles between 200 and 2009. Numbers of sighting along with average numbers of sightings per site jumped dramatically after 2010 and culminating losses of whitebark pine. Sightings of females with COY, as a proportion of total sites, synchronously dropped. Bear observations are from Van Manen et al. (2023). The map in (E) from Robison (2009) show the distribution of sites used by bears in the GYE to exploit moths (yellows dots), excepting sites southeast in the Wind River Mountains, where no bear activity has yet been documented (Ratner 2002). Alpine areas in (B) are shown in green (from Rehfeldt et al. [2012]). Blue areas in (B) identify areas of heavy winter snowpack, with dark blue areas typified by accumulated snow water equivalents >100 cm (from Marcus et al. [2012]). The bar chart in (D) shows the proportions of different foods ingested by grizzly bears when within 500-m of documented moth aggregations; cutworm moths, which account for almost all the local diet, are shown in yellow-green (combined data from Mattson et al. [1991] and White et al. [1998a]).

Moreover, sites where grizzly bears consume moths are in areas that are amongst the most remote from people of any in the Yellowstone ecosystem (Mattson et al. 1991a, French et al. 1994, Gunther et al. 2014; Figure 10e). This matters because remoteness has repeatedly been shown by researchers to be one of the most important spatial factors affecting survival of adult grizzly bears in and near the Yellowstone ecosystem (Mattson et al. 1996; Merrill et al. 1999; Carroll et al. 2001, 2003; Merrill & Mattson 2003; Johnson et al. 2004; Schwartz et al. 2010).

Consumption of moths by grizzly bears, which occurs primarily between mid-July and mid-September, has increased dramatically from essentially nil during the mid-1980s to high levels that have been sustained since the late 1990s (Mattson et al. 1991a, Van Manen et al. 2023a:48-50). Individual sightings of grizzly bears on moth sites have numbered between 200 and 350 during the last ten year (Van Manen et al. 2023a:48-50), implying that a substantial number of individual bears use this food resource—perhaps the majority of those living in east-central portions of the ecosystem (Figure 10a). All the 35 known sites where grizzlies consume moths are located on U.S. Forest Service lands in the Absaroka Mountains east and southeast of Yellowstone National Park (Robison 2009). Six of these sites are located outside of the Primary Conservation Area for GYE grizzly bears, and thus unprotected (Figure 10e).

None of the IGBST publications produced during the last 20 years have explicitly addressed the effects of army cutworm moth consumption on grizzly bear demography or behavior (e.g., Schwartz et al. 2006a, Van Manen et al. 2016). Without such an analysis, the IGBST has no basis for judging what those effects have been or might be in the future, and likewise no basis for differentiating effects attributable to bear densities, as such, from effects attributable to increasing consumption of cutworm moths, especially given that both are highly correlated in time and space (Gunther et al. 2014, Van Manen et al. 2023a:22-24, 36-39, 48-50)

Implications

Inattention to effects of moth consumption on bear demography, behavior, and body condition by Schwartz et al. (2006a), Bjornlie et al. (2014a), Costello et al. (2014), Van Manen et al. (2016), and Corradini et al. (2023) is not tantamount to the absence of an effect. In fact, without any comprehensive analysis, the preponderance of available evidence suggests that, in contrast to effects attributable to increasing bear densities, increased availability and consumption of moths by grizzly bears has likely led to increased accumulation of body fat, higher birth rates (because of the nutritional quality of moths) and decreased late-summer deaths rates (because of remoteness from humans) among bears with access to this food. Moreover, exploitation of moths clearly increased substantially after 2010, likely in compensation for heavy whitebark pine mortality in the Absaroka Mountains during the previous decade (Figure 10b). These conclusions are better supported the alternative conclusion that availability and consumption of moths have had no effect on Yellowstone grizzly bears.

3.8. Effects of Cutthroat Trout Losses

Cutthroat trout were a demonstrably important food for Yellowstone grizzly bears prior to catastrophic declines of the trout fishery in Yellowstone Lake during the 1990s (e.g., Hoskins 1975, Reinhard & Mattson 1990, Mattson & Reinhart 1995, Mattson et al. 2004; Section 3.1). Even so, prospective effects of cutthroat trout on grizzly bears have been dismissed out of hand by IGBST researchers since the early 2000s, including by Schwartz et al. (2006a), Bjornlie et al. (2014a), Costello et al. (2014), and Van Manen et al. (2016). These dismissals invariably invoke Haroldson et al. (2005) and Fortin et al. (2013) as a basis for claiming that use of areas near where bears had previously fished did not decline, and that affected bears were furthermore able to compensate for losses of trout by eating other foods – hence obviating any need to consider how effects of trout declines might have affected demography and behavior of GYE grizzly bears.

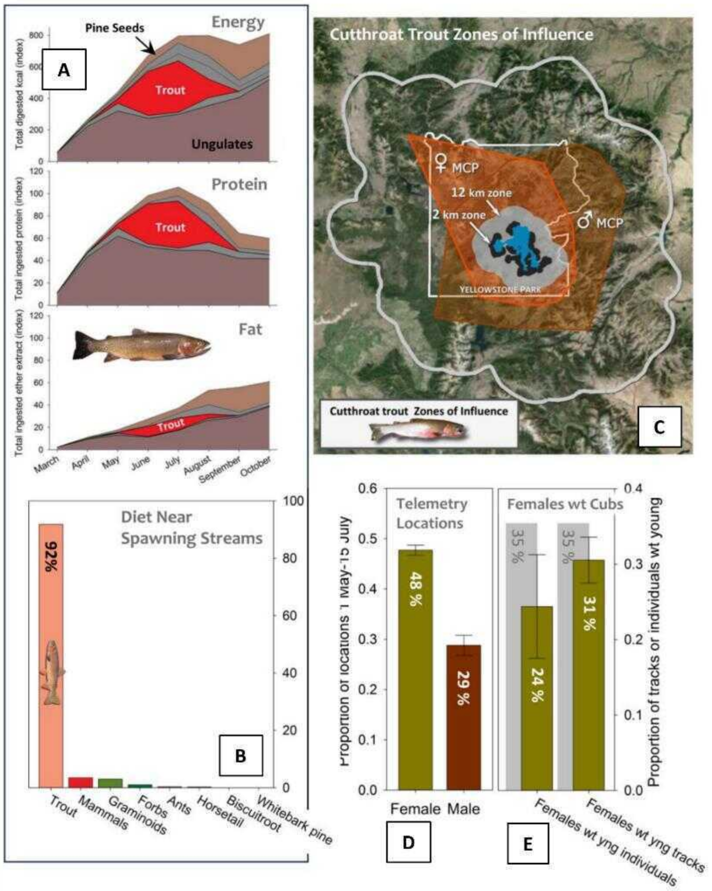


Figure 11. The seasonal trend graphs in (A) show fractional contributions of ungulates (elk & bison, in burgundy), whitebark pine seeds (in brown), and cutthroat trout (in red) to the 1977-1992 diet of Yellowstone's grizzly bears, differentiating digested energy (top) from ingested protein and fat (middle and bottom, respectively). This representation accounts for detectabilities, digestibilities, and monthly population-wide differences in overall levels of consumption based on a corrected sample of >6000 grizzly bear scats. The bar chart in (B) shows percent contributions of different foods to diets ingested by bears concentrated along spawning streams during the 1985-1987 spawning season. The map in (C) shows zones where trout-eating bears were concentrated year-long (12-km) and during the spawning season (2-km), as well as minimum convex polygons encompassing telemetry locations of male and female trout-eating bears (Mattson & Reinhart 1995).

The bar chart in (D) shows the relative proportion of adult female and adult male telemetry locations within 2-km of Yellowstone Lake during the 1977-1993 cutthroat trout spawning seasons, only considering bears with ranges that overlapped spawning streams. The bar charts in (E) show the proportion of all individuals (left) and tracks (right) documented along streams during the 1985-1987 spawning seasons comprised of females accompanied by dependent young (in green) relative to the proportion of each expected by the total in the population (in gray; from Reinhart & Mattson [1990]).

Issues

These claims contravene ample evidence suggesting that trout were important to numerous bears, and that losses of trout were probably behaviorally and demographically consequential: first, because trout were a major source of high-quality food for numerous bears (Section 3.1); second, because trout were disproportionately important to female grizzlies; third, because availability of spawning trout concentrated bears in some of the most secure areas of the ecosystem; and, fourth, because compensatory changes in diet likely exposed bears to greater hazards, both for themselves and their offspring (see Sections 3.12).

Figure 11a graphically summarizes the estimated monthly contribution of cutthroat trout to dietary energy and nutrients of Yellowstone grizzly bears during the 1970s through early 1990s. This estimate is based on analysis of >6,000 scats deposited by grizzly bears throughout the Yellowstone ecosystem, with fecal contents weighted by average nutrient and energy contents and corrected for different digestibilities (cf., Mattson et al. 2004, Lopez-Alfaro et al. 2015). Monthly levels of total ingested energy in Figure 11a vary substantially because of seasonal differences in levels of feeding activity (low in the spring, high in the fall and late summer; Mattson et al. 1991a) as well as numbers of bears active outside dens (Haroldson et al. 2002). Energetic contributions of army cutworm moths are also not included primarily because adequate sampling of bear scats at or near moth sites was logistically difficult.

Trout were clearly an important source of energy and protein for Yellowstone grizzly bears during June and July prior to the 1990s. Most of the bears that exploited spawning trout were concentrated within 12 km of trout spawning streams year-round and within 2 km of streams during the spawning season (Figure 11c; Mattson & Reinhart 1995) at which time they almost exclusively consumed trout (Figure 11b; Reinhart & Mattson 1990). Roughly 12-15% of the bear population was dependent on trout between mid-May and late July – approximately 45-70 grizzly bears out of a total 325 to 570 total bears in the ecosystem (Reinhart & Mattson 1990, Eberhardt & Knight 1995, Haroldson et al. 2005, Van Manen et al. 2023).

Perhaps as important, females bear likely exploited spawning trout more heavily than did males during the 1970s and 1980s (Figure 11d). Trout-eating females spent roughly 1.6 as much time near spawning streams (Figure 11d), although females with dependent young were proportionately under-represented, as denoted by discrepancies between the gray and green bars in Figure 11e. Although scats deposited by females couldn't be distinguished from scats deposited by males, any bear of either sex near a spawning stream during the spawning season was consuming little else but cutthroat trout, suggesting that females were eating more trout during the mid-1980s compared to males.

These results contrast with those of Felicetti et al. (2004), who estimated that bears near spawning streams during 1997-2000 ate only around 0.024-1.09 kg of trout per individual and that males ate 5-times more trout compared to females – at a time when Haroldson et al. (2005) estimated that bear activity around spawning streams was comparable to peak levels observed during the mid-1980s. These patterns are puzzling given the strong relationship between trout densities and bear fishing activity during the 1980s (Reinhart & Mattson 1990), and the fact that grizzly bears could consume as much as 6 kg of trout in a single 40-minute bout (Mattson; personal observation). All of this begs the question of how grizzly bears during the 1990s could have spent time near spawning streams during June and July without consuming much more than 1 kg of trout each – roughly the average size of a single large spawner.

Differences between results of studies during the mid-1980s and late-1990s are plausibly attributable wholly or in part to stark differences in numbers of spawning cutthroat trout (Figure 12), with related effects on relative access to relict spawning streams by female versus male bears. Adult male grizzlies can dominate concentrated food resources such as spawning trout, especially to the exclusion of security-conscious animals such as females with dependent young. If prime fishing opportunities had become spatially restricted after the early 1990s, males would have consequently been the primary winners, and females the primary losers. The result would have been a shift from disproportional use of the trout resource by females to disproportional use by males—leaving females experiencing most of the harm arising from losses of cutthroat trout.

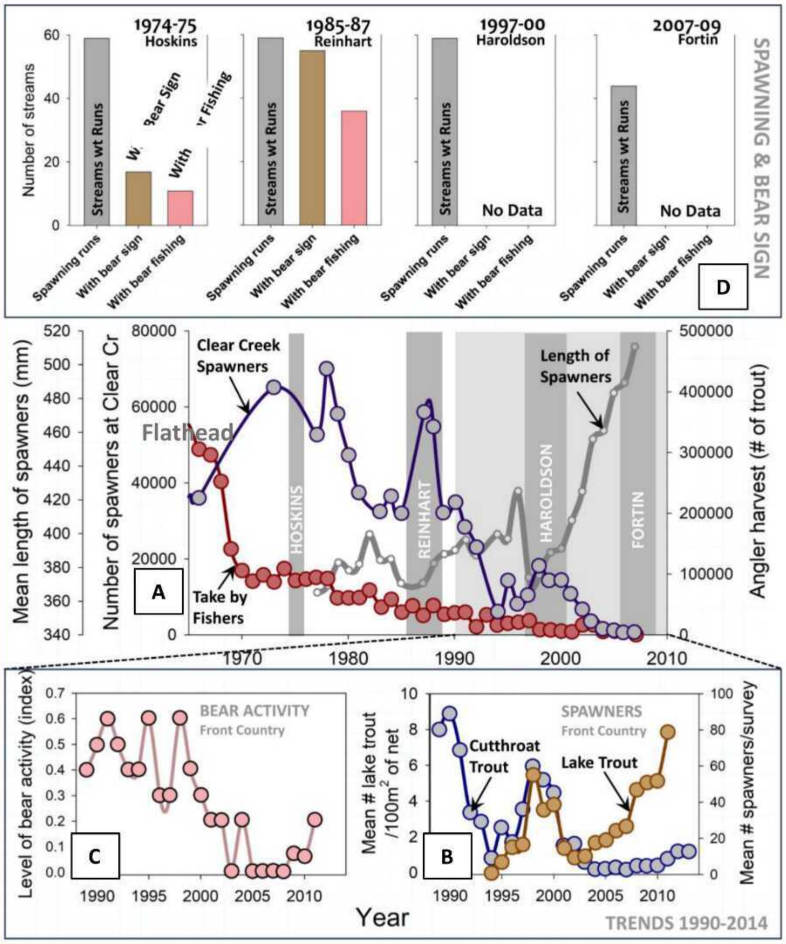


Figure 12. These graphics show (A) longer-term trends in the Yellowstone Lake cutthroat trout population (from Kaeding [2010]) as well as (B) more recent trends in numbers of lake trout and cutthroat trout spawners censused in tributary streams along the north and northwest shores (from IGBST Annual Reports). Indexed levels of bear activity along these same tributary streams are shown in (C), also from IGBST Annual Reports. The bar charts in (D) show results of surveys conducted as part of four studies spanning >30 years, with gray bars denoting numbers of streams where spawning trout were observed, brown bars numbers of streams where grizzly bear sign was detected, and pink bars numbers of streams where evidence of bear fishing was found (Hoskins 1975, Reinhart & Mattson 1990, Haroldson et al. 2005, Fortin et al. 2013). The years during which data were collected during each study are shown above each chart and furthermore denoted by gray vertical bars in (A).

Figure 12 summarizes some key trends relevant to understanding changes that unfolded during the 1990s. Yellowstone Lake's cutthroat trout population exhibited major fluctuations during 1960-2010 (Figure 12a), as indicated by numbers of trout censused in Clear Creek – historically a major spawning stream (blue line) – as well as by numbers of fish killed by human anglers (red line) and average lengths of trout collected by Yellowstone researchers (gray line). Trout numbers peaked during the 1960s, dipped during the early 1980s, resurged during the late 80s, and entered a sustained terminal decline thereafter (data from Kaeding 2010). Larger average sizes of trout indicate lack of recruitment into smaller size classes during periods of decline. Of relevance to these trends, Figure 12b shows numbers of lake trout captured in gill nets (brown line), standardized to reflect level of effort. Predation by non-native lake trout likely drove most declines in cutthroat trout numbers after lake trout were first detected during the mid-1990s.

Consumption of trout by bears tracked trends in numbers of trout, as shown by estimated numbers of spawning streams exploited by grizzly bears during studies spanning a 30-year period (Figures 12d). Each of these studies is differentiated by gray vertical bars and labeled with the name of the lead investigator (i.e., Hoskins 1975, Reinhart & Mattson 1990, Haroldson et al. 2004, Fortin et al. 2013) in Figure 12a. Tributary streams were surveyed during these studies to document bear activity, along with size and duration of spawning runs. Figure 12d summarizes the results of each study in terms of number of streams with spawning runs (gray bars), documented bear activity of any sort (brown bars), and sign of bear fishing (pink bars). As Fortin et al. (2013) and Middleton et al. (2013) document, although declines in numbers of bears active around Yellowstone Lake were catastrophic, cutthroat trout was nonetheless functionally extirpated as a bear food.

Female grizzly bears have probably borne the brunt of declines in trout numbers, resulting in a compensatory turn to eating more meat from elk, bison, and cattle (Sections 3.10 and 3.11) along with probable increases in death rates of adult females and their accompanying cubs and yearlings (Section 3.12). Carrying capacity has also very likely declined in areas occupied by grizzly bears that had previously exploited cutthroat trout. More importantly, this decline would have occurred in the most protected areas of the ecosystem centered on southern Yellowstone National Park. Loss of trout, as well as increasing consumption of army cutworm moths (Section 3.7) and meat from depredated cattle (Section 3.11), have plausibly combined to lure dispersing adolescent or wider-ranging grizzly bears into more lethal environments on the eastern and southeastern ecosystem periphery.

Implications

There is little doubt that functional extirpation of trout in most spawning streams during the 1990s and early 2000s resulted in a major nutritional deficit for bears previously relying on this resource, plausibly resulting in a compensatory shift among affected bears to eating lower-quality foods or preying more heavily on ungulates under risky conditions, with the potential exception of bears that ended up exploiting cutworm moths to the east in the Absaroka Mountains (Fortin et al. 2013, Middleton et al. 2013, Ebinger et al. 2016).

There is thus a good chance that loss of trout not only affected grizzly bear demography in the GYE, but also dispersal and other movements, all of which would have been relevant to IGBST research published since 2000 – but notably neglected by Schwartz et al. (2006a), Bjornlie et al. (2014a), Costello et al. (2014), and Van Manen et al. (2016). Although more immediate impacts of trout losses have likely dissipated, longer-lasting effects are important to understanding trends such as accelerated expansion of the bear population to the east and southeast and demographic consequences arising from increasing exploitation of cutworm moths, cattle, and gut piles (Sections 3.7, 3.10, and 3.11).

3.9. Compensatory Consumption of Meat After 2010

Grizzly bears in Yellowstone have long been known to eat more meat than any other grizzly bear population at mid-latitudes, accounting for >50% of assimilated nitrogen averaged over all bears and >70% of assimilated nitrogen for adult males (Mattson et al. 1991b, Green et al. 1997, Mattson 1997b, Hilderbrand et al. 1999b, Schwartz et al. 2014; Figure 13a). Despite preying heavily on elk calves during mid-May to mid-July, most meat obtained by bears from predation historically came from adult ungulates, including bull elk and moose during the fall, and winter-weakened animals during the spring (Mattson 1997b). This surprisingly heavy predation on vulnerable larger ungulates comports with the tendency of bears to maximize food reward within an acceptable range of risk of injury from prey.

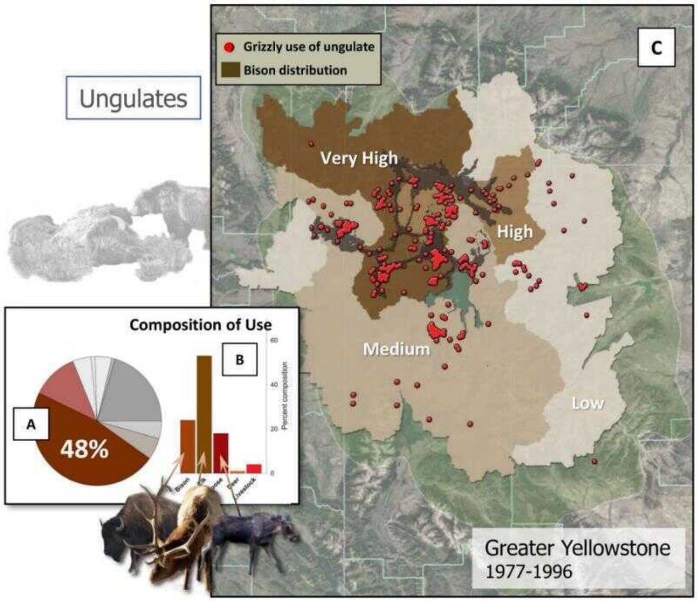


Figure 13. The graphics at left show historical patterns of ungulate exploitation by grizzly bears in the Greater Yellowstone (GYE) ecosystem. The pie diagram in (A) features the 48% of energy and nutrients estimated to have come from ungulates, 1977-1996 (Mattson 1997b, Mattson et al. 2004). The bar graphs in (B) show the proportion of this meat obtained from different ungulate species (Mattson 1997b). Bison is shown in dark, elk in brown, and moose in burgundy. The map in (C) shows geospatial variation, featuring the distribution of bison. Darker shades of brown denote higher levels of consumption (from Knight et al. 1984). Areas shaded darkest brown in (C) correspond with core distribution of bison in the GYE (adapted from Blanton et al. [2015]). Red dots show locations where consumption by grizzly bears was documented 1977-1996 (adapted from Mattson [1997b]).

Consumption of meat from ungulates by grizzly bears was not uniformly distributed in the GYE geospatially during 1977-2003, nor were all ungulate species consumed with equal selectivity (Figure 13c). Exploitation was heaviest in the north and central portions of the ecosystem, coincident with the distribution of bison, and least intensive to the east, in the Absaroka Mountains (Knight et al. 1984, Mattson 1997b, Mattson et al. 2004), where cutworm moths were emerging as a major dietary item during the 1990s (see Section 2.7). Compared to elk, bison and moose were, moreover, exploited by grizzly bears far more heavily relative to their numbers in the ecosystem – bison primarily by scavenging and moose primarily by predation (Figure 13b; Green et al. 1997, Mattson 1997b).

Grizzly bears in the GYE historically compensated by eating more meat from native ungulates during years when whitebark pine seeds were scarce, including meat obtained from the remains of elk killed by big game hunters outside of Yellowstone National Park (Mattson 1997b, Ruth et al. 2003, Haroldson et al. 2004). This compensatory consumption of meat when pine seeds were scarce during the 1970s-1990s logically suggests that grizzly bears would turn in a more sustained way to eating meat from ungulates and possibly calves of domestic cattle if whitebark pine suffered widespread mortality.

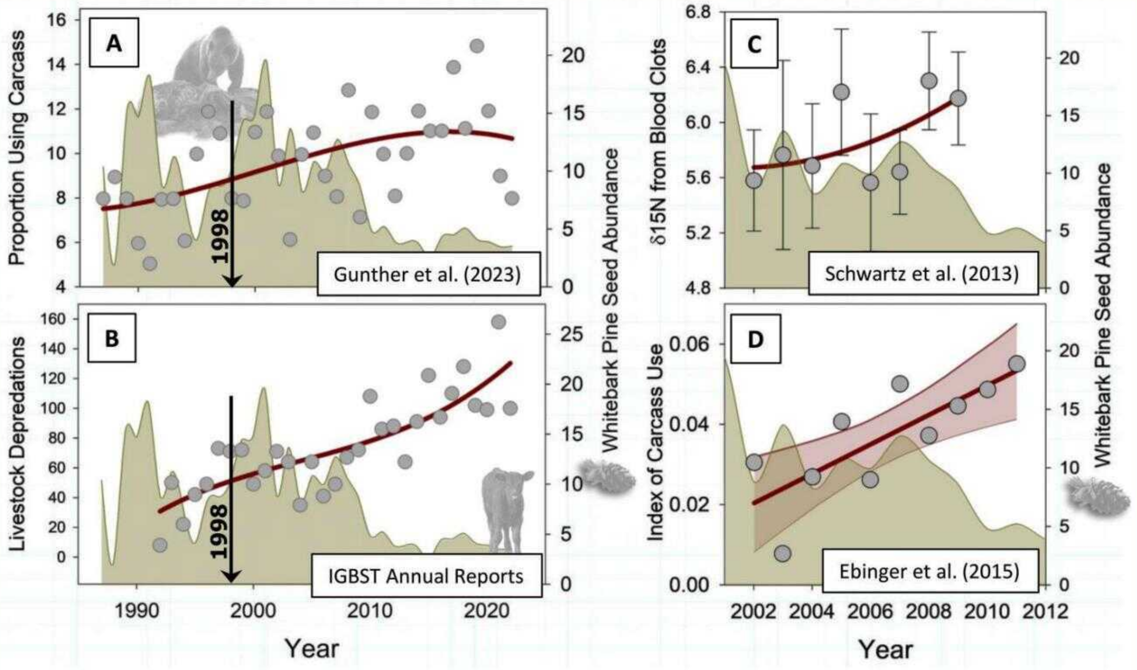


Figure 14. The figures at left show trends in consumption of meat from ungulates by grizzly bears in the GYE derived from different sources of data. Annual values are shown as gray dots; generalized trends as burgundy lines. The baseline year of 1998 is shown for each series of data that encompasses both earlier and later years. Ecosystem-wide trend in availability of whitebark pine seeds is shown in light green. Each panel shows trend from a different identified source using different methods. The proportion of all incidental sightings of bears in Yellowstone Park that involved a bear consuming meat from an ungulate carcass is shown in (A); Numbers of livestock depredations by grizzly bears in the GYE are shown in (B); The relative abundance of animal-origin nitrogen assimilated into body tissues of grizzly bears in the GYE is shown in (C); and relative numbers of grizzly bear telemetry location clusters where consumption of an ungulate was consumed are shown in (D). These four diverse metrics all show the same trend. Consumption of meat from ungulates by GYE grizzly bears has increased over time, but with this trend tending to accelerate after terminal declines in availability of whitebark pine seeds. Source of data are referenced in each panel.

Multiple lines of evidence show that grizzly bears throughout the GYE did, in fact, compensate for losses of whitebark pine and cutthroat trout by eating more meat from ungulates such as elk, bison, and cattle (Figure 14). This increased consumption included elk calves (Barber-Meyer et al. 2008, Middleton et al. 2013), remains of hunter-killed elk (Podruzny 2012, Orozco & Miles 2013), undifferentiated ungulates (Fortin et al. 2013, Schwartz et al. 2014, Ebinger et al. 2016, Van Manen et a. 2023a: Monitoring of Grizzly Bear Foods), and livestock (Gunther et al. 2004, Schwartz et al. 1998-2011: Human-Grizzly Bear Conflicts, Van Manen et al. 2012-2023a: Monitoring of Livestock Grazing). The marked increase in exploitation of ungulates by bears irrefutably began in the early to mid-2000s and accelerated after the terminal demise of whitebark pine around 2010.

However, this increased exploitation of meat occurred while most populations of native ungulates in the GYE were in decline, some precipitously so (Figure 15). Virtually all populations of elk and moose declined substantially after 2000. Declines in the central bison herd (B) began to accelerate around

2005. The trajectory of the bison herd in northern Yellowstone Park stands in stark contrast to all the rest by exhibiting a dramatic increase beginning around 2000. Altogether, these graphics illustrate the substantial heterogeneity in distributions and trajectories of ungulates in the GYE, but with the dominant trend being decline – concurrent with when grizzly bears were subsisting more heavily on meat. This pattern clearly begs the question of where grizzly bears were getting the increasing amounts of meat they ate.

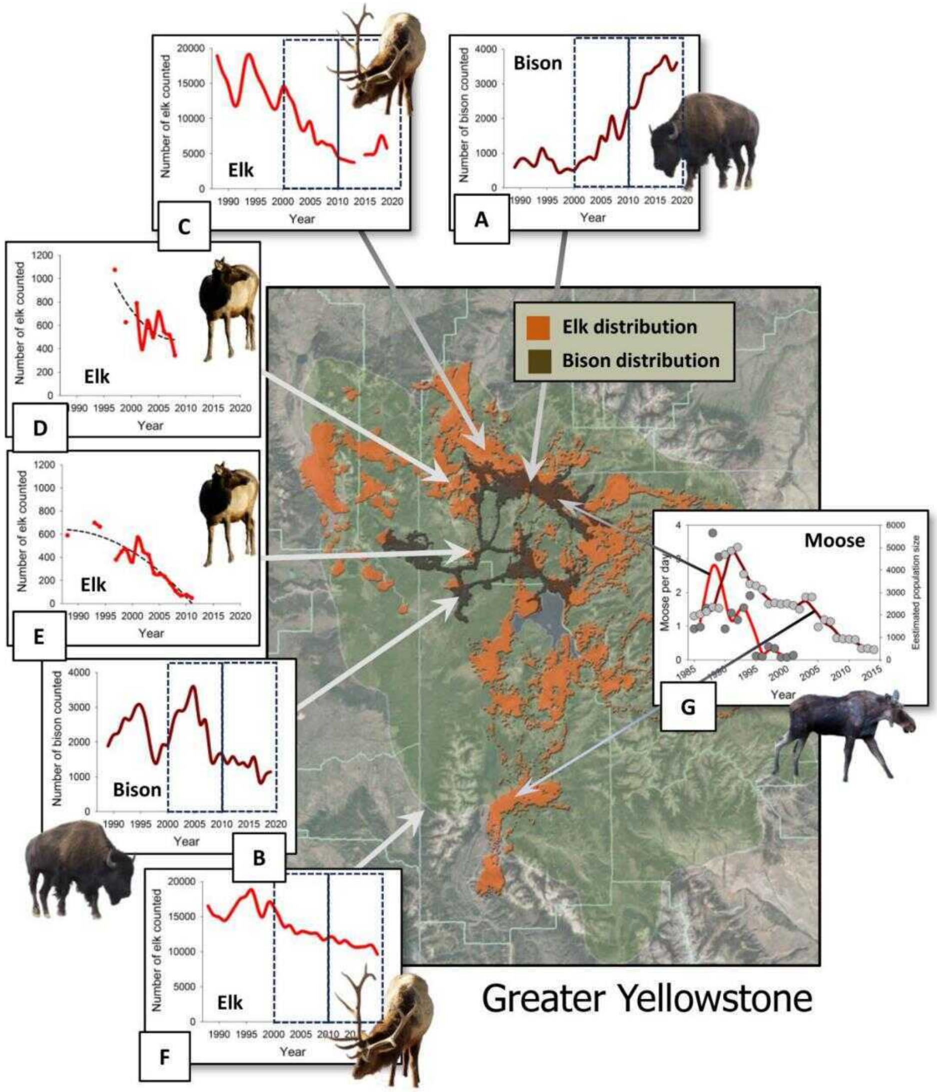


Figure 15. This montage of graphics show temporal and spatial variability in abundance of ungulates in the Greater Yellowstone Ecosystem (GYE), differentiated in the case of elk and bison by different herds. Red lines in the inset panels show trends in in populations expressed as a 3-year moving average. Trends in (D) and (E) were shown as gray fit to observed estimates to fill in gaps between spotty data. In (G), annual counts are shown in addition to moving averages for indices of population size for moose herds in the Jackson, Wyoming (light gray dots), area and in and near Yellowstone's Northern Range (dark gray dots). Virtually all populations of elk and moose have declined substantially since 2000. Declines in the central bison heard (B) began to accelerate around 2005. Trajectory of the bison herd in northern Yellowstone Park stands in stark contrast to all the rest by exhibiting a dramatic increase beginning around 2000. Altogether, these graphics illustrate the substantial heterogeneity in distributions and trajectories of ungulates in the GYE, but with the dominant trend being decline.

Implications

None of these dynamics related to consumption of meat have been explicitly accounted for by IGBST researchers in analyses of grizzly bear condition, behavior, or demography. The question of where bears are obtaining increasingly important meat has also not been directly addressed (albeit indirectly by Wells et al. 2019), which is inexplicable given that these dietary changes were happening in the wake of heavy whitebark pine mortality and functional extirpation of cutthroat trout as a grizzly bear food (Section 3.8). This failing is especially germane to short-comings of the analysis reported by Corradini et al. (2023) given the well-documented extent to which consumption of proteinaceous foods can affect accumulation of lean body mass (Farley & Robbins 1995; Jacoby et al. 1999; Hilderbrand et al. 1999b; Rode & Robbins 2000; Rode et al. 2001; Felicetti et al. 2003a; Robbins et al. 2007; McLellan 2011; Robbins et al. 2012; Erlenbach et al. 2014) and the extent to which availability of meat to GYE grizzly bears has varied geospatially. Alternatively, it is hard to construe direct causal links between bear density and declining lean body mass, as asserted by Corradini et al. (2023).

3.10. Increasing Depredation-Related Conflicts

Much of the meat consumed by grizzly bears post-2010 has likely come from exploiting cattle on public-land grazing allotments located on the periphery of grizzly bear distribution (see Figure 8i), including allotments on the Bridger-Teton and Shoshone National Forests (Figure 16a, 16b, and 17b; Wells et al. 2019, Van Manen et al. 2023a). Levels of depredation-related conflicts have been orders-of-magnitude greater in the GYE during the last two compared to previous three decades despite a long history of sympatry between cattle and grizzly bears, notably on allotments in the upper Green River and Wind River drainages of Wyoming (Figure 17b). This trend is also true for livestock-related conflicts on rangelands in Tom Miner Basin at mid-elevations of Paradise Valley in Montana (Figure 17a).

Public land grazing allotments that have been spared noteworthy increases in depredation after 2010 are restricted primarily to areas near army cutworm moth aggregation sites in alpine areas of Wyoming’s Absaroka Range (Figures 8i and 16b). These sites saw a major increase in levels of grizzly bear activity after 2010 (Section 3.7), suggesting that, as in the case of increased meat consumption, increases in exploitation of fat-rich moths by grizzly bears have likely been in compensation for loss of whitebark pine seeds (see Section 3.7). Parenthetically, these substantial increases in levels of bear activity on moth sites have been synchronous with comparative stasis in size of the GYE bear population (Van Manen et al. 2023a), which debars a significant effect attributable to increasing numbers of bears.

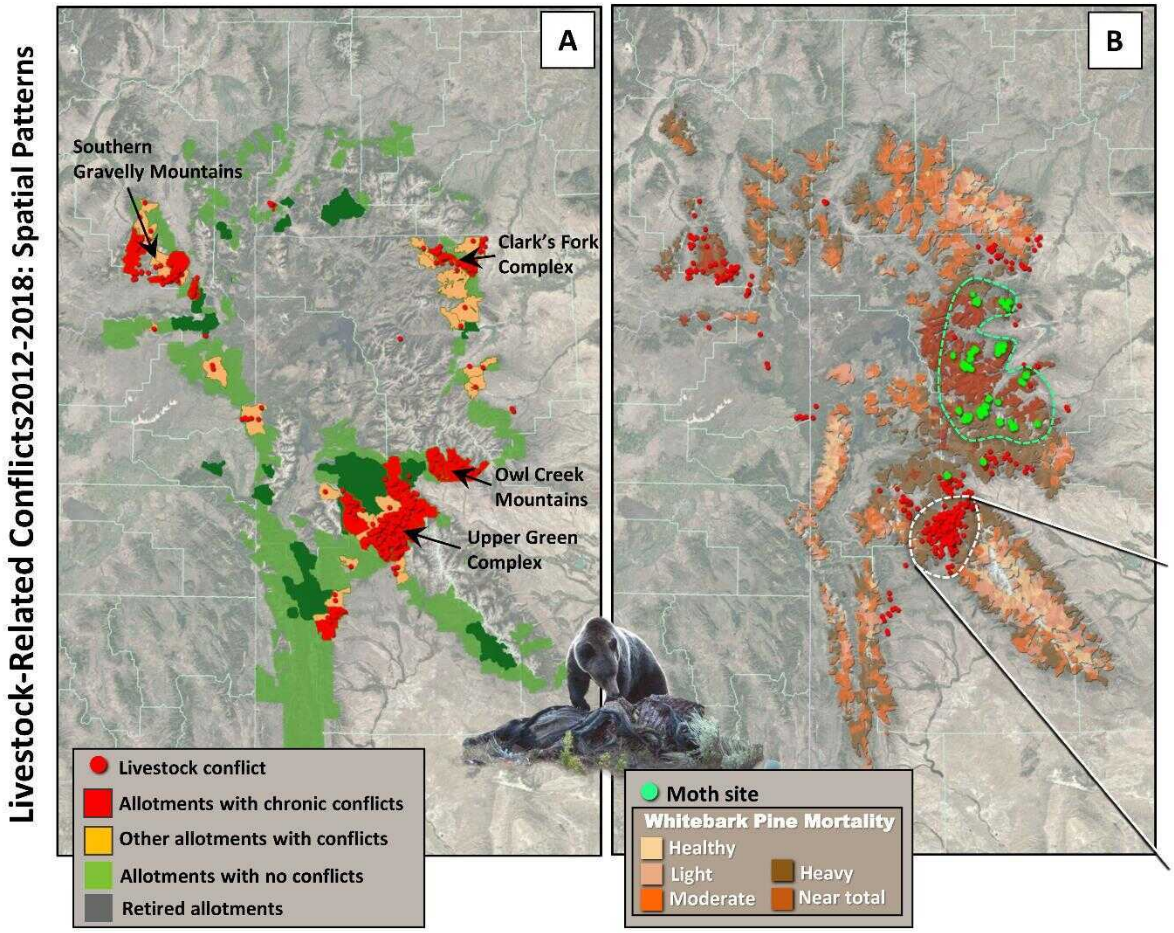


Figure 16. These maps offer a visual synopsis of geospatial patterns of livestock-related grizzly bear-human conflicts in the Greater Yellowstone Ecosystem, emphasizing patterns in the Upper Green River and Owl Creek Mountains areas of Wyoming. Much of the cattle-related depredation in the GYE occurred in these areas between 2012 and 2018. Map (A) shows grazing allotments in the GYE, differentiating those with chronic depredation (red), from those with more episodic depredation (orange) and those without any documented grizzly bear depredation as of 2018 (Wells 2017). Allotments shaded dark green were retired either before or during 2012-2018 (National Wildlife Federation 2015). Specific incidents of depredation are shown as red dots (Van Manen et al. 2012-2019). The map in (B) shows depredations, again as red dots, relative to mortality of mature cone-producing whitebark pine between 2000 and 2009 (Macfarlane et al. 2013: in shades of brown) and sites where grizzly bears were known to consume army cutworm moths (green dots; Robison 2009). Losses of whitebark pine were especially severe in middle portions of the Absaroka Mountains and around the Upper Green River, which is where depredations on cattle by grizzly bears were concentrated post-2010, with the exception of areas near where grizzly bears had the option to feed on army cutworm moths. These patterns, as well as others, suggest that grizzly bears compensated for losses of whitebark pine by consuming more cutworm moths, or where moths were not available, by depredating on cattle – especially cow-calves. As important, allotments on which grazing was retired did not experience any depredations, notably the Spread Creek-Black Rock allotments west of the Upper Green River Drainage.

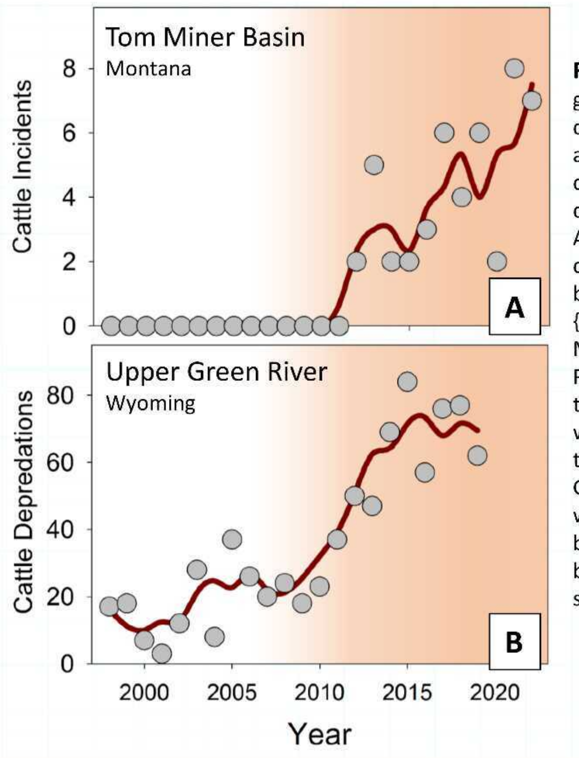


Figure 17. These trend graphs show numbers of grizzly bear-cattle conflicts associated with depredation on cow-calves in (A) Tom Miner Basin at the northern limits and (B) the Upper Green River drainage at the southern limitsof grizzly bear distribution in the Greater Yellowstone Ecosystem . Annual numbers of depredations are shown as gray dots, and a three-year moving average as a dark burgundy line (data from Schwartz & Haroldson {1999-2004], Schwartz et al. [2005-2011], and Van Manen et al. [2012-2022], Montana Fish, Wildlife & Parks [2015]). The vertical orange shading denotes the terminal decline of whitebark pine. Losses of whitebark pine were severe in middle portions of the Absaroka Mountains and around the Upper Green River and around Tom Miner Basin, after which depredations on cattle by grizzly bears in both areas escalated dramatically. Notably, grizzly bears and cattle had been sympatric in both areas since before 1998.

Implications

Although Wells (2017) and Wells et al. (2019) addressed spatial patterns of grizzly bear depredation on livestock, very little attention was given in these publications to the rapid increase in depredations after losses of whitebark pine, the likely compensatory nature of this increased exploitation, the mitigating effects of nearby sites where bears could consume cutworm moths, and compounding effects of nearby heavy mortality of whitebark pine trees. Bjornlie et al. (2014), Costello et al. (2014) and Van Manen et al. (2016) gave no consideration to this phenomenon in their analyses focused on changes in grizzly bear demography and behavior. This lack of attention is even more remarkable given the geospatial aspects of increasing grizzly bear depredation and the demonstrably lethal effects of depredation-related conflicts on bear survival.

3.11. Effects of Meat Consumption on Bear Demography

Increases in livestock depredation by grizzly bears in the GYE have led to a substantial escalation in numbers of bears killed because of livestock-related conflicts since around 2008 (data from Schwartz et al. 1998-2011, Van Manen et al. 2012-2023a). This increase, together with an antecedent increase in numbers of bears killed during conflicts with big game hunters has resulted in mortalities resulting from meat-related conflicts with humans proportionately more than doubling since 2000 (Figure 18a).

These increases in bear mortalities arising from meat-related conflicts have fueled a near four-fold increase in numbers of grizzly bears annually known to die in the GYE (Figure 18b), leading, in turn, to a 2.5-fold increase in numbers of known bear deaths as a proportion of total estimated population size (Figure 18c; total population size from Van Manen et al. [2023a]). This increase in the ratio of dead to live bears has occurred while proportions of known deaths attributable to natural causes have declined, casting into doubt the role of natural mortality in curbing growth of the GYE grizzly bear population since 2008 (see Section 4, *in toto*, and 6.1). Meat-related deaths are thus more plausibly implicated in slowing population growth.

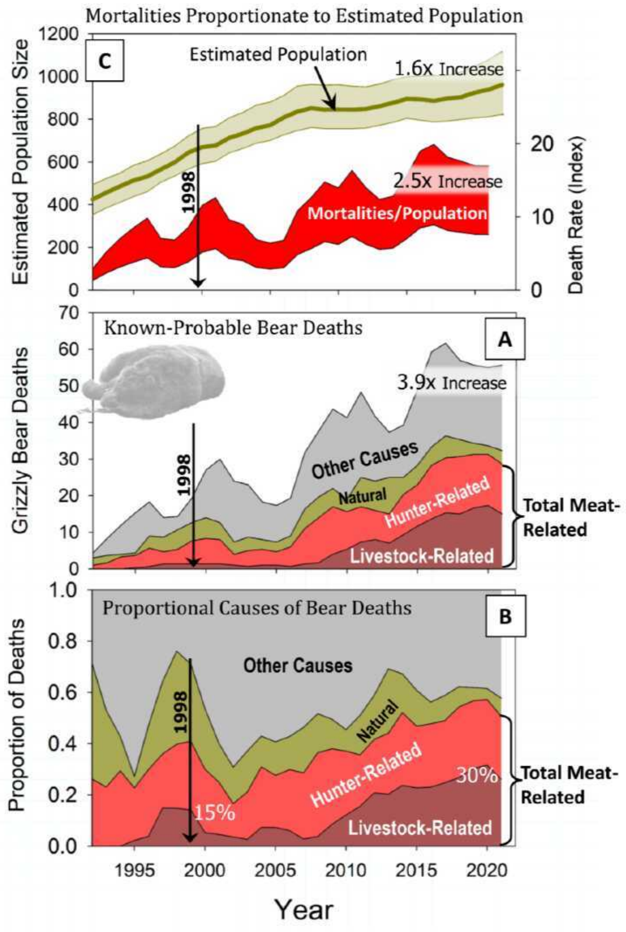


Figure 18. The figures at left show trends in annual numbers of known or probable grizzly bear deaths in the GYE along with probable causes as a 3-year running average. The benchmark year of 1998 is also shown. Panel (A) shows absolute number of deaths differentiating those resulting from retaliation for livestock depredation (in burgundy) from those arising from encounters with big game hunters (in red) and natural (green) and residual (gray) causes. Panel (B) shows these causes proportionally. Grizzly bear deaths arising from conflicts with people over meat (i.e., livestock and remains of hunter-killed animals) increased 5-fold after 1998 and proportionately doubled. Most of these increases occurred during and after terminal losses of whitebark pine between 2005 and 2010. Panel (C) shows total 3-year-averaged grizzly bear mortalities as a proportion of estimated total population size. Known and probable mortalities were adjusted to estimate total grizzly bear mortality using two different multipliers, a lower value from Interagency Grizzly Bear Study Team Annual Reports 2013-2021 and a higher value from Lamb et al. (2023). Mortalities as a proportion of live bears have increased 2.5-fold since 1998, with most of this increase again occurring after terminal losses of whitebark pine.

Longer-term, removals of grizzly bears in the GYE because of predation on livestock shifted after 1998 from incidents predominantly involving depredation on sheep to incidents almost exclusively (>90%) involving depredations on cow-calves (Figure 19a; data from Schwartz et al. 1998-2011, Van Manen et al. 2012-2023a) – a shift that resulted largely from closure during the 1990s of most allotments permitted to graze sheep within the distribution of GYE grizzly bears (National Wildlife Federation 2015). More important than this shift from conflicts involving sheep to conflicts involving cattle, the sex and age composition of bears killed because of livestock-related conflicts changed from predominantly (>60%) adult male grizzly bears prior to 2018 to predominantly other sex-age classes thereafter (Figure 19b). Even more problematic from a demographic perspective, the proportion of female deaths doubled from around 20% prior to 2016 to nearer 40% after 2020. Of these, roughly half were reproductive-aged females.

This substantial increase in female mortality resulting from retaliations against predation on cow-calves compromises prospects for the GYE grizzly bear population for two key reasons. For one, growth of brown and grizzly bear populations has repeatedly been shown to depend on high survival rates among females – especially reproductive-aged females (Knight & Eberhardt 1985, Wiegand et al. 1998, Schwartz et al. 2006a, Mace et al. 2012, Gosselin et al. 2015). For another, growth rate of the GYE population has substantially declined towards stasis beginning around 2007, concurrent with terminal declines of whitebark pine and marked increases in consumption of meat from anthropocentric sources (Figure 18a, Van Manen et al. 2023a).

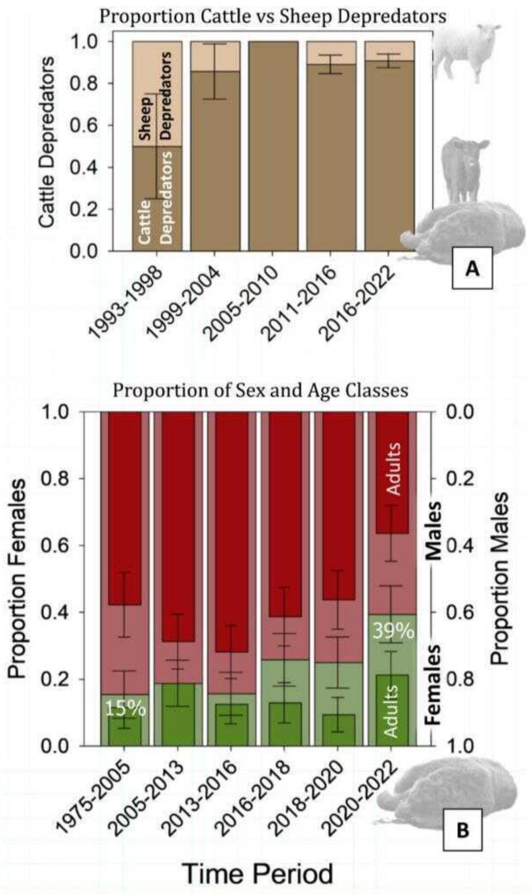


Figure 19. The two bar charts at left show in (A) the proportional break-down of grizzly bears killed in retaliation for depredation on sheep versus cattle and in (B) the sex and age class of killed depredators. The proportion of depredators that killed cattle is shown in brown in (A) for five different 6-year periods. Bears involved in cattle depredation have accounted for virtually all those killed since 1999, in contrast to a preponderance involved in sheep depredation during earlier years. The sex-age composition of bears killed because of depredations are shown in (B) for time periods defined to provide comparable sample sizes. Males are shown in shades of burgundy, females in shades of green, and adults of each in darker hues. The representation of females increased substantially after 2016, and more than doubled during 2020-2022 compared to 1975-2016. By contrast, adult males declined from representing the preponderance (>60%) of depredators during 2005-2018 to accounting for proportionately nearly half as many during 2020-2022. These trends suggest that females are more often being killed because of depredation-related conflicts, of which almost all involve cow-calves.

The increasing representation of females among bears killed to prevent or retaliate for livestock depredation is indicative of a convergence of male and female bear diets on meat, but obtained under risky conditions (Mattson 1997b, Schwartz et al. 2014), all of which reflects major environmental change in the GYE since roughly 2005. More important, there is good reason to think that female grizzly bears will continue to comprise a large portion of bears killed because of future livestock-related conflicts, with implications for the future composition of grizzly bear deaths.

Nutritionally, a dietary shift towards consuming more meat has probably not been detrimental. Mattson et al. (2004) show that meat is a high-quality bear food, and that, during fall, ungulates can offer bears a substantial quantity of fat. As a result, there is no reason to expect major changes in female fecundity, which is consistent with recent data on reproduction (e.g., Van Manen et al. [2023a]).

The problem with meat consumption arises from the entailed hazards for any grizzly bears engaging in this activity (Section 3.12). Figures 18a and 18b highlight the extent to which increasing numbers of grizzly bears have been dying because of conflicts with big game (primarily elk) hunters. There is clearly a strong temporal correlation between declines in cone availability and increases in meat-related grizzly bear conflicts and deaths. Given that bears seem to be compensating for losses of whitebark pine by eating more meat (Section 3.9), these increases in meat-related grizzly bear deaths are not plausibly coincidental.

Implications

Rather than being attributable to “density-dependent effects,” increased death rates of cubs and yearlings in Yellowstone post-2000 (Van Manen et al. 2016, 2023a:38) are more plausibly ascribed to increased hazards for these vulnerable young bears arising from their mothers eating more meat. These hazards for young bears derive partly from the human-associated hazards incurred by their mothers, but also from hazards associated with increased predation by wolves and other bears when care-taker females consume a concentrated high-quality food characteristically used by male bears and other carnivores (Mattson et al. 1992b, Mattson 2000, Ben-David et al. 2004, Gende & Quinn 2004, Gunther & Smith 2004, Quinn et al. 2017, Lincoln & Quinn 2019).

As a bottom line, rapid increases in total known and probable grizzly bear deaths in the Yellowstone ecosystem post-2010 are correlated with terminal declines in availability of whitebark pine seeds (Figures 18a and 18b). Taken together, these meat-related increases in mortality constitute compelling evidence for deleterious population-level effects arising from loss of whitebark pine as well as cutthroat trout (Section 3.8), with additional foreseeable negative effects. Inattention to meat-related mortality in IGBST publications during the last two decades constitutes yet another important failing in analyses by Van Manen et al. (2016, 2023a) and casts further doubt on conclusions in these publications regarding putative effects of conspecific density.

3.12. Hazards Associated with Exploiting Different Foods

The demographic implications of bears consuming different diets are axiomatically defined at a population level by effects on both birth and death rates. Effects on fecundity are predictably mediated by effects on the condition of reproductive females and the extent to which those effects translate into reproductive rate. Effects on death rate are dictated by the characteristic hazards associated with using a particular food. A high-quality food with positive effects on birth rates can either be associated with foraging opportunities concentrated in highly secure habitat or the opposite. The latter set of circumstances where a high-quality food lures an animal into a lethal environment has become the focus of scientific inquiry organized under the rubric of “ecological traps” (e.g., Delibes et al. 2001, Schlaepfer et al. 2002, Hale & Swearer 2016), which is interrelated with but distinct from source-sink dynamics (Kristan 2003).

The concept of ecological traps is not new to bear researchers. Nielson et al. (2006, 2010), Northrup et al. (2012), and Lamb et al. (2017, 2018, 2020), among many others, have deployed this concept in assessing the spatial aspects of challenges facing conservation of grizzly bears in Alberta and British Columbia. Moreover, there have been several congruent landscape-level assessments of hazards for Yellowstone grizzly bears (Carroll et al 2001, 2003; Merrill & Mattson 2003; Johnson et al 2004; Schwartz et al. 2010b) which have been directly relevant to judging the hazards incurred by bears using different foods with different geographic distributions (e.g., livestock, whitebark pine, and cutthroat trout) – albeit without explicit integration under the rubric of ecological traps.

Despite these precedents, the IGBST has not deployed the potentially insightful concept of ecological traps in research reported since Schwartz et al. (2010b) published a spatial analysis of hazards for grizzly bears in the GYE. Nor has the IGBST deployed an explicit framework by which the nutritional benefits and entailed hazards of a given diet or dietary shift are simultaneously considered. More to the point, the IGBST has consistently examined nutritional aspects in isolation from effects on survival, as well as without regard for past research on importance of the Big 4 foods (e.g., Corradini et al. 2023; see Section 3.1).

Implications

Inattention by IGBST researchers to dietary hazards, especially in the form of ecological traps, debars confidence in conclusions reported in most of the Study Teams publications, notably Fortin et al. (2013), Gunther et al. (2014), Van Manen et al. (2016a), and Corradini et al. (2023). Credible inquiry requires the explicit integration of hazards and nutrition because hazards incurred by bears can vary substantially, even when using foods of otherwise similar nutritional quality. Of relevance to GYE grizzly bears, hazards are much lower for bears consuming whitebark pine seeds, trout, and moths in characteristically secure environments compared to bears consuming a diet of meat from ungulates, livestock, or any other food that brings bears into conflict with people (Figure 20; Sections 3.7-3.11; also, Mattson et al. [1992a], Mattson [1998], Pease & Mattson [1999], Gunther et al. [2004], Schwartz et al. [2006a],).

More to the point here, IGBST researchers have failed to characterize major grizzly bear foods according to a conceptualization that distinguishes high-quality foods associated with hazardous environments from high-quality foods associated with secure environs. These researchers have furthermore failed to differentiate whether hazards were incurred primarily by dependent young, independent bears (adults and adolescents), or both (Figure 20). This latter distinction is important because 80-90% of all independent-aged grizzlies die from human-related causes (e.g., Schwartz et al. 2006a), whereas many dependent young bears die for “natural” reasons, including predation by other bears (Schwartz et al. 2006a, Van Manen et al. 2016). Hazards associated with humans are thus thrown into sharp relief in any worthwhile assessment of dietary shifts among adult bears, whereas hazards associated with potential natural predators are a more prominent consideration in assessing changes for cubs and yearlings.

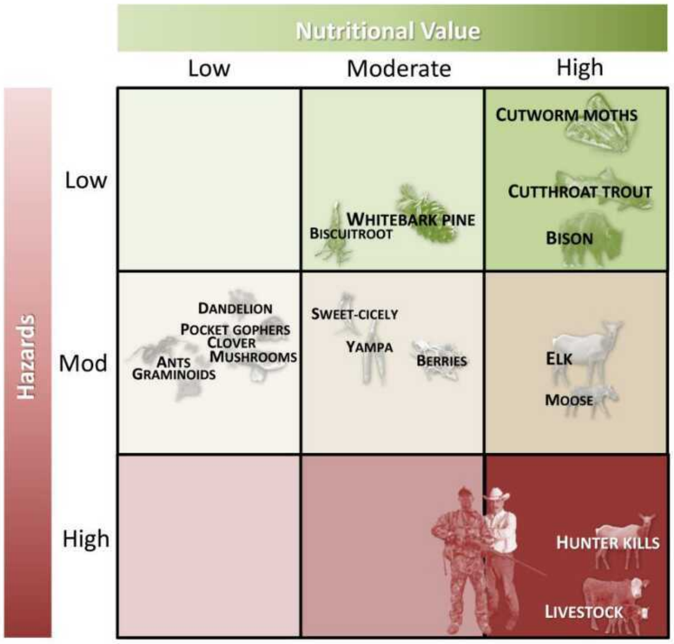


Figure 20. This figure shows a matrix of nutritional value horizontally and hazards vertically associated with exploitation of characteristic foods by adult and adolescent grizzly bears in the Greater Yellowstone Ecosystem. Individual food items are shown, with nutritional value taken from Mattson et al. (2004) and hazards from numerous sources, including Gunther et al. (2004), Middleton et al. (2013), and Wells et al. (2019). Of the highest-quality foods, cutworm moths, cutthroat trout, and bison are the safest for bears to consume, largely because these foods occur in remote areas or the protected confines of Yellowstone National Park. Exploitation of meat from livestock and animals killed by big game hunters is most hazardous because risk of conflict with humans is extremely high.

4. Issues with Demographic Analyses and Applications

The following sections address a suite of issues explicitly related to methods and data used by the IGBST in analyses of GYE grizzly bear demography. Collectively, the identified problems call into question the veracity of not only the IGBST's methods and conclusions, but also derivative management applications. Because raw data are currently held under monopolistic arrangements that preclude independent inquiry (Section 5.5), most of what's presented here is based on circumstantial evidence. Even so, this circumstantial evidence calls into question virtually all research regarding demography of the GYE grizzly bear population published during the past 20+ years (e.g., Cherry et al. 2002; Schwartz et al. 2016a; Manen et al. 2014b, 2016, 2023a, 2023b). Although there is scant basis in circumstantial evidence for reaching definitive conclusions about trend and size of the GYE grizzly bear population, there is nonetheless ample support for the existence of problematic bias and uncertainty that has not yet been addressed. Because IGBST researchers monopolize government data and resources and serve as public trustees, they are obligated to satisfactorily address – rather than reflexively dismiss (e.g., Section 5.4) – the many issues identified in following sections.

4.1. Method-Based Artifacts in Estimates of Population Size and Trend

Estimates of grizzly bear population size in the GYE by IGBST researchers during the past 30 years have exhibited instantaneous year-on-year increases of sometimes 100s of bears that are *prima facie* not only implausible but also biologically impossible (Figure 21). Yet these increases have been routinely billed by naïve or politically motivated journalists and grizzly bear managers as real (see Section 2). This uncritical publicizing of IGBST grizzly bear population estimates has contributed to public perceptions of sky-rocketing bear population growth and a consequent shaping of policy environments favorable to removing ESA protections for the GYE bear population.

As a factual matter, estimated population increases during recent decades have been largely an artifact of changing methods rather than any real change in population size (see also Sections 4.2-4.6). Prior to 2007, interannual changes in estimated *minimum* numbers of bears in the population were used to indicate population trend. During 2007-2015, estimates of *total* population size were based on a statistical adjustment to 3-year running sums of females with cubs-of-the-year (COY) that were thought to be unique individuals (the Chao2 method; Keating et al. [2002], Cherry et al. [2007]). This estimated total number of reproductive-aged females was then adjusted by multipliers to account for fractions of remaining sex and age classes (see for example, Schwartz et al. [2008]. During 2013-2020, these same basic methods were employed, but with the fraction of male bears substantially increased based on an estimated increase in survival rates for this population segment (Van Manen et al. 2014). In 2021, this same basic approach was again used, but with a substantial increase in estimated numbers of unduplicated females with COY resulting for use of new methods that substantially discounted distances between sightings of this cohort as a basis for determining which were of unique individuals (Van Manen et al. 2023b). In 2022, yet another method was deployed that incorporated estimated numbers of females with COY and updated estimates of population vital rates (i.e., an Integrated Population Model or "IPM"). IPM methods were then used to retrospectively estimate population size during previous years (for details and data on these estimates see Pease & Mattson, unpublished; Knight et al. 1987-1993, 1997; Knight & Blanchard 1994-1996; Eberhardt & Knight 1996; Haroldson et al. 1998; Schwartz et al. 1999-2011; Van Manen et al. 2012-2023a; Van Manen et al. 2023b).

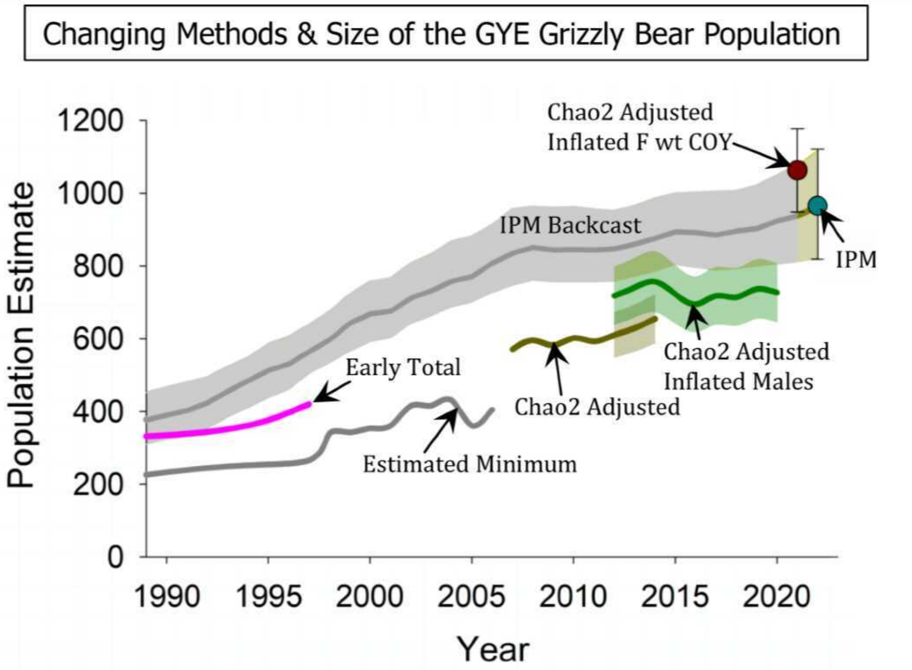


Figure 21. This figure summarizes different estimates of population size for GYE grizzly bears based on seven different methods used between 1989 and 2022. Estimates derived from different methods are shown in different colors. Lavender shows trend in estimated *total* size of the population from Pease & Mattson (unpublished) and Eberhadt & Knight (1996). The dark gray line 1989-2006 shows the *minimum* number of bears estimated to be in the GYE population. The dusky and bright green lines (with associated confidence intervals) show estimated *total* population size using a method based on unduplicated counts of females with cubs-of-the-year (COY) multiplied by various factors to account for fractions of other sex, age, and reproductive classes. The increase in estimate size post-2011 resulted from inflating the estimated fraction of male bears in the population. The estimate for 2021 used the same basic method but inflated estimated number of females with COY by reducing the distance threshold for defining unique females. Finally, the estimate for 2022 was based on a method (Integrated Population Model or IPM) that integrated counts of females with COY and updated estimates of population vital rates. This method was then backcast to retrospectively estimate population size for previous years. Results of this exercise are shown in shades of gray. Managers and journalists frequently make claims about growth in size of the GYE population based on comparing estimates produced by these various incommensurate methods, analogous to comparing apples and oranges.

At face value, this summary of methods reinforces the extent to which putative increases in size of the GYE grizzly bear population invoked in the media and government decision-making during the past 30 years were – and continue to be – an artifact of methods and not real changes in population size. Each change in methods instantaneously added sometimes 100s of grizzly bears on paper to estimated total population size – without any change in real numbers of bears in the ecosystem. As recently as 2022, revised methods reduced estimated size of the population by 100 paper bears – independent of any real change (Van Manen et al. 2023a). Confusion regarding these large changes in estimated population size has been further compounded by distinctions regarding whether estimates held for the entire population or only for the portion of bears residing within an area designated for population monitoring (the Demographic Monitoring Area or DMA).

Implications

Each of the changes in method used to estimate size and trend of the GYE grizzly bear population could be considered an improvement, trending towards estimates that were more precise and less biased (but see Sections 4.2-4.6). Even so, changes in estimates were predictably mystifying to, or at least taken at face value by, managers and members of the public. For unclear reasons, IGBST researchers failed to publicly clarify the extent to which these changing estimates of population size and trend were an artifact of changing methods.

Regardless of motivation, neglect of fiduciary educational duties by the IGBST predictably aggravated public confusion and abetted claims by those invoking politicized IGBST science to support removal of ESA protections for GYE grizzly bears (see Sections 2 and 6.4). If nothing else, evasive statements by IGBST scientists reinforced rather than corrected perceptions that changes in estimated size arising from changing methods were, in fact, real. These prevarications fed perceptions of partisan scientific practice (e.g., Wilkinson 1998, Ketchum 2019) and more objectively eroded the standing of IGBST researchers as "honest brokers" of scientific information (cf., Pielke 2007).

4.2. Bias Arising from Search Effort and Sightability

There is, furthermore, good reason for skepticism about estimates of size and trend for the GYE grizzly bear population produced by recent methods, specifically the Integrated Population Model (IPM; Van Manen et al. 2023a). These IPM-based estimates continue to be informed primarily by annual counts of unduplicated females with cubs-of-the-year (COY), albeit with adjustments introduced by updated estimates of grizzly bear vital rates (Section 4.1). As has been the case for all previous estimates based on unduplicated counts of females with COY (e.g., Doak & Cutler 2014a, 2014b), annual estimates of population size produced by the IPM continue to be highly correlated with efforts by researchers to observe this cohort, as well as changes in overall sightability of bears.

Figure 22 illustrates the extent to which IPM-based estimates of population size and aerial search efforts by IGBST researchers are correlated. Trend in population size is shown in Figure 22a; trends in 3-year-averaged estimates of unduplicated females with COY in Figure 22b; and trends in 3-year-averaged hours spent by observers during aerial overflights systematically looking for bears in Figure 22c (data are from Van Manen et al. 2023a). Even a cursory visual examination suggests that all three are strongly correlated, borne out by statistical relations shown in Figures 22d-22f. Annual estimates of unduplicated females with COY explain 96% of the variation in annual estimates of total population size (Figure 22d), whereas hours of observation flights explain 94% of variation in annual estimates of unduplicated females with COY (Figure 22e) – as well as 96% of the variation in annual estimates of total population size (Figure 22f).

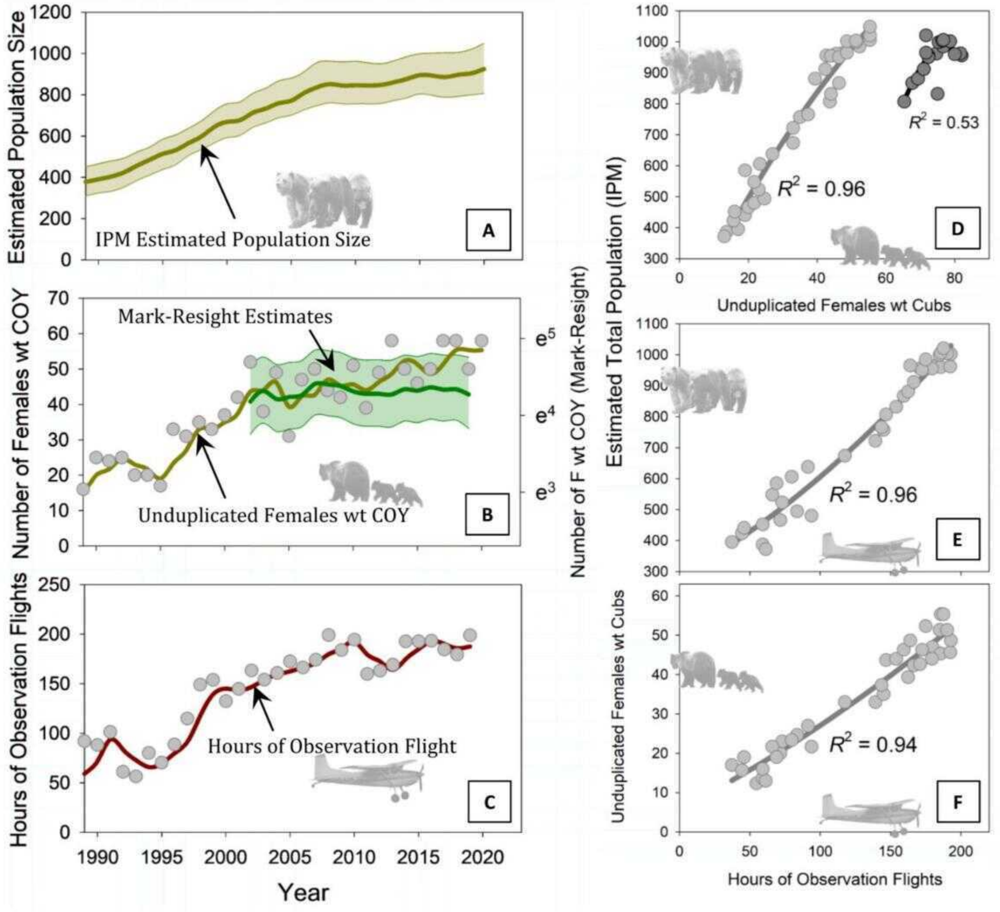


Figure 22. The panels above illustrate problematic correlations between estimated size of the GYE grizzly bear population (as per the IPM, see Figure 13) and potentially confounding bias introduced by observer effort. As described in Figure 13, all recent annual estimates of population size have been largely informed by annual observations of unique (or unduplicated) females with cubs-of-the-year (COY). Many of these females with COY are observed during aerial overflights specifically designed to sight bears. Other observations are taken from at-large sources. The extent to which estimates of population size track estimated numbers of females with COY is evident in comparing (A) and (B). The extent to which both track observer effort (i.e., hours of observation flights) is evident by comparing panel (C) with panels (A) and (B). These relations are shown statistically in panels (D)-(F). Annual estimates of females with COY explain 96% of the variation in annual estimates of population size, and hours of observation flights likewise explains 96% of variation in estimated bear numbers as well as 94% of estimated unduplicated females with COY. All of this could be construed as meaning that observations of females with COY and derivative estimates of total population size are largely an artifact of observer effort rather than real population trends.

The likelihood that GYE grizzly bear population estimates are confounded by bias is compounded by the extent to which these estimates have also been highly correlated with increasing numbers of bears using army cutworm moths in alpine areas of the Absaroka Mountains (Figure 20; Section 3.7). Any grizzlies feeding at these sites were almost certain to be seen by aerial observers (Figure 21a; French et al. 1994, O'Brien & Lindzey 1998), in contrast to grizzly bears consuming pine seeds under typically dense forest canopies (Mattson 2000) which stood only a 7% chance of being seen. As relevant, bears feeding on ungulate carcasses had >30% chance of being observed. The concurrence of plummeting pine seed consumption and increasing exploitation of moths and meat (see Sections 3.2, 3.7, and 3.9) suggests that *per capita* sightability of bears increased substantially during the past 20-30 years, increasing, in turn, the odds that any given bear would have been seen, whether during aerial overflights or by observers on the ground.

Figure 23b illustrates how closely trends in estimated size of the GYE grizzly bear population tracked numbers of sites where grizzly bears were observed consuming moths. This visual approximation is corroborated by the fact that number of utilized moth sites and absolute numbers of bears observed on these sites each year explained 91% and 80%, respectively, of variation in annual estimates of bear numbers (Figures 23c and 21d).

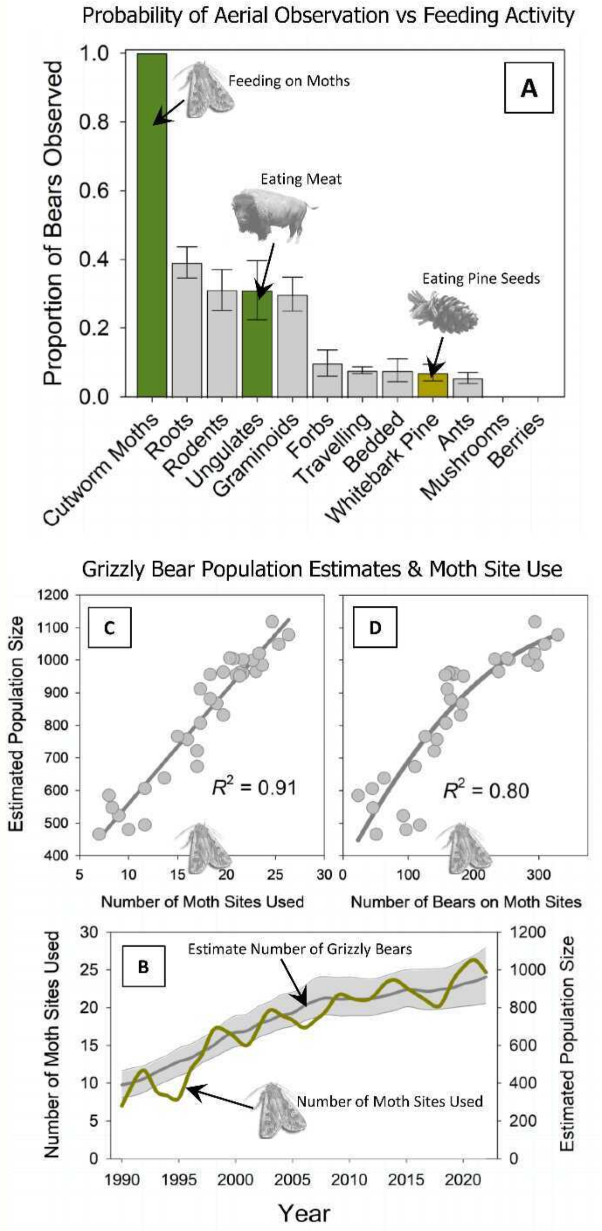


Figure 23. The panels at left illustrate the extent to which changes in aerial observability of grizzly bears associated with changes in diet and habitat use could have biased estimates of population size and trend for the GYE grizzly bear population. The bars in (A) are proportional in height to the likelihood that a grizzly bear would have been visually observed from the air during radio-tracking flights as a function of the kind of activity that bear was engaged in (determined from later ground visits). Likelihood of observation varied by orders of magnitude. Notably, bears consuming army cutworm moths and meat from an ungulate were >10- and >3-times more likely to be seen, respectively, compared to bears eating whitebark pine seeds. Given that consumption of pine seeds has plummeted, and consumption of moths and meat has increased, these differences have major implications, in turn, for observations of females with COY and estimates of total population size (see Figure 14).

This potential bias is substantiated by how closely estimated numbers of GYE grizzly bears track number of moth sites annually used by grizzly bears (B). Statistically, number of exploited moth sites explains 91% of the variation in annual estimates of grizzly bear population size (C). Similarly, absolute numbers of bears observed on moth sites explains 80% of variation in population estimates. These relations could be construed as meaning that estimated numbers of GYE grizzly bears are largely an artifact of changes in sightability of bears associated with changes in food availability and diets.

Implications

One could conclude from these relations that annual estimates of total grizzly bear population size produced by the IPM are almost wholly an artifact of efforts by agency researchers to find females with COY each year and changes in diet and habitat use that have made grizzly bears easier to observe by ground and aerial observers. Put another way, statistical relations this strong demand an irrefutable explanation of how they might exist in the absence of bias that fatally compromises the validity of methods used to estimate size and trend of the GYE grizzly bear population – including the IPM (see also Doak & Cutler [2014a, 2014b]).

This last point should not be construed as suggesting that the GYE grizzly bear population has not grown during the past 30 years. Nonetheless, observations as simple as the ones presented here cast doubt on the veracity of current estimates of population size and trend as well as any related assertions about size and trend made by GYE bear managers and IGBST researchers. As a bottom line, despite official representations to the contrary, there is, in fact, considerable uncertainty about the status of the GYE grizzly bear population.

4.3. Risky Methods for Managing Mortality Rates

The IGBST uses known fates of radio-marked grizzly bears to estimate annual mortality rates for different sex-age classes of grizzly bears (e.g., Schwartz et al. 2006a; Van Manen et al. 2016, 2023). More specifically, these calculations involve estimating the likelihood that a given radio-marked bear would have died during a given year at a given age. A range of death rates centered on these historical estimates have been used in population simulations to derive benchmarks for managing grizzly bear mortality. These simulations associate different population trajectories with different estimated death rates that would, in theory, achieve different management objectives, i.e., growth, statis, or decline (Harris et al. 2006, Interagency Grizzly Bear Study Team 2012, Van Manen et al. 2023b). As a logical derivative, management applications have assumed that real-time rates at, above, or below these benchmarks will allow managers to maintain, decrease, or increase the bear population.

However, in application, mortality rates used to inform managers on a real-time basis are calculated using a method that fundamentally differs from methods used by the IGBST to estimate death rates of radio-marked bears and derivative management benchmarks. Putative death rates are calculated each year for management purposes as the ratio of *estimated* total dead (D) to *estimated* total live bears (N), not as the likelihood that radio-marked bears would have died during a given year (Greater Yellowstone Subcommittee 2016). In other words, annual estimates of bear deaths are divided by corresponding annual estimates of total population size to yield what is essentially an indexed death rate (i.e., D/N, a ratio of dead to live bears) for each of the monitored sex-age classes of grizzly bears, which is then compared to management benchmarks.

Total numbers of *dead* bears used in the D/N calculations are estimated using methods described in Cherry et al. (2002; see Section 4.4). Up until 2020, total numbers of *live* bears were based directly on

Chao2-based estimates of total reproductive females (Keating et al. 2002, Cherry et al. 2007) coupled with multipliers to account for proportions of dependent young, adolescent females, and independent males in the population (Section 4.1). The 2016 Greater Yellowstone Conservation Strategy allows for annual calculations of D/N to be the future basis for adopting different goals at different population thresholds. For example, if population size were estimated to be ≤675, 675-747, or >747 bears, then goals could prospectively change from managing for increase or stasis to managing for decline (Yellowstone Ecosystem Subcommittee 2016).

Issues

One assumption in this approach adopted by managers is that there will be future equivalence between population growth rate and historical death rates estimated from fates of radio-marked bears (e.g., Interagency Grizzly Bear Study Team 2012, Greater Yellowstone Subcommittee 2016). If nothing else, this assumption is tenuous because it does not deal with variation in birth rates. Population growth is, axiomatically, the difference between birth and death rates. In other words, one half of the equation is left out of explicit real-time consideration.

The only presumed corrective for a mismatch between historical and real-time demographic rates is through annual updates incorporating recent data from radio-marked bears (Van Manen et al. 2023a, 2023b). Even so, updated estimates of demographic rates will always be driven largely by old data simply because large sample sizes – larger than samples provided by recent data – are needed for adequate statistical precision (Section 4.5). Management responses are, moreover, triggered only when prescribed death rates are exceeded 3 years in a row (Greater Yellowstone Subcommittee 2016). All of this creates lags in responses by managers to unfolding conditions that are further compounded by 4 to 11-year lags in reliable detection of population declines using Chao2-based estimates of total population size (Van Manen et al. 2023b).

Another important assumption underlying management applications is that the calculation used to estimate annual death rates (estimated total dead bears [D]/ estimated total population size [N]) correlates perfectly with death rates estimated from known fates of radio-marked bears—and with a 1:1 slope. As it turns out, the exact relationship between benchmarks based on *known fates* of individual bears and *the index* used to annually monitor death rates is unknown. Certainly, there is no equivalence between the methods used to calculate each metric. Put another way, even if managers calculated a putative population-wide death rate of 7.6% for adult females during a given year, there is no way to know whether this rate was real, much less equivalent to benchmark standards.

This is a case where apples are being compared to oranges and where, moreover, managers and the IGBST have not identified potentially violated assumptions or evaluated consequences of discrepant methods (cf., Mattson 1997b). As the IGBST acknowledges (Interagency Grizzly Bear Study Team 2012, Van Manen et al. 2023b), methods by which total dead and live bears are annually calculated are prone to substantial variability and bias of a nature that can, in turn, both amplify or dampen bias in a relationship with benchmark mortality rates that are already unknown. Hence, the nature and magnitude of change in bias from one year to the next is, and will continue to be, unknown — compounding problematic lags introduced by monitoring and management methods.

More specifically, as the IGBST notes in Table 2.1 of its 2012 review of population monitoring methods, the method for estimating total mortality is "slightly low," largely because substantial variation arising from changing causes of mortality is not accounted for (Interagency Grizzly Bear Study Team 2012; see also Sections 4.4 and 4.5). Historically, methods for estimating population size using the Chao2 method were also biased low, which mitigated some of the problems arising from under-estimating total dead bears (Interagency Grizzly Bear Study Team 2012, Van Manen et al. 2023b). However, that changed in 2020 when population estimates based on the Chao2 method and associated multipliers were instantaneously increased by around 35% through the employment of new criteria for identifying unduplicated females with cubs-of-the-year (see Section 4.1, Figure 21, Van Manen et al. 2023b). This abrupt increase in estimated population size erased any mitigations that might have been introduced by under-estimating live bears (N) pre-2020, with a resulting unknown but likely substantial increase in likelihood that D/N under-estimated death rates.

Compounding these biases and uncertainties, increasing aerial search efforts and sightabilities of bears in the GYE have likely increased over time, resulting in dubious increases in estimated numbers of females with COY and derivative estimates of total population size (N in the D/N calculation), both with no known relationship to true population size (see Section 4.2). At the same time, estimates of total mortality have varied in unknown ways relative to biases introduced by "heterogeneity" (Cherry et al. 2002, Interagency Grizzly Bear Study Team 2012; Section 4.4). More specifically, if true causes have been increasingly shifting to those less likely to be detected and recorded (for example, by malicious killers or unscrupulous big game hunters; see Section 3.11), then estimates of total bear deaths (D) will have been correspondingly under-estimated.

Implications

As a bottom line, methods developed by the IGBST for use by GYE grizzly bear managers to guard against over-killing grizzly bears are beset by substantial bias and uncertainty. This arises from multiple causes, including (1) using a method for estimating death rates that has no known relationship to the standards being used to guide management (the apples and oranges problem); (2) substantial biases affecting methods for estimating both total numbers of annual deaths (the death rate numerator; Section 4.4) and females with COY during a given year (the death rate denominator); and (3) bias and outright error affecting multipliers used to derive estimates of total population size (Sections 4.5 and 4.6, below). This chain of potentially compounding problems debars confidence in methods used for monitoring grizzly bear death rates of GYE grizzly bears.

4.4. Problematic Method for Estimating Numbers of Dead Bears

The IGBST uses a method developed by Cherry et al. (2002) to calculate total numbers of grizzly bear deaths in the GYE each year based on a proportional estimate of unreported mortalities – a value that is then used in the numerator of the calculation used to annually index death rates (the D in D/N; see Sections 4.3 and 4.5). This index is compared to benchmark rates to determine whether numbers of deaths are compatible with different management objectives – a process that is prey to several concerning biases and uncertainties described more fully in Section 4.3. Here I focus more explicitly on uncertainties and biases associated with the Cherry et al. (2002) method for estimating total numbers of dead bears.

Issues

One significant problem with this method is a well-recognized tendency to underestimate true mortality (Interagency Grizzly Bear Study Team 2012: Table 2.1; Cherry et al. [2002]). Any underestimation axiomatically increases the likelihood that death rates will be underestimated as well, especially if the denominator – estimated population size (N) – is proportionately inflated (see Sections 4.2 and 4.3). This concern is lent weight not only by discrepancies between proportional estimates of unreported bear mortalities produced by the Cherry et al. (2002) method when compared to estimates by methods applied in other ecosystems, but also by implausibly little interannual variation. This variation is an astoundingly small 4% of the annual average (i.e., Coefficient of Variation; data from IGBST Annual Reports). Leaving aside implausibly small interannual variation, the proportion of unreported mortalities produced by the Cherry et al method (roughly 25%) averages 2 and 2.5-times less than the average of proportions reported for other ecosystems using different methods (roughly 58%; e.g., Dood et al. 1986; McLellan et al. 1999, 2018; Austin et al. 2004; Lamb et al. 2023). Alone, these prospective problems cast doubt on using the Cherry et al. (2002) method for precautionary management of any bear population.

But there is another major problem, prominently noted by Cherry et al. (2002): "The assumption of a constant reporting rate for radio-collared bears over time was important in…application of the method to the count data. This assumption could be violated if, for example, the probability of a death being reported depended on the cause of death and these causes changed over time…there is some evidence that reporting rates have declined in recent years." In other words, if causes of death are trending towards those that are less likely to be reported, then the Cherry et al. (2002) method will be prey to ever-increasing under-estimation of total deaths. Given the increasing toll being taken on GYE grizzly bears by lethal encounters with elk hunters in remote areas (Figure 18), this is indeed likely to be the case.

Moreover, estimates of total deaths are likely to be further biased by intensity of efforts to capture and radio-collar grizzly bears. This bias arises from the fact that deaths of radio-collared bears are not subject to the multiplier produced by the Cherry et al. (2002) method to estimate unreported unknown mortalities. In other words, if ever more effort is being exerted to capture bears, resulting in ever-more radio-marked bears, there will likely be a larger number of deaths each year attributable to marked bears and thus not subject to any adjustment accounting for unknown mortalities—this simply as a function of effort on the part of researchers and managers and without any intrinsic relationship to numbers of bears dying. This systematic bias is almost certainly exacerbated if numbers of bears being captured and radio-collared are increasing as a proportion of total estimated population size.

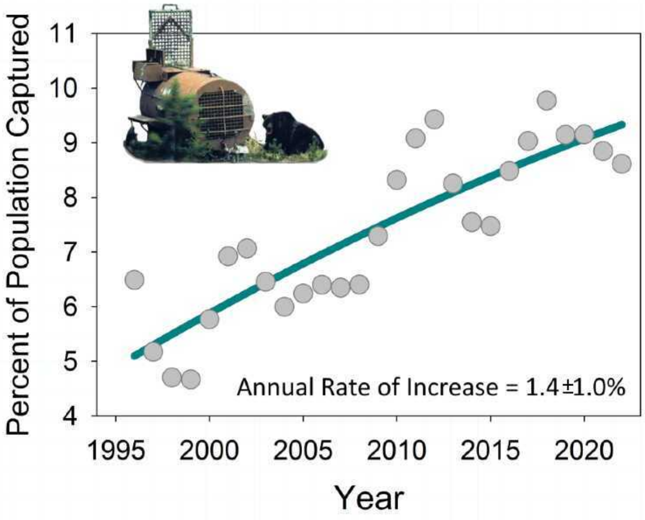


Figure 24. This figure shows trend in the numbers of grizzly bears captured each year in the Greater Yellowstone Ecosystem as a percent of total estimated population size. Percent captures is shown as a 3-year running average. Data for numbers of captures and total estimated population size are from Van Manen et al. (2023). Captures and imputed trapping effort increased during 1993-2022 at an annual rate of roughly 1.4%, resulting in a near-doubling of relative numbers of captures, imparting major bias to estimates of grizzly bear density based on cumulative bear captures.

Figure 24 shows that grizzly bear captures have, in fact, increased at a far more rapid rate than any probable change in total population size, which is consistent with capture effort alone magnifying the extent to which total grizzly bear mortality has been under-estimated. Numbers of bears captured each year have increased since 2000 at an annual rate approximately 3% greater than estimated rate of increase for the total population (Van Manen et al. 2023a). Ergo, a larger fraction of the population is being marked, predictably yielding a larger number of dead bears that are radio-collared—amounting to roughly a 4% rate of fractional increase per year since 2000. Even barring consideration of other problems, this increase alone arbitrarily deflates estimates of unreported mortality produced by the Cherry et al. (2002) method.

Implications

The IGBST fails to acknowledge these several problematic biases affecting its promoted method for estimating total numbers of dead bears in the Yellowstone grizzly bear population. The IGSBT additionally fails to recognize or acknowledge the extent to which these biases amplify risk. Perhaps more important, unacknowledged biases have predictably increased over time, resulting in greater underestimation of total mortality. Consequently, there is a good chance that death rates have been likewise increasingly underestimated, leading to increased errors by managers regarding the sustainability of current levels of mortality.

4.5. Death Rates that are Lagged and Implausible

As I preview in Section 4.3, the IGBST uses estimates of death rates derived from fates of radio-marked bears at several critical junctures in the methods it has promulgated for monitoring and managing mortality of Yellowstone's grizzly bears. For one, these rates are the basis for seminal management benchmarks (Section 4.3) and, for another, as a basis for calculating proportions of different sex-age classes in the population used, in turn, as multipliers for deriving total population estimates (Section 4.1).

These multipliers can obviously have major effects on total population estimates. For example, beginning in 2012 the IGBST began using a larger multiplier to account for number of independent males, arguing that the most recent estimate of death rates for males using data from 2002-2011 had decreased (Section 4.1; Interagency Grizzly Bear Study Team 2012). Hence there were presumably more males in the population than had been previously thought. The difference between population estimates using the old and new multipliers averaged 107 bears for 2012-2014, which amounted to an instantaneous 17% increase in estimated total population size (Figure 21).

Axiomatically, this substantial increase in the denominator (N) for calculating the index used to monitor mortality rates (D/N; see Section 4.4) translated into a 15% decrease in death rates calculated from real-time survey data. In other words, depending on the multipliers that account for proportions of sex-age classes in the population, estimates can be more or less arbitrarily either substantially over or under a given threshold or benchmark for mortality rates (as per Greater Yellowstone Subcommittee 2016).

Issues

Estimates of death rates derived from fates of radio-marked bears thus need to be unimpeachable. But there are two major problems with these rates, one of which is chronic, and the other especially evident during the past 20 years. The chronic issue arises from inherent insensitivities of death rates calculated from fates of radio-marked bears to rapidly changing conditions. Reliable estimates depend on large sample sizes (e.g., the known fates of 50-100 individuals for each sex-age class), and the only way to produce a large sample size is to include data that span numerous years. In other words, these death rates (or, inversely, survival rates) are chronically slaved to the past and, in an environment such as Yellowstone's, ten years can rapidly become irrelevant to the present and near future (see Sections 3.1-3.11). This problem holds, moreover, for all demographic estimates obtained from fates of radio-marked bears, including birth rates. As a result, even annual updates of demographic parameters with estimates using a single previous year's data (as per Van Manen et al. 2023a) stand little chance of offering critical insights into rapidly evolving environmental and demographic trends.

But the more important *prima facie* problem is the extent to which death rates derived from fates of radio-marked bears are not only discrepant from, but also fundamentally at odds with, straight-forward and unambiguous trends in numbers of grizzly bears dying in the Yellowstone ecosystem.

Figure 25 illustrates the extent of this problem using data from Knight et al. (1992, 1993, 1997), Knight & Blanchard (1994-1996), Haroldson et al. (1998), Schwartz et al. (1999-2011), and Van Manen et al.

(2012-2023a). The red dotted lines in Figures 25a and 25b are indicators of population-wide death *rates*, based on a more direct (A) and a more indirect (B) measure.

Figure 25a shows *total* estimated bear mortality (using methods in Lamb et al. [2023]) as a percentage of *total* estimated population size (shown in green along with credible intervals). This ratio, which directly indicates death rates, has been steadily climbing since 1990, punctuated by a near two-fold increase that correlated with culminating losses of whitebark pine during the late 2000s.

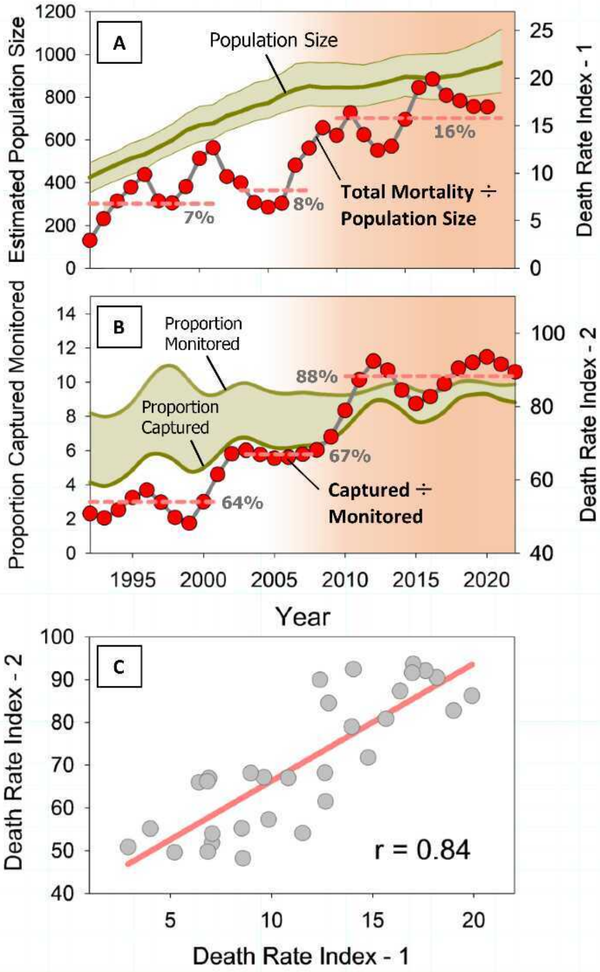


Figure 25. The panels in (A) and (B) at left show trends in indicators of annual death rate for GYE grizzly bears referenced to retrospective estimates of total population size by Van Manen et al. (2023). Panel (A) shows population size (plus confidence intervals) in green. The red dotted line shows a 3-yr running average of *total* estimated grizzly bear mortality divided by *total* population size, which provides an estimate of total population death rate (Death Rate Index – 1). The horizontal dashed lines show average indexed death rates for different periods of time correlated with valence shifts in death rate, notably post-2007 increases associated with culminating losses of whitebark pine losses. Panel (B) shows the proportion of the population that was annually monitored (top lighter green line) and captured (bottom darker line). The red dotted line shows percent captured divided by percent monitored, which indicates the level of attrition of captured bears over time and is also an indicator of death rate among adolescent and adult bears (Death Rate Index -2). Values associated with valence shifts in this metric are also shown in (B). The bottom graph (C) shows a strong correlation between the two indices. These indicators suggest that morality rates increased dramatically after culminating losses of whitebark pine in the late 2000s – by as much as a third to two-fold compared to previous years.

Figure 25b shows the proportion of the total population that was annually captured (darker green line) and monitored (lighter green line), with a clear narrowing of the gap between these two values. The only plausible way this could happen is if there was increasing attrition of captured bears each year either because of death or lost collars, with the first cause more likely than the second. The ratio of captured to monitored bears is thus another logical – albeit more indirect – indicator of total death rate. Here again there was a substantial increase in this measure after culminating losses of whitebark pine. The strong correlation between these two independently derived indicators of death rate (r = 0.84) shown in (C) suggests that they contain significant information about an underlying phenomenon, i.e., real grizzly bear death rates.

Implications

The marked contrast between trends shown in Figure 25 and trends in death rates reported by the IGBST (e.g., Schwartz et al. 2006a, Interagency Grizzly Bear Study Team 2012, Van Manen et al. 2016, 2023a) pose a paradox. Which trends are to be believed? Both cannot be true. I would argue that the data I present here (all from IGBST databases and Annual Reports) are straight-forward and hard to refute, whereas the death rates estimated by the IGBST from fates of radio-collared bears derive from assumption-laden, complex, and refutable models. There is good reason to believe unambiguous trends based on straight-forward data, especially when differences between derived indicators are so dramatically different from estimates of death rates for radio-marked bears.

The implications of this cursory analysis are potentially consequential given the extent to which IGBST estimates of annual death rates play such a pivotal role in monitoring population size and trend as well as deriving management benchmarks (Section 4.3). If estimated death rates reported by the IGBST are both flawed and biased, then there is little basis for giving credence to demographic results produced by the IGBST for research for management purposes. Perhaps more to the point, given the monopolistic hold the IGSBT maintains on all GYE grizzly bear data (Section 6.6), the burden is upon Study Team researchers to unequivocally demonstrate how the results I present here can be reconciled with their estimates of death rates.

4.6. Suspect Estimates of Population Growth

Arguments detailed in Sections 4.1-4.5 along with the critique by Doak & Cutler (2014a, 2014b) provide cause for skepticism about IGBST estimates of population trend. Doak & Cutler (2014a, 2014b) showed that estimates of population growth rate had likely been over-estimated by the IGBST using both the Chao2-based method and more complex calculations based on death and birth rates estimated from known fates of radio-marked grizzly bears. More specifically, Doak & Cutler found that Schwartz et al. (2006) and IGBST estimations thereafter had not accounted for effects of senescence on both birth and death rates of female grizzly bears, and that when accounted for, female survival and population growth rates (as estimated by Harris et al. 2006) dropped significantly.

Van Manen et al. (2014) claimed to have rebutted the original Doak & Culer (2014a) analysis. Aptly enough, the response of Doak & Cutler (2014b) to this presumed rebuttal was entitled "Doth Protest too Much." More specifically, Doak & Cutler (2014b) found that the Van Manen et al. (2014) response was larger confirmatory of their original critiques. To quote Doak & Cutler: "[the Van Manen et al.] results show that incorporating senescence sharply reduces previously estimated population growth from 1983 to 2001"; and "[the Van Manen et al.] study shows that there is so much uncertainty in population estimates that inferences about population trends are extremely weak." In other words, the collective results presented not only by Doak & Cutler (2014a, 2014b), but also by Van Manen et al. (2014), show that population growth rate from 1983-2001 was over-estimated by the IGBST, and that the methods used by the IGBST for monitoring the Yellowstone grizzly bear population are at best tenuous.

Insofar as methods for monitoring and management are concerned, the evidence described here suggests that mortality benchmarks for the GYE grizzly bear population are too liberal by virtue of being linked to inflated estimates of population growth—which means that purported management objectives will not be achieved by employing these rates. More specifically, a 7.6% and 15% mortality rate for females and males, respectively (cf., Interagency Grizzly Bear Study Team 2012, Greater Yellowstone Subcommittee 2016), will likely *not* maintain a stable population, but rather yield unintended declines. Given all the other problems with methods for monitoring mortality rates described in Sections 4.4-4.6, there is a good chance that these sorts of declines will not be detected or addressed in a timely manner, and certainly not in a way that would allow a meaningful response, further delayed by prospective lags between environmental degradation and demographic responses (see also Doak [2015] and Van Manen et al. [2023b]).

Implications

Given these considerations as well as current monopolistic research arrangements, the IGBST needs to, first, substantively address rather than reflexively deny potential unreliability of its current indicators of mortality and population growth rates and, second, recommend that benchmark mortality rates used for monitoring and management be revised downward by several percentage points to acknowledge and account for the prospectively liberal bias of rates currently in use—for example, from 7.6% down to 5.6% for females at a population size of ≤674.

4.7. A Problematic Density Measure and "Density-Dependence" Concept

The IGBST claims in virtually all its publication since 2005 that changes in demography of Yellowstone's grizzly bear population have been driven largely – if not solely – by changes in population density, entraining "density-dependent effects." This claim contributes to dismissal of effects attributable to changes in abundance of whitebark pine or any other food. The primary basis for often-repeated claims about the dominance of density effects are Van Manen et al. (2016) as well as Schwartz et al. (2006a), who earlier reported detecting an effect of conspecific density on bear survival rates. According to this thesis, declines in survival rates of cubs and yearlings are driven by increasing bear densities. These declining survival rates translate into an effect that governs growth of the grizzly bear population. As I describe here, this claim suffers from invoking a naïve conception of density-dependence and from critical—even fatal—failings of the analyses reported in Schwartz et al. (2006a) and Van Manen et al. (2016; see Sections 3.2-3.12). Claims that density has increased since around or even before 2000 are additionally contradicted by some straightforward evidence.

Issues

Population-wide densities of grizzly bears did not appreciably change in the Yellowstone ecosystem during 1990-2022, contrary to claims by Van Manen et al. (2016) and Corradini et al. (2023). Figure 26 summarizes relevant data from Van Manen (2023a), including the latest retrospective estimates of population size based on the IPM (see Section 4.1; Figure 26a, in gray) and increases in population distribution (in brown), with both estimates confined to the area designated for monitoring the GYE bear population (i.e., Demographic Monitoring Area [DMA]). As illustrated in Figure 26b, simple math (population size divided by distribution area) shows that an increasing number of individuals was spread out over a proportionally comparable increase in distribution within the DMA, with a resulting stasis in population-wide bear density that was within the bounds of uncertainty. If anything, population-wide bear densities peaked slightly during 2002-2007 and subsequently declined concurrent with terminal losses of whitebark pine (Section 3.2). Taking this pattern at face value, minimal annual variation in density debars credible statements about putative increases in density within the GYE DMA, and furthermore does not support claims that increasing bear densities have been driving virtually all changes in demography of the GYE grizzly bear population during the past 20 years (e.g., Schwartz et al. 2006a, Van Manen et al. 2016).

Problems with the methods employed by Schwartz et al. (2006a), Bjornlie et al. (2014a) and Van Manen et al. (2016) warrant close examination. In the case of Schwartz et al. (2006a), the authors used a time-specific population-wide index of "density" derived solely from annual counts of females with COY. As I describe in Section 4.2, this index of population size almost perfectly mirrors changes in efforts by researchers and managers to find bears along with changes in the intrinsic sightability of the bears they were seeking, leaving the correlation between annual counts of females with COY and actual population size unknown and therefore suspect. The index used by Schwartz et al. (2006a) moreover does not account for steady increases in the distribution of the population (e.g., Schwartz et al. 2006b, Bjornlie et al. 2014b), which introduces further unaccounted-for bias. Compounding these intrinsic problems is the fact that Schwartz et al. (2006a), like Van Manen et al. (2016), did not control for a number of major temporal changes in abundance of key foods that were correlated with their purported index of bear density (e.g., cutthroat trout, elk, bison, and army cutworm moths; see Sections 3.2-3.11), which debars any isolation of a density effect and introduces major statistical problems related to covariance of explanatory variables.

In contrast to Schwartz et al. (2006a), Van Manen et al. (2016), Bjornlie et al. (2014a), and Corradini et al. (2023) used a purported index of population density that varied not only by year, but also by a grid of cells sized to approximate the extent of female home ranges. Because of this spatial and temporal resolution, the Bjornlie/Van Manen index gives the reassuring impression of high-resolution precision to those looking at their results with an uncritical eye. Briefly, the density index used by these authors is directly based on the number of bears trapped and radio-marked in a given area during a given year, weighted by estimated survival rates to "extrude" [sic] these bears forward and backward through time, after which the "extruded" bears are stacked and added to come up with a purported area-specific index of density.

However, this index has no known relationship to the parameter it purports to represent and has not been validated by any independent direct measure of population density, notably based on non-intrusive sampling of grizzly bear genotypes systematically collected through hair-snaring (e.g., Boulanger et al. 2018, Lamb et al. 2019). The index is, moreover, contaminated by bias introduced by increasing efforts to capture bears each year, resulting in an increasing percentage of the estimated total grizzly bear population being captured and radio-collared over time (Figure 24; data from Van

Manen et al. 2023a). Van Manen et al. (2016) and Bjornlie et al. (2014a) claim to have validated this index *prima facie* biased by trapping effort through correlations with two additional metrics that also have no known relationship to density and thus provide no credible substantiation.

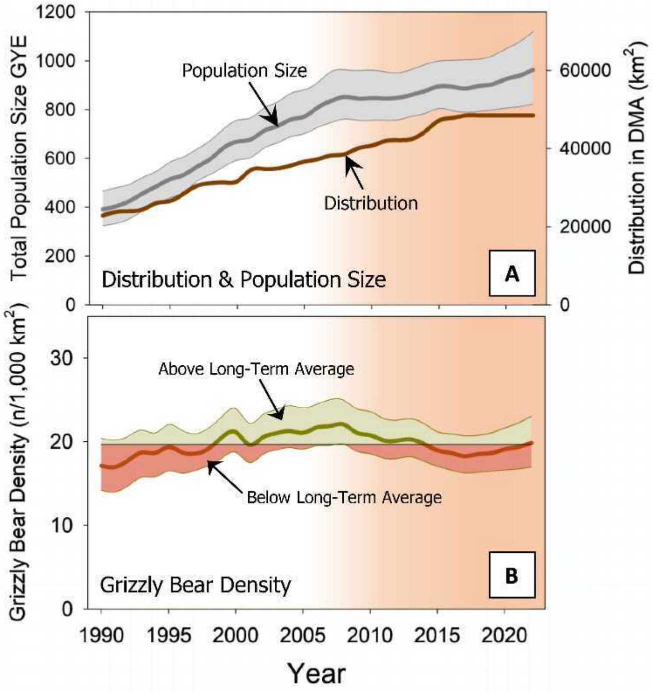


Figure 26. The figures at left illustrate the extent to which density of grizzly bears in the Greater Yellowstone Ecosystem (GYE) Demographic Monitoring Area (DMA) *has not* increased during the last 30 years. Trend lines in (A) show estimated total distribution (brown line) and population size (gray line and uncertainty interval), both within the DMA. The trend line and uncertainty interval in (B) shows grizzly bear density within the DMA calculated as population size divided by aerial distribution. Areas shaded green show periods when either the main trend or uncertainty interval were above the 30-year average; areas shaded red show periods when either were below the long-term average. Areas shaded orange denote the terminal decline of whitebark pine. Densities were above the long-term average only during circa 2006-2008, otherwise there has been no trend. All data are from Van Manen et al. (2023).

This failing is compounded by the fact that neither Bjornlie et al. (2014a) nor Van Manen et al. (2016) accounted for numerous other major changes in Yellowstone's grizzly bear habitat—also correlated in both time and space with their purported density index (Sections 3.5-3.10). As a result, these authors have no defensible basis for isolating an effect of density, even assuming the index they use is valid.

Finally, the IGBST deploys a simplistic and often misleading conception of "density-dependence" that offers little insight into population dynamics. As one well-respected population ecologist put it: "Density is not a mechanism" (Charles Krebs [1995, 2002]). What he meant by this is that birth and death rates of animals are driven by levels of predation, disease, and intra- and interspecific competition, as well as by the quality and abundance of foods – not directly by density. If population density has any effect at all, it is through affecting factors such as conspecific predation and competition. Invoking density *per se* as an explanation for any demographic phenomenon is equivalent to assuming that animals are ping-pong balls spatially moving at random, with each ball equal in its effects on the others.

To the extent that density has any effect, it necessarily interacts with carrying capacity (but see Section 4.8) and changes in the microscale and mesoscale distributions of individual bears driven by availability of food and associated diets. In other words, at the same exact density, the frequency and lethality of interactions among bears can vary substantially depending on total abundance of foods and the extent to which these foods are concentrated in time and space—as with differences in British Columbia between coastal areas with salmon spawning runs and interior areas with abundant but widely-distributed berries. The upshot of this is that a simple shift in diet among Yellowstone's female grizzly bears from pine seeds to terrestrial meat could substantially modify levels of interactions with other bears – especially males – without any change in bear densities.

Parenthetically, as I point out in Sections 3.8, 3.11, and 3.12, changes in cub and yearling survival rates can be plausibly explained by changes in foraging behaviors of female bears, without resorting to dubious and poorly conceptualized claims regarding population density. Any decline in survival of cubs and yearlings has more likely been a consequence of adult female grizzlies eating more meat and incurring substantially more hazards for their dependent offspring (Mattson et al. 1992b, Mattson 2000, Ben-David et al. 2004, Steyaert et al. 2013, Penteriani et al. 2020)—hazards primarily, but not solely, related to increasing odds of predation by other adult bears and perhaps wolves.

Implications

Given all the problems with the Van Manen/Bjornlie population density index, the burden rests on IGBST researchers to reconcile contradictions, on the one hand, between the best available science regarding population size and distribution and, on the other, use of an index that is *prima facie* unproven in analyses that fail to account for most of what has likely affected grizzly bear birth and death rates (see Sections 3.1-3.12). Any valid inference about effects of conspecific densities on demography depends, moreover, on deploying a credible conceptualization of “density-dependence”.

4.8. A Problematic Carrying Capacity Concept

Carrying capacity (*K*) is a notoriously ambiguous concept encompassing interactions among conspecifics, interactions of species with the environment, and even interactions with potential predators (e.g., Clark et al. 1975, Picton et al. 1986, Dhondt 1988, Del Monte-Luna et al. 2004). Given the scope and complexity of these dynamics, it’s not surprising that *K* has been difficult to apply in practice, or, when applied, done with considerable naiveté (Tansley 1935, Chapman & Byron 2018). Ecologists have long recognized that *K* can theoretically vary substantially – even catastrophically – in time and space because of changes in environmental productivity or changes in intra- and interspecific interactions, in turn affecting every aspect of demography.

In theory, numerous dynamic interactions limit the number of conspecifics that can occupy a given area at a given time. However, in practice, *K* is virtually impossible to measure anywhere but in a petri dish. Ecologists have consequently resorted to various changes in demography to signal whether a wildlife population might be approaching carrying capacity, including declines in female fecundity, decreased neonate survival, delayed reproductivity maturity, increased scramble competition, greater intraspecific strife and predation, and stalled population growth. However, even at best, these indices are beset by lagged responses (Sections 4.2 and 4.5, and below) as well as potentially complex or otherwise unknown relations to the phenomenon of interest, i.e., carrying capacity. Change in any one of these demographic measures could be attributable to factors such as predation, changing diets, and redistribution of foods, all while independent of or lagging well behind fundamental changes in the environment.

Issues

Picton et al. (1986) recognized over 30 years ago that carrying capacity for grizzly bears in the Greater Yellowstone Ecosystem was dynamic and beset with measurement problems. However, the dynamic, complex, and lagged nature of relations between bear demography, environmental productivity, conspecifics, and human predators seems to have eluded researchers and managers in the GYE, who routinely invoke a naïve conception of carrying capacity (along with "density-dependence"; see Section 4.7) to explain virtually every aspect of bear demography. This naivete is evident not only in likening *K* to a "sardine can" able to support only a fixed number of bears (e.g., "we are packing more sardines in the sardine can": Frank Van Manen, May 5, 2015) but also construing stabilization of population growth as direct evidence for limits imposed by a fixed ceiling on habitat productivity (Van Manen et al. 2016, Corradini et al. 2023).

Moreover, when critically scrutinized, the available credible evidence suggests that dietary shifts alone – rather than any approach to a fungible *K* – drove reductions in cub and yearling survival as well as increases in adult mortality that together plausibly caused decreases in population density and growth rate (Sections 3.8, 3.10, 3.11 and 4.5). Likewise, dietary shifts rather than any putative approach to *K* likely allowed bears to maintain body fat concurrent with decreases in lean body mass (Section 3.5 and 3.7).

More specifically, there is clear evidence that loss of whitebark pine resulted in greater consumption of army cutworm moths in Wyoming's Absaroka Mountains (Section 3.7) along with increased exploitation of anthropogenic meat outside of Yellowstone National Park (3.9), especially on livestock allotments near the ecosystem periphery (Section 3.10). Increased consumption of anthropogenic meat unambiguously drove a near 4-fold increase in grizzly bear mortality largely between 2006 and 2022 (Figures 18a and 18b), constituting a >2.5-fold increase in known and probable mortality pro-rated to total population size (i.e., mortality rate), which correlates with when population size plateaued (Figure 18c). During the same time, natural mortality, a putative effect of conspecific densities when near *K*, declined as a proportional cause (Figure 18b). To the extent that cub and yearling mortality increased during recent years (Van Manen et al. 2016, 2023), these increases correlate quite strongly with increased risk of conspecific predation that predictably arose from increased exploitation of meat by mothers of dependent young bears beginning around 1998-2000.

Relations between carrying capacity and grizzly bear demography are further complicated by temporal and spatial lags in effects of *K* on vital rates. Over 20 years ago, Doak (1995) explicitly related the concept of lag effects to dynamics of the Yellowstone grizzly bear population. More recently, data from McLellan (2015) plausibly demonstrated lagged effects of a grizzly bear population in the North Fork of the Flathead River drainage of British Columbia and Montana in response to a dearth of huckleberries (*Vaccinium membranaceum*). Growth rate for this population is shown in Figure 27a as a 6-year moving average of annual change in population size (i.e., ʎ = lambda). Green dots represent population density and gray squares represent population growth rate. A key take-away from the Flathead data is that growth rate began to decline almost as soon as huckleberry production dropped in 1996, but didn't turn negative until roughly 5-years later. More importantly, population size, as such, didn't begin a substantial long-term decline until 10-11 years after the berry famine began.

Lag effects are thus relevant to judging the status of Yellowstone's grizzly bear population, not only relative to major changes in abundance of high-quality foods during the last 20+ years, but also any related changes in carrying capacity. Figure 27b shows trends for Yellowstone's grizzly bear population rendered in terms comparable to those of the North Fork bear population. The darker green line shows estimates of population density based on concurrent estimates of population distribution and size using the IPM method (from Van Manen et al. 2023a), which is less biased than the Chao2 method used exclusively by the IGBST between 2007 and 2020 (Section 4.1, Figure 21). The dark gray squares represent a 6-year running average of population growth rate derived from sequential population estimates.

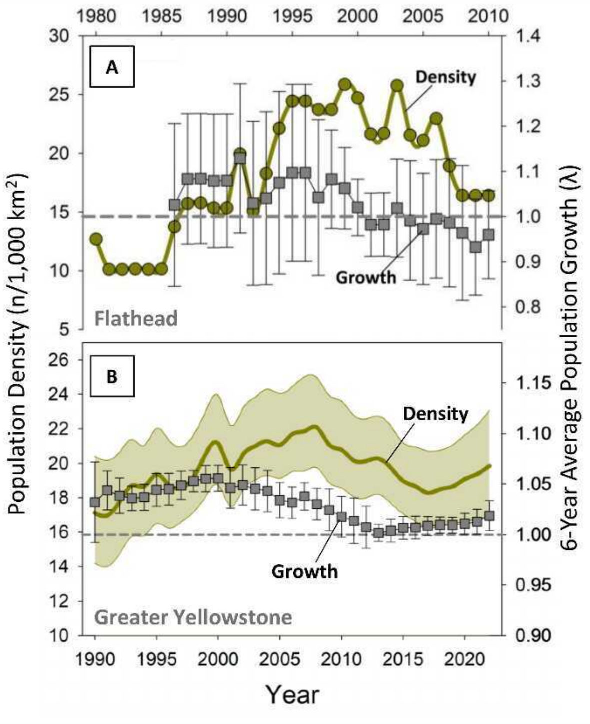


Figure 27. These graphics show trend data for grizzly bear populations in (A) the North Fork of the Flathead for 1980-2010 (data from McLellan 2015), and (B) the Yellowstone grizzly bear population for 1990-2022. Dark green dots and lines represent best estimates of density, and dark gray squares derivative estimates of population growth rate (ʎ; as a 6-yr running average). Uncertainty bars around estimates of growth rate represent standard deviations. Trends from both populations show growth rates declining roughly six-seven years before significant stasis or even decline in population density is evident and five-years after major declines in a key food resource began – huckleberries in the North Fork and whitebark pine seeds in Yellowstone.

A key take-away from Figure (27b) is that average population growth rate began to decline around 2000, concurrent with declines in whitebark, and roughly seven years before population density began to drop – all at a time when population size appeared to be more-or-less stable, if not slightly increasing.

Implications

The IGBST narrative holding that density-dependent effects arising from a population approaching K have driven stalled population growth, an expanding distribution, and increased cub and yearling mortality of grizzly bears in the GYE during the past 20-30 years *is not* supported by the available evidence. This narrative is, moreover, at variance with research showing that bears are *more,* rather than *less*, likely to disperse and go farther when local densities of conspecifics are below *K* (i.e., inverse or negative density dependence; Støen et al. [2006], Zedrosser et al. [2007], Roy et al. [2012], Moore et al. [2014]).

As a bottom line, random encounters among bears driven by implausible increases in population density are unlikely to have driven changes in demography and distribution of the GYE grizzly bear population during recent decades (Figure 22b), especially when conceptualizations of carrying capacity are deficient. Any invocation of carrying capacity to explain trends is further compromised by the near impossibility of measuring this feature of the environment; guaranteed lags between changes in *K* and bear vital rates; and complex as well as uncertain relations between carrying capacity and demographic measures commonly used to indicate change in *K* (as per Schwartz et al. [2006a] and Van Manen et al. [2016, 2023a]).

5. Issues Related to Genetic Health of GYE Grizzly Bears

Genetic health of the Greater Yellowstone Ecosystem (GYE) grizzly bear population featured prominently in 2017-2020 litigation contesting removal of ESA protections by the U.S. Fish & Wildlife Service (USFWS; Section 2). In the rule removing protections, the USFWS argued that the GYE grizzly bear population had not experienced any worrisome loss of genetic diversity since being isolated and that current diversity was sufficient to maintain genetic viability, with the proviso that managers could, at their discretion, translocate as many as two bears per decade to the ecosystem to augment genetic diversity. The USFWS further argued that size of the population at the time (750+ bears) substantially exceeded the 500 bears needed for long term viability (U.S. Fish & Wildlife Service 2017).

These claims were contested in court on the basis they misrepresented or misinterpreted the best available science; that documented loss of diversity was indeed problematic; and that 500 bears were not sufficient to ensure long-term genetic health. These arguments prevailed over those of the USFWS in court at both the federal district and federal appellate levels (Section 2; U.S. District Court for the District of Montana, Missoula Division, 2018, U.S. Court of Appeals for the Ninth Circuit 2020).

The following two sections address flaws in arguments made by the USFWS in its 2017 delisting rule as well as dubious aspects of IGBST science invoked by the Service to justify several key claims (i.e., Kamath et al. 2015). The USFS not only misrepresented or misunderstood the best available science regarding sizes of populations needed to ensure long-term genetic health and adaptation (Section 5.1), but also the literal and statistical significance of genetic losses since isolation of the GYE grizzly bear population in the late 1800s-early 1900s (Section 5.2). The IGBST publication relied upon by the USFWS to bolster several key claims (Kamath et al. 2015) was, in common with other IGBST research, furthermore beset with suspect results and conclusions (Section 5.2).

5.1. Population Viability

There are several reasons to doubt claims that a population of 500 bears (i.e., censused population or N_c) is sufficient in size to ensure long-term genetic viability. As a preface, any judgements regarding whether a given censused population is adequate for maintaining genetic health and evolutionary potential depend on the standards adopted for defining acceptable risk of extirpation or decline. Likelihood of extirpation is most often used as the standard for judging centuries-long effects of genetic processes, whereas “quasi-extinction” thresholds are often adopted for assessing decades-long effects of variable environmental and demographic processes. Quasi-extinction benchmarks are used not only to mitigate the uncertain effects of long-term projections, but also as means of flagging when populations have declined to critical levels warranting augmented conservation efforts (Ginzberg et al. 1982, Doak et al. 2015, McGowan et al. 2017, Carroll et al. 2019). Even so, adopting one or the other of these standards depends on whether the greater focus is on genetic or demographic outcomes, with potentially orders-of-magnitude effects on estimated risk.

Other determinations with comparable effects on results of population viability analyses include adopted time frames and acceptable levels of risk, as well as the extent to which genetic, demographic, and environmental processes are included in models for projecting population size and extinction. Again, orders-of-magnitude differences in results of risk analyses can arise simply from adopting <1% risk of an adverse outcome within the span of 40 animal generations as a standard, rather than a less cautious <10% risk of adverse outcomes over a period of 100 years. Although acceptable timeframes and risks are partly subjective, a consensus has emerged that 40 generations and a 1% chance of an adverse outcome is appropriate for judging the effects of long-term genetic processes such as drift, selection, mutation, inbreeding, outbreeding, and more.

That having been said, differences in life span and life histories militate against adopting a single time frame for all animal species. Although one year might be appropriate for judging the effects of genetic processes on a species such as *Drosophia melanogaster*, with a generation length of 10 *days*, one year is an absurdly short time span for a similar analysis of species such as grizzly bears, with generation lengths of 10-11 *years* (Harris & Allendorf 1989, Tallmon et al. 2010, Kamath et al. 2015). Although 100 years was more-or-less arbitrarily adopted by Shaffer (1981, 1983) for his ground-breaking analysis of population viability for grizzly bears, the current scientific consensus holds that 40 generations is the more appropriate time span for reckoning risks to genetic viability (Reed et al. 2003, Traill et al, 2007, O'Grady et al. 2008). In the case of grizzly bears this equates to roughly 400 years (e.g., Shaffer & Samson 1985, Shafer 2022).

Effective population size (N_e) provides a link between numbers of animals in a population at any given point in time (*census* population, N_c) and levels of acceptable risk and time frames adopted for projecting genetic health. The technical definition of N_e is remarkably abstruse, but, in general terms, N_e represents the number of individuals contributing genetically to the next generation. N_e can be a proxy for numbers of animals breeding during a single season (N_b), albeit typically representing a higher fraction of the total population (Charlesworth 2009, Waples et al. 2014). For most species the ratio of N_e to N_c is in the range of 0.1 to 0.25, with a harmonic mean of 0.13 (e.g., Lande 1995, Frankham 2010, Palstra & Fraser 2012, Frankham et al. 2014). This ratio of 1/10th to 1/4th of total population size captures most estimates made for populations of brown and grizzly bears (0.06-0.40; harmonic mean = 0.13; e.g., Harris & Allendorf [1989], Paetkau et al. [1998], Miller & Waits [2003], Craighead et al. [2006], Tallmon et al. [2010], Méndez et al. [2014], Barrueto et al. [2023]).

Estimating sizes of grizzly bear populations needed to safeguard (e.g., <1% risk) against extinction or even quasi-extinction for periods as long as 400 years is fraught. Credible forecasting using methods such as population viability analysis (PVA) not only needs to account for genetic processes, but also demographic and environmental variation. The last typically entails introducing factors such as characteristic environmental variability, occasional catastrophes, and even systematic change in carrying capacity (*K*, see Section 4.8). Even though these kinds of modeling exercises can never predict the future, they do provide important information regarding the nature and relative importance of various risks, as well as a range of population sizes allowing for precautionary management of populations (e.g., Wolf et al. 2015, Lawson et al. 2021).

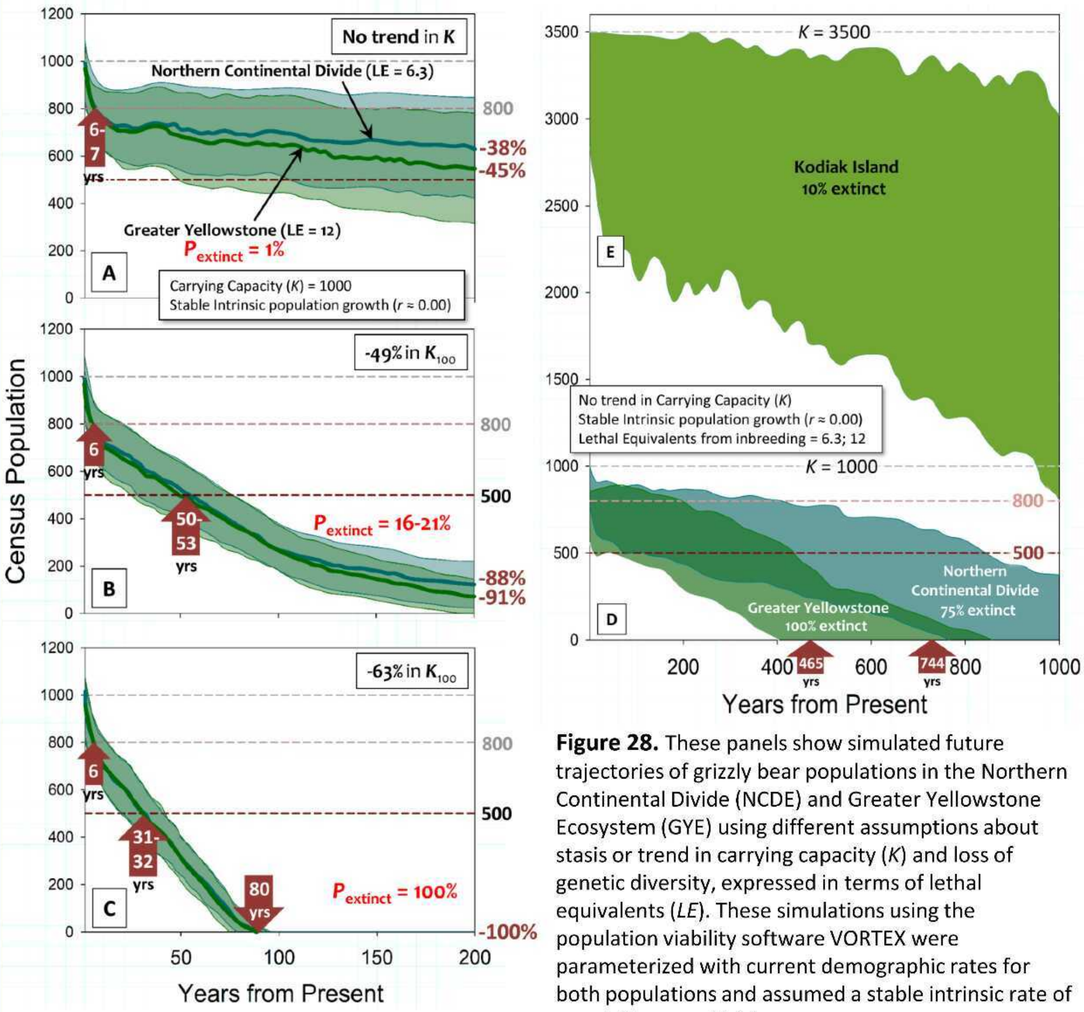


Figure 28. These panels show simulated future trajectories of grizzly bear populations in the Northern Continental Divide (NCDE) and Greater Yellowstone Ecosystem (GYE) using different assumptions about stasis or trend in carrying capacity (*K*) and loss of genetic diversity, expressed in terms of lethal equivalents (*LE*). These simulations using the population viability software VORTEX were parameterized with current demographic rates for both populations and assumed a stable intrinsic rate of population growth (*r*).

The results in (A) show projected future tends for the next 200 years (20 bear generations) assuming no decline in *K*, density-dependent population regulation, and environmental variation calibrated to historical ranges in the GYE. Median population declines for the NCDE and GYE ranged from 38-45%, with 1% of simulations resulting in extirpation of the GYE population. Results in (B) and (C) assumed progressive declines in *K* totaling 49% in (B) and 63% in (C) by the end of the 200-year projection. Roughly 16-21% of simulations resulted in extirpation of the NCDE and GYE populations in (B) and 100% by 80 years in (C), with corresponding median population declines of *c*. 90% and 100%. Median population sizes dropped below 500 within 50-53 years in (B) and 31-32 years in (C). Simulated trends in (D) are based on the same assumptions and parameters as in (A) but projected out 1000 years (100 bear generations). Seventy-five percent of these simulations resulted in extirpation of the NCDE population and 100% in extirpation of the GYE population, with median times to extirpation of 744 (70+ generations) and 465 years (40+ bear generations), respectively. As a point of contrast, results in (E) show projections for the sizable but isolated population of brown bears on Kodiak Island (current N ≈ 3,400). Much of these results are driven by environmental variation, feedback from an approach to *K*, and slow but steady loss of genetic diversity.

In addition to insights provided by PVAs, the long-standing, much debated, but still valid 50/500 rule of thumb continues to provide a link between N_e and N_c (e.g, Franklin 1980, Lande 1988, 1995, Spielman et al. 2004, Jamieson & Allendorf 2012). In this case, “50” refers to the size of N_e needed to guard against inbreeding depression (a shorter-term consideration), whereas “500” is considered enough to balance genetic losses due to genetic drift and genetic increases due to mutation (a much longer-term concern). When used in combination with mean ratios of N_e to N_c, these rules of thumb roughly translate into censused populations of approximately 380 and 3,850 animals, respectively. This range is remarkably consilient with estimates of minimum population sizes (MVPs) derived from PVAs or recommended by geneticists as being needed to ensure viability of species such as grizzly bears. These reported or recommended MVPs average around 3,700 bears, but with a range from 1,850 to 10,000 (Lande 1995, Lynch & Lande 1998, Miller & Waits 2003, Reed et al. 2003, Brook et al. 2006, Sinclair et al. 2006, Traill et al. 2007, Puranen-Li et al. 2014).

Issues

There are several straightforward problems with claims by the USFWS that a population of 500 bears is adequate to sustain long-term genetic health. First is the marked discrepancy between standards tacitly employed by the USFWS to judge risk and the current consensus among geneticists regarding not only appropriate standards, but also benchmarks for minimum viable populations. Even under ideal conditions, a population size of 500 would only guard against shorter-term risks of inbreeding depression and provide little assurance of long-term (e.g., 400-year) evolutionary and adaptive potential. This number is, moreover, only 1/7th of that recommended for MVPs of large mammals. The closest explicit approximation of an MVP for grizzly bears comes from Traill et al. (2006), who estimated that around 3,800 animals were needed, which is also seven times greater than 500. Importantly, even the two largest grizzly bear populations in the contiguous United States – in the Greater Yellowstone (GYE) and Northern Continental Divide (NCDE) Ecosystems – are estimated to be only around 1,000 animals each – 1/3rd to 1/4th what is needed (cf., Costello et al. 2022, Van Manen et al. 2023a).

These shortfalls of current grizzly bear population sizes and standards used by the USFWS for judging risk to genetic health are further emphasized by illustrative analyses of population viability using a well-established software package called VORTEX (Lacy & Pollak 2021, Lacy et al. 2021). This software can be used to project interacting dynamics that account for environmental, demographic, and genetic variation, parameterized to simulate a specific species or population. Outcomes are represented in various ways, including probabilities of extinction or quasi-extinction, median times to both, and changes in future population sizes and composition. In this case, I parameterized the model using vital rates from the GYE (Schwartz et al. 2006a, Van Manen et al. 2016) and NCDE (Costello et al. 2016) grizzly bear populations and input parameters for estimated environmental variation using historical data from the GYE. I represented loss of genetic diversity as plausible rates of accumulating lethal equivalents (LE) derived from applicable literature (Allendorf & Ryman 2002, Jamieson & Allendorf 2012, Frankham et al. 2014, Lacy & Pollak 2021). I furthermore explored the effects of systematic declines in carrying capacity, as might be expected with potentially catastrophic climate warming (cf., World Meteorological Association 2023).

Figure 28 shows the results of these grizzly bear-centric simulations projected 200 (A-C) and 400 years (D) into the future. Vital rates in all simulations were set to deterministically represent a population that was stable one year to the next (i.e., $\lambda = 1.0$, $r = 0.0$). Even so, population sizes declined in all simulations. In scenarios with a fixed carrying capacity of 1,000 bears (A), median population declines amounted to around 40% at the end of 200 years, largely because of environmental variation and losses of genetic diversity. Losses were even more dramatic when systematic reductions in K were introduced.

A slight downward trend (B) yielded not only a 50% reduction in *K* by 200 years, but also an approximate 90% chance of extirpation for both the NCDE and GYE bear populations. As important, both populations had dropped below around 500 bears by around 50 years. A moderate downward trend in *K* (C) resulted in 100% probability of extinction by around 80 years, despite only a 63% total drop in carrying capacity after two centuries.

Figure 28d emphasizes the toll that losses of genetic diversity and endemic variation can take on populations of even 1,000 bears in environments with a fixed carrying capacity when simulations are projected more than 40 generations (i.e., 400-1,000 years). Notably, the GYE population went extinct in 100% of simulations, with most occurring between 450 and 750 years into the future. The NCDE population went extinct in 75% of the millennium-long projections. The simulations shown in (E) represent projections for the Kodiak Island brown bear population, which is often represented as being immune to the effects of genetic impoverishment and environmental variation. Even this population of an estimated 3,400 bears was projected to go extinct during 10% of the 1000-year simulations, with most projections also showing progressive population declines.

Implications

None of these projections are meant to be literal forecasts or predictions. Nonetheless, they constitute a compelling heuristic showing the prospective vulnerability of bear populations as large as even 1,000 animals, especially when there are declines of any magnitude in carrying capacity. These simulations also emphasize not only the inadequacy of a 500-bear – or even 800-bear – recovery standard, but also the hubris of adopting as well as arguing for such a standard in the first place. This conclusion is reinforced by the fact that these sorts of standards are substantially deviant from the current scientific consensus holding that freely interbreeding grizzly bear populations should number 3,000-4,000 animals in size to ensure long-term viability.

5.2. Current Genetic Health

GYE grizzly bears have not only been isolated from grizzly bears elsewhere for at least 120 years (Merriam 1922) but are also genetically impoverished compared to bears in nearby populations. Most prominently, trait-specific alleles are 7-25% less diverse among GYE grizzly bears compared to bears in the NCDE population (i.e., Yellowstone grizzlies are less heterozygous; Miller & Waits [2003], Haroldson et al. [2010], Mikle et al. [2016]). This comparative impoverishment predictably threatens long-term genetic health of the GYE bear population (Allendorf et al. 2006, Allendorf et al. 2019, Shafer 2022), consistent with a recent inbreeding rate estimated to be 2.3% (Miller & Waits 2003). The most pronounced losses of genetic diversity, including allelic richness (Allendorf & Leary 1986, Greenbaum et al. 2014), likely occurred during a population bottleneck that lasted from ~1900 to 1980 when $N_e \approx$ 75-90 and $N_c \approx$ 300-350[2] (from estimates in Miller & Waits [2003], including $N_e/N_c \approx 0.27$).

Issues

There is little doubt about the current genetic isolation, diminished heterozygosity, and inbreeding of GYE grizzly bears – all associated with an historical population bottleneck. However, there is considerable uncertainty about recent size and trend of effective population size (N_e), despite consensus that N_e likely ranged between 50 and 100 bears for roughly 100 years – from the late 1800s through the 1980s (Miller & Waits 2003, Kamath et al. 2015). Uncertainty about more recent trends in size of N_e, N_b (i.e., number of breeders), and N_e/N_c during the 1990s-2000s arises primarily from the *prima facie* implausibility of estimates produced by Kamath et al. (2015), which in turn underpin most claims made by the USFWS regarding genetic health of the GYE population. Figures 29 and 30 illustrate the problem.

Figure 29 shows trend in census (N_c) and effective (N_e) populations sizes for the GYE grizzly bear population for 1982-2007 – in Figure 29a as raw numbers and in 29b as a ratio (N_e/N_c). Estimates of N_c are from Van Manen et al. (2023a). Estimates of N_e are from Kamath et al. (2015). The colored areas bounding trend lines are "credible intervals". The horizontal lines at the bottom of Figure 29b are the average and standard deviation of N_e/N_c values from numerous other studies of mammals, including bears (see Section 5.1).

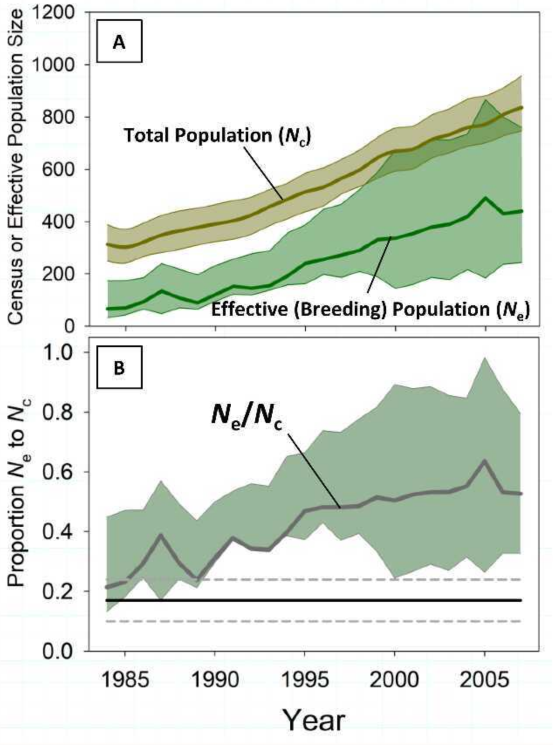


Figure 29. The trend graphs at left summarize estimates of effective population size (N_e) and census (or total) population size (N_c) for the GYE grizzly bear population, 1984-2007. Estimates of N_e are from Kamath et al. (2015); estimates of N_c are from Van Manen et al. (2023a). The technical definition of N_e is remarkably abstruse, although in crude terms N_e approximates the number of individuals contributing genetically to a population and is typically in the range of 13-24% of total population size (N_c) at any given point in time. The trend lines in (A) show both values along with credible (or uncertainty) intervals. Remarkably, the upper range of a ballooning uncertainty interval for N_e converges on and even overlaps with total population size during 1999-2007. The proportion of effective to total population size is shown in (B), again with uncertainty intervals. The horizontal black and dashed lines show the mean and standard deviation of values for this ratio from numerous authoritative publications. The ratio calculated using estimates of N_e from Kamath et al. (2015) averages an unprecedented and implausible 0.54 (± 0.28-0.88) during 2000-2007 and an equally implausible 0.41 (± 0.37-0.64) during 1991-1999.

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[2] This population estimate belies frequent published claims that the GYE grizzly bear population dropped below 200-275 animals during the 1970s.

Estimates of N_e produced by Kamath et al. (2015) generally tracked N_c, but at an accelerating rate. Annual growth rate of N_e during 1984-2000 was ~10%, roughly twice the 5% growth rate for N_c during this same period. On the face of it, this disparity is implausible. How could numbers of bears contributing genetically to the population increase *twice* as fast as total population size for more than 15 years? There is no defensible explanation. Even more notably, the upper bound of uncertainty for N_e overlapped N_c from 1995 through 2007, reflected in average values of N_e/N_c ranging between 0.4 and 0.6 for the same period (Figure 29b). This ratio far exceeds values from other mammal studies (see Section 5.1) – including an estimate of 0.25-0.3 by Miller & Wait (2003) for the same population.

Moreover, the fact that values of N_e/N_c derived from estimates produced by Kamath et al. (2015) doubled between 1982-1994 and 1995-2007 suggests that critical methodological assumptions were violated. As Kamath et al. (2015) acknowledge, methods for estimating N_e are complex, fraught with pitfalls, and prone to violation of critical assumptions (Wang 2005, Luikhart et al. 2010, Hare et al. 2011, Waples & England 2011, Palstra & Fraser 2012, Waples et al. 2014, Wang 2016). This is especially the case for long-lived non-monogamous species such as grizzly bears that have overlapping generations, produce multiple litters during a lifetime, and exhibit significant spatial population structure (cf., Steyaert et al. 2012).

This constellation of confounding factors is manifest in problematic results from Kamath et al. (2015), suggesting that these authors either used compromised data or violated critical assumptions – or both. More specifically, contrary to claims made by Kamath et al. (2015), interannual instability of estimates for N_c/N_e signals not only that assumptions were violated, but also that the ratio produced by these authors was not suitable for reconstructing trend or estimating current genetic health (Waples 2010, Schregel et al. 2012, Ruzzante et al. 2016, Beichman et al. 2018). Of relevance, authors of the only other bear study to produce estimates of the N_e/N_c ratio as high as those of Kamath et al. (2015) were skeptical of their results, although they deemed them sufficient for reconstructing *trend* in N_e (rather than absolute value) only because values of N_e/N_c were, in contrast to those of Kamath et al. (2015), stable from one year to the next (Schregel et al. 2012).

Approximations of N_e and N_b derived directly from demographic data for the GYE grizzly bear population cast further doubt on estimates of both made by Kamath et al. (2015). The assumption underlying such a comparison is that N_e is demographically approximated by total number of breeding adults, summed over multiple breeding cycles, accounting for the small percentage of adult males that fail to successfully breed at all. Likewise, N_b is approximated by the number of females breeding each year (i.e., roughly one-third of the total) added to numbers of successfully breeding males, which are likely to be less than numbers of breeding females. Parenthetically, breeding success of males is highly uncertain given scant information (but around 70%; e.g., Craighead et al. 1995, Bellemain et al 2006, Shimozuru et al. 2019). Numbers of breeding females can be enumerated directly from Chao2-adjusted counts of unduplicated females with COY (see Section 4.1). Numbers of adult males can be estimated from their proportion in the population (0.164; derived from IGBST Annual Reports, 2007-2014).

Figure 30 shows these demographic approximations together with estimates from Kamath et al. (2015) for N_b in (A) and for N_e in (B) and (C) during 1984-2007. The green shaded areas in (A) and (B) show discrepancies between demographic and Kamath et al. (2015) estimates, with annual estimates of the latter shown as a bright green line. The red shaded areas in (A) and (C) are proportional to values from Kamath et al exceeding demographic estimates. Estimates of N_b from Kamath et al were consistently greater than demographic estimates, but especially during 1984-1994 when estimates by Kamath et al were an implausible two-fold more than the number of bears available to breed during any given year. By contrast, estimates of N_e from Kamath et al averaged nearly 100 more than the total estimated number of reproducing animals in the population during 1996-2007, consistent with inflated estimates of N_e/N_c for this later period.

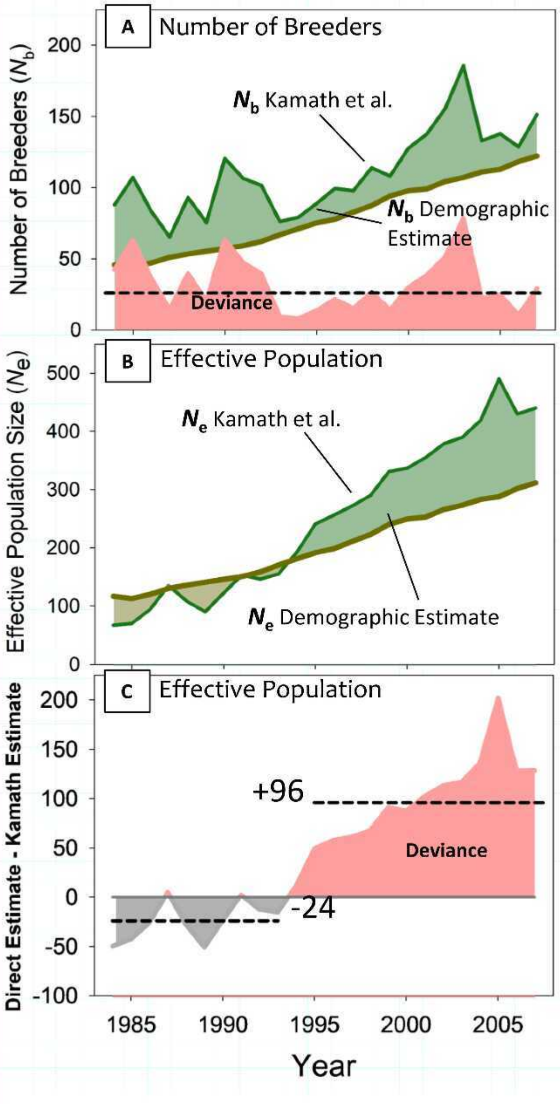

Figure 30. The panels at left illustrate discrepancies between (A) numbers of breeder (N_b) and (B-C) effective population sizes (N_e) estimated by Kamath et al. (2015) from genetic data versus results for the same calculated directly from demographic data (see below for details). All demographic results are based on population estimates reported by Van Manen et al. (2023a). The trend lines in (A) show numbers of breeders from Kamath et al in bright green and demographic estimates in dusky green. The red shaded area in (A) shows the numeric discrepancy between these two estimates. Estimates from Kamath et al. are consistently higher, especially during 1984-1993. Panel (B) shows trend lines in the same colors for the two sources but comparing estimates of effective population size (N_e). Estimates by Kamath et al. for N_e were similar to those derived from numbers of reproductive-aged bears in the population during 1984-1993 but exhibited a rapid comparative escalation after 1995. Panel (C) shows this deviation, with discrepancies averaging -24 during 1984-1993 and +96 during 1995-2007, comparable to the trend shown for N_e/N_c in Figure 29.

Methods: N_b and N_e were approximated from demographic data by first estimating different sex, age, and reproductive cohorts in the population. Annual numbers of reproductive-aged females were derived directly from 3-year sums of Chao2-adjusted counts of unduplicated females with COY. Proportions of dependent young (0.312) and males (0.164) and females (0.258) ≥ 2-years old were calculated from numbers reported in Annual Reports 2007-2014. The proportion of reproductive-aged males was calculated based on the same ratio of adults to adolescents as was used for the female cohort. Only 70% of adult males were estimated to reproduce (Craighead et al. 1995, Bellemain et al. 2006, Shimozuru et al. 2019), both cumulatively (for N_e) and as a portion of females available to breed each year (1/3rd of the total for N_b). This 70% value accounted not only for unsuccessful breeders but also potential split paternity litters.

Kamath et al. (2015) reported one additional implausible result, highlighted by a stark contrast with Miller & Waits (2003). The latter investigators estimated an inbreeding rate of 2.3% per generation for GYE grizzly bears during most of the twentieth century. Kamath et al. (2015) estimated the rate to be

0.2% – roughly 10-fold less – for the 1980s-2000s. This difference presumably arose from including data from one more generation of bears. Readers are left with the impression that this difference was real and not artifactual. If so, a convincing explanation is needed for how an estimate for a process that characteristically unfolds over multiple generations (i.e., inbreeding) could have changed by an order of magnitude simply by adding data from one to two generations of animals, especially for a species with traits such as those of grizzly bears (cf., Allendorf et al. 2013). Those looking at the results of Miller & Waits (2003) and Kamath et al. (2015) are confronted with needing to believe one or the other but not both. Given the dubious nature of results pertaining to N_e, N_b, and H reported by Kamath et al. (2015), those of Miller & Waits (2003) seem more believable.

Implications

Discrepancies between results of Kamath et al. (2015) and those of Miller & Waits (2003), as well as from estimates derived directly from demographic data, cannot be explained simply by methodological differences. Under such circumstances, estimates of N_b and N_e from genetic models are *prima facie* implausible when they substantially exceed numbers of bears potentially making a reproductive contribution to the population, exhibit significant temporal instability, and are substantially discrepant from trends in estimated population size. As with other suspect IGBST research, the authors of Kamath et al. (2015) are burdened with providing a compelling explanation for how their results can be reconciled with the problematic patterns described here. Absent a convincing explanation, results from Kamath et al. (2015) – including those related to implausibly low rates of inbreeding – can not be invoked as a credible basis for claims regarding the past genetic history or current genetic health of GYE grizzly bears.

5.3. Trucking Bears

The 2017 rule removing ESA protections for the GYE grizzly bear population (see Section 2) allowed for discretionary translocation of grizzly bears from elsewhere into the population if warranted by adverse trends in genetic diversity (U.S. Fish & Wildlife Service 2017). In a reversal of this prospective policy, plans for translocation were authoritatively adopted in 2023 as non-discretionary policy by the USFWS, Montana Department of Fish, Wildlife & Parks, and Wyoming Game & Fish Department, primarily to legally buttress a third effort in 2024 to remove ESA protections for grizzly bears in the GYE (Koshmrl 2023). Of relevance, the second, 2017, rule was overturned in federal district and appellate courts partly because the involved judges concluded that the USFWS had misrepresented relevant research on genetics of the GYE bear population and downplayed risks to genetic health (Sections 2, 5.1, and 5.2).

The new 2023 plans call for translocating “two to four” adolescent female or male bears per decade to the GYE from the Northern Continental Divide grizzly bear population, although it is unclear what will inform exact numbers. Managers apparently assume that a handful of translocated bears will contribute enough genetic material to mitigate inbreeding and losses of heterozygosity among GYE grizzly bears, presumably based on the so-called “one migrant per generation rule”. This rule holds that infusion of genes from one individual can theoretically forestall the deleterious effects of inbreeding under circumstances where there is equilibrium between genetic drift and migration, $N_e \approx N_c$ (effective population size ≈ census population size), immigrants survive and reproduce at the same rate as residents, different genotypes have equal fitness, and migrants are sourced by a random process from a large pool of populations (Spieth 1974).

Issues

If any of the assumptions validating the one migrant per generation rule are contravened, more migrants would be needed to achieve the same genetic effect – potentially as many as 10-20 or more per generation (e.g., Mills & Allendorf 1996, Vucetich & Waite 2006). As it turns out, circumstances affecting the prospective transplanting of bears from the NCDE to the GYE lead to violation of all the assumptions legitimizing the one migrant per generation rule, implying that for theoretical reasons alone, human-assisted migrants would need to number nearer 10-20 rather than two-four per decade.

Not surprisingly, the benefits of transplanting bears to remedy potential inbreeding are complicated by yet other considerations. Alleviating loss of allelic richness due to genetic drift – a different phenomenon than loss of allelic heterozygosity due to inbreeding – prospectively increases numbers of required migrants above and beyond what might be entailed by violated assumptions of the one migrant per generation rule (Greenbaum et al. 2014). There is also the potential for *outbreeding* depression – the loss of locally adapted alleles – especially if animals from populations that have been isolated for a significant period are swapped between substantially different environments (Edmands & Timmerman 2003, Frankham et al. 2011). This latter issue is relevant to grizzly bears given that there is evidence of outbreeding in bears translocated among dissimilar environments in Alberta (Shafer et al. 2014), and because diets of bears in the GYE and NCDE and so different[3].

There is also evidence from success rates of previous efforts to translocate grizzly bears that potentially informs numbers of transplants needed to sustain long-term genetic health of GYE bears. Efforts to augment a perilously small population of grizzly bears in the Cabinet Mountains of Montana with animals translocated from nearby southeastern British Columbia and the NCDE were undertaken during two periods spanning a total of 19 years – 1990-1994 and 2005-2019 (Kasworm et al. 2022). Notably, of the 22 translocated bears, only three contributed genetically to the Cabinet Mountains population, and of these three, just one contributed 87% of documented offspring.

This translates into a per bear success rate of 13% or, if extrapolated to translocations of bears from the NCDE to GYE, a total of 15-30 bear per decade needed for the successful infusion of genes from the idealized two-four animals. If, more realistically, successful infusion of genes from 10-20 animals were needed, 75-150 bears would need to be transported. Even more cautionary, these relatively pessimistic numbers don't account for the fact that bears translocated into the Cabinet Mountains were sourced from similar environments and introduced into an area with comparatively little competition from other

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[3] See Mattson (2000), Mattson et al. (2004), and Gunther et al. (2014) for bear diets in the GYE, and Kendall (1986), Mace & Jonkel (1986), and Aune & Kasworm (1989) for bear diets in the NCDE. Meat and army cutworm moths currently dominate the diet of the former (see Sections 3.7 and 3.9) and berries the diet of the latter.

grizzly bears, unlike more adverse circumstances predictably typifying transfer of bears from the NCDE to the GYE.

Research by Mikle et al. (2016) documenting the history and biogeography of genetic impoverishment and rescue among NCDE grizzly bears is also instructive. Heterozygosity (H_o) of grizzly bears in areas south of Glacier National Park (NP) was estimated in 2004 to be 7-11% lower than that of grizzly bears inside the park ($H_o \approx 0.67\text{-}0.7$ vs 0.75), presumably because the southern population was partially isolated and subject to an unsustainable grizzly bear trophy hunting for nearly 100 years (Mattson 2019). Data collected during 2009-2012, five-eight years after the initial 2004 survey, showed that H_o had increased in southern portions of the NCDE by 0.0-0.07 (roughly 0-10%) to levels comparable to those of bears in Glacier NP and northern Canada (Paetkau et al. 1998). Notably, this occurred during a period when natural exchange of immigrants among three regions of the southern NCDE numbered roughly 33.4 *per year* and accounted for 35-50% of all detected individuals.

Although this history is encouraging, it nonetheless highlights not only the prospectively formidable logistical challenges of transplanting bears from the NCDE to the GYE, but also the imperative to establish natural immigration as a long-term corrective for genetic health. There is no simple way to translate the genomic history of bears in the NCDE into a recipe for translocating bears from this ecosystem to the GYE largely because dynamics in the NCDE arose from a veritable swamping of local gene pools by genetic infusions from natural immigrants. Nonetheless, the data presented by Mikle et al. (2016) suggest that transplanted bears would ideally number nearer 100 per decade rather than two-four, especially given that H_o of GYE grizzly bears is at a greater comparative deficit – roughly 25% lower than H_o of NCDE bears, and two-three times greater than the deficit of bears in southern portions of the NCDE roughly 20 years ago.

If managers chose to ignore evidence supporting the need to translocate nearer 100 bears per decade and instead persisted with plans to translocate just two-four, adaptive changes could theoretically be triggered by monitoring trends in genetic diversity and composition of GYE grizzly bears. However, this sort of strategy has little prospect of success simply because managers would have limited ability to detect losses of heterozygosity or allelic richness, even in a population of 1,000 bears. As Allendorf et al. (2019) expressed it: "Even if it were possible to sample all the offspring each year and estimate the effective number of breeders (N_b), there would still be a lag time of many generations before a trend could be detectable."

Implications

Current plans to redress inbreeding of the GYE grizzly bear population by translocating a handful of bears each decade from the NCDE have weak theoretical support and are at variance with available evidence regarding odds of success. There is also little prospect of adaptively remedying unsuccessful efforts through monitoring genetic composition and diversity of GYE bears. Grizzly bear managers and researchers need to acknowledge weaknesses of current plans and the prospectively formidable logistical challenges associated with translocating bears to address current issues with genetic health of GYE grizzly bears.

6. Problematic Scientific Practices

The flawed IGBST science described in Sections 3-5 did not arise in a vacuum. These patterns were a result of practices configured not only by the history introduced in Section 2, but also more importantly by how that history interacted with basic psycho-social human impulses and institutionalized incentives, disincentives, and norms. As a fundamental premise, humans – including scientists – are not particularly rational, at least in a formalized linear sense of the word (Kahneman 2011), and institutions often end up being corrupted to serves the purposes of those with organizational and societal power (e.g., Lasswell 1948, Lasswell & Kaplan 1950).

Science is a set of norms, standards, and practices expressly designed to overcome bounded subjectivities in pursuit of a shared intersubjective understanding of the world rooted in shared tangible evidence (e.g., Section 6.1). Even so, implementation of scientific ideals is a chronically fraught and imperfect enterprise given that these ideals routinely run counter to deeply rooted human impulses such as confirmation bias, bounded rationality, groupthink, and group loyalties – not to speak selfish impulses that lead researchers to prioritize career advancement and monopolization of data over more transcendent collective undertakings (see Sections 6.2-6.3).

Friction between the ideals of science and fundamentals of human nature has led philosophers and sociologists of science to fill tomes, not only describing this problematic interface, but also prescribing prospectively chimerical remedies (e.g., Popper 1959; Kuhn 1970a, 1970b). One could further argue that the entire institutional edifice of academe and affiliated research-focused government agencies is devoted to not only curbing human impulses that overtly run counter to ideals of scientific practice, but also channeling those same impulses to serve the transcendent scientific enterprise – which is laudable up to the point where institutional leaders fall prey to subverted self-serving goals such as increased funding and political influence.

In what follows, I both describe and explain patterns of practice that have led to the fall of IGBST researchers from scientific grace. These corruptive patterns include a fundamentally flawed analytic enterprise (Section 6.1), the pervasive influence of special interest funding and group loyalties (Section 6.2), the assiduous perpetuation of a monopoly on relevant data (Section 6.3), and the invocation of remedies rooted in a fallacious conception of peer review (Section 6.4).

6.1. Specification of Hypotheses and Models

Hypotheses – formalized and testable speculations about how systems work – are intrinsic to scientific inquiry. In laboratory settings, researchers can randomly assign a treatment (e.g., a specific dose of medication) to animals or objects that are sequestered from all other extraneous effects and otherwise as homogeneous as possible (e.g., pure bred albino Wistar rats). This kind of rarefied circumstance allows researchers to isolate the effect of a single factor and undertake critical tests of so-called "null" hypotheses, allowing for the provisional rejection of effects attributable to specific treatments (Wold 1956, Fisher 1960).

However, outside of laboratories, employment of hypotheses is a fraught and complicated undertaking (e.g., Lakatos 1970, Putnam 1974, Quinn & Dunham 1983, Funtowicz & Ravetz 1993, Holling 1998). Without meeting stringent standards, hypothesis testing during inquiry into complex natural systems can easily lead to unsubstantiated or even erroneous conclusions if key issues are not addressed. The suite of alternate competing hypotheses – possible explanations for an outcome of interest – must encompass all plausible effects, not just a select few chosen based on professional or political expediency (Chamberlin 1890, Hillborn & Stearns 1982, Simmons et al. 2011. Betini et al. 2017; see Sections 2 and 5.3). As a logical consequence, hypotheses must be matched by well-designed statistical analyses and data sufficient to reliably address the range of speculated effects (Hillborn & Mangel 1997).

Treatment of uncertainty also needs to be clearly defined and justified up front. Most researchers default to reducing the odds of erroneously concluding that some factor (e.g., abundance of whitebark pine) affected an outcome of interest, when in fact it didn't (minimization of Type I errors). However, there are often good reasons to minimize the opposite, i.e., concluding that a factor had no effect when, in fact, it did (minimization of Type II errors). These kinds of determinations need to be accompanied by a justification that addresses the nature and asymmetry of risks associated with incurring one kind of error versus the other – including endangerment or extirpation of at-risk populations (Schrader-Frechette 1991, Schrader-Frechette & McCoy 1993, Barry & Oelschlaeger 1996). In the case of grizzly bears, erroneously concluding a population is increasing when in fact it is in decline (Type I error) is more consequential and often harder to reverse than the adverse error (Type II error).

Quintessential scientific practice, whether reckoned in terms of laboratory or field ideals, is rarely evident in ecological research undertaken in open natural systems (cf., Fisher 1960, Quinn & Dunham 1983, Cochran 1983). Ecological arenas of research are beset by numerous factors simultaneously affecting an outcome of interest, with these complexities compounded by exigencies of measuring all potentially relevant effects and accounting for temporal-spatial correlations among impinging factors. Under such circumstances, definitive isolation of a single effect (e.g., conspecific bear densities) is unlikely.

Issues

In theory, IGBST research during the past 10+ years has tacitly invoked 'treatments' comprised of exposing individual bears or bear cohorts to different bear densities and diets while holding the effects of all other factors constant. In practice, this theory is little more than hypothetical. Bear researchers cannot randomly assign treatments (e.g., exposure to a specific density of conspecifics) in a way that excludes or somehow controls all other effects arising from systematic differences or other variation among bears and their environments. There are thus no unambiguous null hypotheses or related "critical" tests that allow researchers to reject some effect (e.g., attributable to variation in abundance of pine seeds; cf., Green [1979], Cochran [1983], Oreskes [2003]). Perhaps even more important, there is little corresponding basis for reaching definitive conclusions about whether an effect does exist and, if so, with what impact (e.g., densities of conspecifics). At best, a provisional conclusion ends up being supported by the transient weight of evidence (Oreskes et al. 1994, Oreskes 2003).

Modeling offers the only prospective means of tentatively controlling for the effects of numerous interacting factors typifying grizzly bear research (see Sections 3 and 4, *in toto*, also Wold [1956], Green [1979], Cochran [1983], Hilborn & Mangel [1997], Burnham & Anderson [1998]). However, this sort of provisional statistical "control" for intervening effects requires that special conditions be met. In particular, the suite of factors considered for inclusion in a model must be biologically plausible and sufficiently replete to cover relevant demographic and ecological dynamics. In the case of Yellowstone grizzly bears, this includes likely effects arising from changes in foods, habitats, interactions with humans, and interactions with other bears – including real-time or lagged effects arising from temporal and spatial correlations among candidate factors. Failure to anticipate or adequately estimate even a few major effects compromises use of models for inference because unaddressed factors introduce potentially substantial unknown bias (Hilborn & Mangel 1997) – as holds for essentially all IGBST research published since 2000 (Sections 3.1-3.12).

Even under ideal circumstances, best practices for modeling ecological systems are difficult to meet. Among the most demanding, albeit arcane, requirement is that a modeling strategy produce results with minimal residual bias arising from systematic rather than random variation within modeled categories or relationships – or, in other words, under conditions where there are no substantive effects attributable to covariates not considered in the model and where variation of ultimate modeled responses is essentially random (Kyburg 1969, Dawid 1979, Rosenbaum 1984).

Credible inference from observational studies depends on meeting this standard (cf., von Mises 1957, Kyburg 1969, Dawid 1979, Holland 1986). Mismatches of classes to underlying variation in key parameters, as in Bjornlie et al. (2014a) and Corradini et al. (2023), violates this fundamental statistical requirement, as does pronounced temporal or spatial heterogeneity of covariates (e.g., measures of whitebark pine abundance), as in Costello et al. (2014) and Van Manen et al. (2016; cf. Greenwald & Robins 1985). This kind of bias arising from deficient modeling cannot be corrected by statistical gymnastics or *pro forma* invocation of jargon (c.f., Morgan & Henrion 1990). The best that can be provided by more sophisticated methods such as the General Additive Models and hierarchical Bayesian methods so prominently advertised by IGBST researchers (e.g., Cherry et al. 2002, Van Manen et al. 2023b) is greater insight into the nature and extent of uncertainty (Oreskes et al. 1994, Gelman et al. 2003, Oreskes 2003).

Ecologists and field biologists also routinely confront measurement and sampling errors (Wold 1956, Diamond 1986). Problems with study design and implementation introduce not only additional uncertainty, but also bias, i.e., the deviation of whatever's being measured from real patterns in the focal object of interest. When indices are used, as in representations of bear densities by the IGBST (Section 4.7), as much systematic bias as possible needs to be removed, and any remaining bias both disclosed and accommodated as part of inferences leading to research conclusions. The true magnitude of uncertainty surrounding estimates also needs to be transparently represented – rather than reflexively disputed – regardless of whether this uncertainty arises from non-random sampling or systemic bias. Of relevance to this last point, uncertainty (or "credible") intervals for statistical estimates produced by the IGBST have a history of being implausibly small as well as potentially misleading (Pease & Mattson 1999; Interagency Grizzly Bear Study Team 2012; Doak & Cutler 2014a, 2014b).

Cumulatively, when inadequately parameterized statistical models are accompanied by bias- and error-prone measurements, hypotheses are unenlightening, statistical models routinely suffer from specification error, analyses more often produce spurious results, and misinterpretation is commonplace – as holds for almost all IGBST research since 1998 (see below). The invocation of model parsimony (i.e., selection on the basis information criteria) or the latest statistical methodology – as so often done by IGBST researchers – cannot rescue a research enterprise from these sorts of problems (cf., Hilborn & Mangel 1997, Burnham & Anderson 1998, Oreskes 2003, Brewer et al. 2016, Coelho et al. 2019).

Implications

IGBST publications routinely pose selectively sparse hypotheses that are then subjected to inadequate statistical tests, almost invariably involving a straw man contest between an effect of whitebark pine loss and an effect of bear density (see Section 2). This deficient framing predictably yields analysis results that are habitually interpreted as evidencing a dominant effect of conspecific densities. The absence of results attributable to whitebark pine seeds – or any other food – are explained in terms of resilience by grizzly bears to all but catastrophic changes in habitats and diets (see Section 3.1). More specifically:

- *Gunther et al. (2014)*: (i) Claimed to test whether whitebark pine seeds were a critical food for Yellowstone grizzly bears by examining dietary diversity and absence of whitebark pine in established bear home ranges; (ii) Used a measurement of whitebark pine distribution that substantially under-represented the extent of mature cone-producing trees (Section 3.3); (iii) Failed to adequately address variation in nutritional values of foods (Section 3.1); and (iv) Neglected hazards associated with consumption of different diets (Section 3.12).
- *Costello et al. (2014)*: (i) Claimed to test whether changes in bear movements and distributions were caused by conspecific densities or abundance of whitebark pine cones; (ii) Used a substantially under-specified model that did not account for any other environmental effects or dietary changes (Sections 3.4-3.9); (iii) Relied on weak connections between hypotheses, analysis, and conclusions; (iv) Employed a dubious measure of bear density (Section 4.7); and (v) Used a flawed conception of density-dependent effects (Sections 4.8-4.9).
- *Bjornlie et al. (2014a)*: (i) Claimed to test whether changes in home range size were caused by conspecific densities versus abundance of whitebark pine; (ii) Employed substantially under-specified hypotheses and models that did not account for any other environmental effects (Sections 3.4-3.9); (iii) Structured the analysis according to a design that fundamentally misrepresented temporal availability of whitebark pine seeds (Sections 3.2 and 3.4); (iv) Used a measurement of whitebark pine distribution that substantially under-represented the extent of mature cone-producing trees (Section 3.3); (v) Employed a dubious measure of bear density (Section 4.7); and (vi) Used a flawed conception of density-dependent effects (Sections 4.8-4.9).
- *Van Manen et al. (2016)*: (i) Claimed to have tested the effects of conspecific density versus whitebark pine abundance by statistically estimating temporal and geospatial effects of both on grizzly bear fecundity and survival; (ii) Hypotheses and models were substantially under-specified

because numerous other environmental effects were not considered (Sections 3.4-3.9); (iii) The estimated spatial extent and temporal abundance of whitebark pine seeds was fatally compromised by measurement errors (Sections 3.2-3.3); (iv) Hazards associated with different diets were not accounted for (Section 3.12); (v) Used a dubious measure of bear density (Section 4.7); and (vi) Employed flawed conceptions of carrying capacity and density-dependent effects (Sections 4.7-4.8).

- *Corradini et al. (2023)*: (i) Posed ambiguous hypotheses as a basis for testing the presumed effect of temporal changes in abundance of three high-quality foods versus conspecific density on body composition of Yellowstone grizzly bears; (ii) Grossly neglected within-class variability of food abundance by lumping data under more-or-less arbitrarily defined decadal blocks (Sections 3.4-3.5); (iii) Neglected trends and effects of other unacknowledged foods, notably army cutworm moths (Section 3.7); (iv) Used a dubious measure of bear density (Section 4.7); and (v) Employed a flawed conception of density-dependent effects (Sections 4.7-4.8).

The structure of hypotheses and related measurements and tests by IGBST researchers in all these publications failed to meet standards of credible scientific practice. Hypotheses and models were routinely underspecified, meaning that only a highly rarefied and prospectively biasing subset of plausible environmental and demographic effects was considered. Classifications often mismatched factors of interest and were compromised by further systematic bias. Measurements introduced additional undisclosed errors and uncertainty. In short, given the complexity of the ecological system affecting Yellowstone's grizzly bears, the cumulative weight of these failings warrants skepticism about almost all conclusions reported in IGBST publications during the past twenty years.

6.2. Politicized Science: A Social, Psychological, and Institutional Perspective

The fundamental flaws in IGBST science described in Sections 3-5, and 6.1 beg the question of how these failings could have been cumulatively neglected, overlooked, uncorrected, or even willfully embraced during the process of scientific inquiry and publication. The politicized history described in Section 2 provides important context for how IGBST research was shaped and even corrupted. However, these external effects were predictably amplified by social-psychological dynamics, including in-group loyalties and perverse institutional incentives created the U.S. Geological Survey (USGS), USFWS, and state wildlife management agencies comprising the IGBST.

Issues

IGBST researchers routinely assert that they are neutral scientists who merely query data collected from Yellowstone grizzly bears and their environment without interjecting their values. As one Team Leader expressed it, "We bend over backwards to see that the science remains neutral…We let the numbers do the talking" (Kevan 2011). These sorts of claims are belied by this critique as well as a definitive corpus of inquiry into human social-psychology, organizational dynamics, and scientific practice.

The evidence contravening naïve assertions of objectivity on the part of scientists is so extensive that it defies a cursory review. Social scientists who study researchers and their practices have exhaustively documented pervasive influences of subjectivity and bias (e.g., Berger & Luckmann 1967, Kuhn 1970, Feyerabend 1975, Leopold 1978, Quinn & Durham 1983, Gavin 1989, Longino 1990, Proctor 1991, Sinclair 1991, Rousch 1995, Functowicz & Ravetz 1993, Sarewitz 1996, Hilborn & Mangel 1997, Pielke 2007). There are no unambiguous self-evident questions, hypotheses, or models. "The data" or "the numbers" are not sentient semiotic beings that somehow speak for themselves. To the extent that any data "speak", the vocabulary is largely dictated by the questions researchers ask and the effects they chose to investigate. All these factors largely predetermine research results, which are further shaped by the bounds placed individually and collectively on permissible inquiry – as evident in IGBST research. There is no value-free or otherwise "neutral" science (e.g., Proctor 1991, Restivo 1994, Sarewitz 1996).

In addition to the pervasive play of subjectivity, funding indisputably shapes what research is done, by whom, and to what purpose. From a societal and scientific perspective, the configuring effects of research funding can range from beneficial, to benign, to corrupt, largely as a function of who provides funding and the motivations of involved scientists (Sarewitz 1996, Greenberg 2001). At the beneficial end of this spectrum, scientists compete for funding from the National Science Foundation awarded by panels of esteemed peers who strive for objectivity and merit. At the other extreme, profit-seeking corporations use opaque processes to channel money to researchers who almost invariably provide science bolstering *a priori* agendas – most notoriously so in the case of the international tobacco industry and the scientists it recruited to do research (Kessler 2001). Interestingly, the dynamics associated with IGBST funding more closely resemble those of a corruptive corporate enterprise than those of a highly competitive and transparent process overseen by scientific peers.

The IGBST is governed by USGS business practices that have increasingly come to resemble those of a for-profit enterprise during the last two decades. Beginning in the 2000s, budgetary allocations by Congress to the USGS declined in real dollar terms while administrative costs proportionately mounted (https://www.usgs.gov/bpi/budget-archives). To balance the books, USGS progressively resorted to covering its expenses through 12-25% administrative overhead levied on outside funding largely originating from federal or state management agencies. USGS scientists have, moreover, increasingly needed to obtain outside funding to pursue any research as well as cover their salaries. In the case of the IGBST, much of this outside funding has come from the USFWS and, more indirectly, from state wildlife management agencies.

These financial dependencies have come with increasing emphasis in USGS policies on treating entities that provide funding as "partners" and in places literally as "customers" for whom science is a "product" (https://www.usgs.gov/survey-manual/50015-customer-service-policy). The parallels to a for-profit business are striking, except that figurative profits are more subtly absorbed into operational budgets. All this creates a predictable sense of dependency by researchers in the IGBST on funding from partner agencies, notably the USFWS. Along with this dependency comes tacit – albeit strong – incentives to provide products that serve the "customer's" wants and needs (e.g., Etzkowitz et al. 1998, Ottesen et al. 2002, Martinson et al. 2005). In the case of USFWS decision-makers, there is clear evidence in documents listed as *Supplemental Information* that these wants and needs have included producing science to rebut judicial decisions voiding 2007 and 2017 rules that removed ESA protections for GYE grizzly bears (see Section 2).

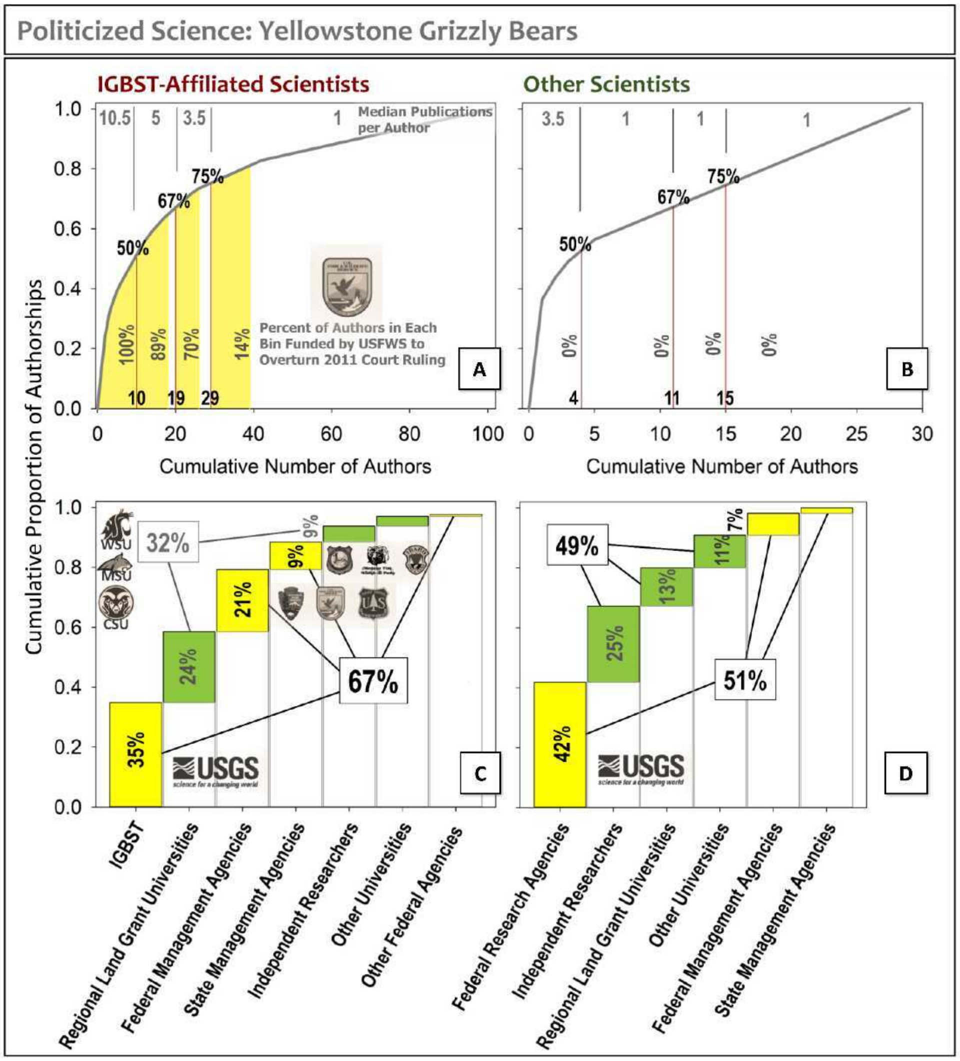

Figure 31. These graphics are illustrative of how funding sources and affiliations have manifest in publications by IGBST-affiliated researchers relative to independent scientists who also published analyses related to Yellowstone grizzly bears – often contesting claims made by the IGBST. Figures (A) and (B) show cumulative publications between 1995 and 2022 attributable to authors credited with a diminishing average number of papers. Scientists who together published 50% of IGBST-affiliated research had an average 10.5 papers each, as opposed to an average 3.5 papers for unaffiliated scientists. Authors credited with only one paper each accounted for only 20% of IGST-affiliated publications versus authorships on over 50% of unaffiliated publications. This disparity suggests the difference between a coordinated and comparatively homogenous IGBST-affiliated research team versus more diversity among those who were unaffiliated. More telling, the yellow shaped portions of each bin in (A) and (B) are proportional to the number of publications that were partially or wholly funded by the USFWS. None of the research by independent researchers was funded by the agency, whereas between 70% and 100% of the authors producing multiple IGBST-affiliated publications were (on average between 3.5-10.5 papers each). Figures (C) and (D) partition authorship of USGS-affiliated and independent research by institutional affiliations, again as cumulative numbers. Bins shaped yellow denote authorships of government-employed researchers who cumulatively accounted for 67% of those on IGBST-affiliated publications versus 51% unaffiliated publications. Notably 25% of unaffiliated authorships were by researchers who represented themselves as "independent."

Reliance by the IGBST on outside funding has been accompanied by the formation of a community of managers and researchers vested with authority over grizzly bear research and management. This community, or "team," has facilitated coordination and communication. At the same time, though, attendant social-psychological dynamics have come with a predictable downside, notably a predilection for ingroup loyalty, groupthink, and confirmation bias. Social and psychological researchers have demonstrated that all these phenomena can have powerful influences on people in social groups (e.g., Janis 1972, Klayman & Ha 1987, ‘t Hart 1990, Mullen et al. 1992, Klayman 1995, Schafer & Crichlow 1996, Nickerson 1998) – including groups of researchers such as the IGBST (e.g., Kuhn 1970, Klayman & Ha 1987, Kolowski 1996, MacCoun 1998). The predictable consequence is a tendency for group members to favor certain hypotheses and questions, confirm prior biases and expectations when interpreting new evidence, and defend group interests against perceived outside attacks – all of which is amply evident in the IGBST and its publications (see especially Sections 2, 5, and 6.1).

Figure 31 provides a visual snapshot of how financial influences, organizational identifications, and group loyalties have manifest in publications by IGBST-affiliated researchers during 1995-2022 (Figures 31a and 31c), with publications by unaffiliated researchers who also focused on GYE grizzly bears provided as a point of contrast (Figures 31b and 31d). Much of this latter body of research contested claims made by the IGBST. The caption of Figure 31 provides more information on the design of each panel, but the basic points are relatively straightforward. Authorship of IGBST-affiliated research papers was cumulatively much less diverse compared to that of papers by unaffiliated authors (Figures 31a and 31b), consilient with the fact that authorships of the former were likewise more heavily weighted towards researchers who worked for the IGBST or closely affiliated management agencies (Figures 31c and 31d). Equally important, roughly 74% of all authorships on IGBST-affiliated publications were attributable to researchers who were funded wholly or in part by the USFWS, with most of these authorships attributable to researchers who contributed to >6 papers each. As a bottom line, these data do not paint a picture of diverse identities, affiliations, or financial obligations among those holding a monopoly on data pertaining to the Yellowstone grizzly bear population.

This penchant for perspectives defined by group loyalties and dependencies is also evident in public statements by those participating directly or indirectly in media discourses about grizzly bear management. Figures 32 and 33 summarize statements made in the media, not only by people with a spectrum of partisan perspectives, but also by those representing themselves as scientists or spokespeople for management agencies. These statements either explicitly or tacitly defined problems and solutions for grizzly bear policy and management in the GYE, typically with direct or oblique reference to the desirability of removing ESA protections. Many statements also claimed to express “facts” about grizzly bears, bear habitats, and people. These communications, often in the form of quotes, were obtained from a comprehensive collection of regional and national newspaper articles published during 2005-2010. The full diversity of quotes was distilled into a handful of comparable statements that were identified with policy participants, who were then clustered to identify and characterize “discourse coalitions” – people with shared perspectives and narratives (Mattson & Chambers [2009] and Mattson & Clark [2012] provide more detailed descriptions of methods). “Factual” statements were also subjectively scored, ranging from 0 in instances where the “fact” contravened all available research to 6 in instances where the statement was supported by replicated research results.

The captions in Figures 32 and 33 provide more detail on the included diagrams, especially those pertaining to results of cluster analysis. However, the basic patterns are clear. First, public statements by people involved in debating grizzly bear management are not only diverse, but also fundamentally different in how “problems” are defined (Figure 32). “Facts” are also selectively marshalled and featured to support a given perspective (Figure 33). Many “facts” are even at variance with available evidence, scientific or otherwise (Figure 32c). Not surprisingly, having one's favored definition of "the problem" prevail in public debates about grizzly bear management is central to the political process, with scientific "factual" information serving primarily to advance an agenda that serves one's special interests (cf., Weiss 1989, Rochefort & Cobb 1994, Dery 2000).

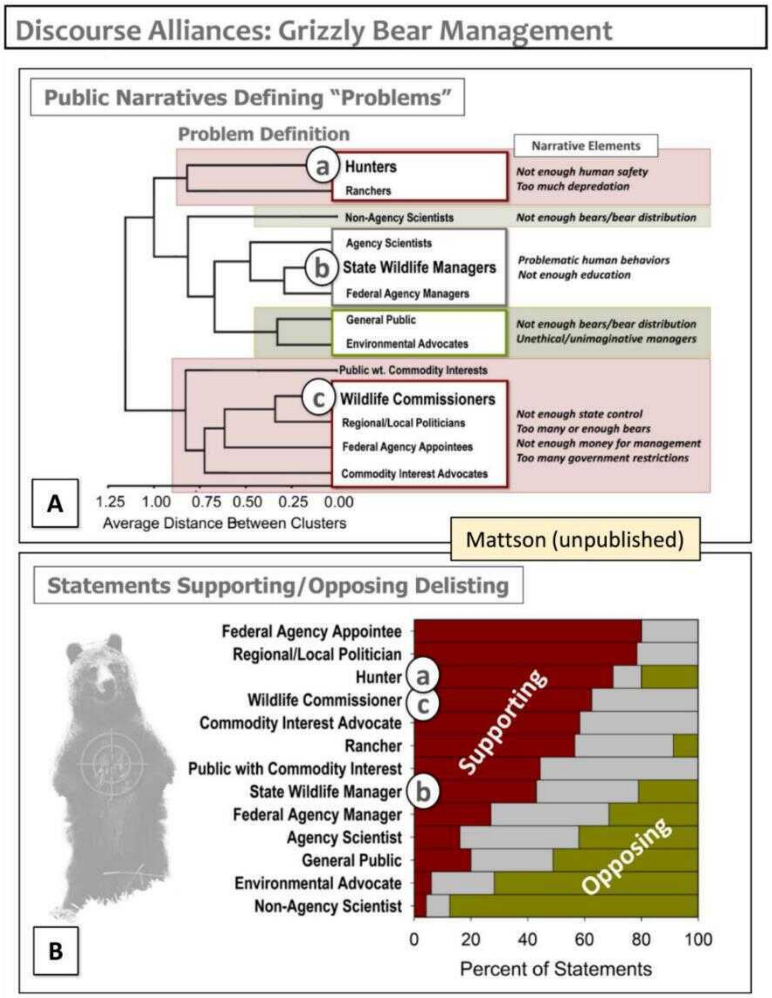

Figure 32. The figures at left show how different participants in policy debates over GYE grizzly bears cluster based on similarity of perspectives expressed in the print media during 2005-2010. The graphic in (A) is a cluster diagram, with different cluster branches farther right signifying greater similarity among policy participants identified at the terminus of cluster limbs. The phrases farthest right synopsize key perspective or narrative elements shared by participants in clusters identified as (a), (b), and (c). Cluster (a) was defined by hunters and ranchers who expressed concern about levels of depredation and lack of human safety. Cluster (c) consisted of leaders of state and federal management agencies along with regional politicians and individuals identified with commodity interests who insisted there were too many grizzly bears, not enough state control or authority, and too many government restrictions. The last less well-defined cluster (b) consisted of scientists and mid-level state and federal managers who thought that central problems related to problematic human behaviors and lack of public education, loosely affiliated with environmental advocates and members of the general public who thought there were too few bears.

The graphic in (B) distills expressed perspectives in terms of whether they explicitly or tacitly supported or opposed removal of ESA protections for GYE grizzly bears. The horizontal length of different colored portions of each bar corresponds with the proportion of statements supporting (burgundy) or opposing (green) delisting, with gray denoting statements that were ambiguous about the topic. Each horizontal bar is identified with discourse participants names in (A). Hunters, ranchers, regional politicians, and leaders of federal and state management agencies overwhelmingly supported delisting. Environmental advocates and non-agency scientists were overwhelming opposed.

Those who most ardently promoted removal of ESA protections for GYE grizzly bears included not only people and their political allies with interest in grazing public rangelands and extracting commodities such as timber from grizzly bear habitat, but also the leadership of federal and state agencies involved in managing grizzly bears and their habitat (Figure 32a). The narrative fielded by these policy advocates held that federal regulations were onerous, there were too many bears in too many places, and that states deserved absolute authority over bear management – all supported by unreliable facts purporting to substantiate removal of ESA protections (Figure 33). Interestingly, statements from scientists who did *not* work for state or federal agencies aligned closely with those of environmental advocates and fielded factual statements that scored as being the most credible of any by participants in public debates.

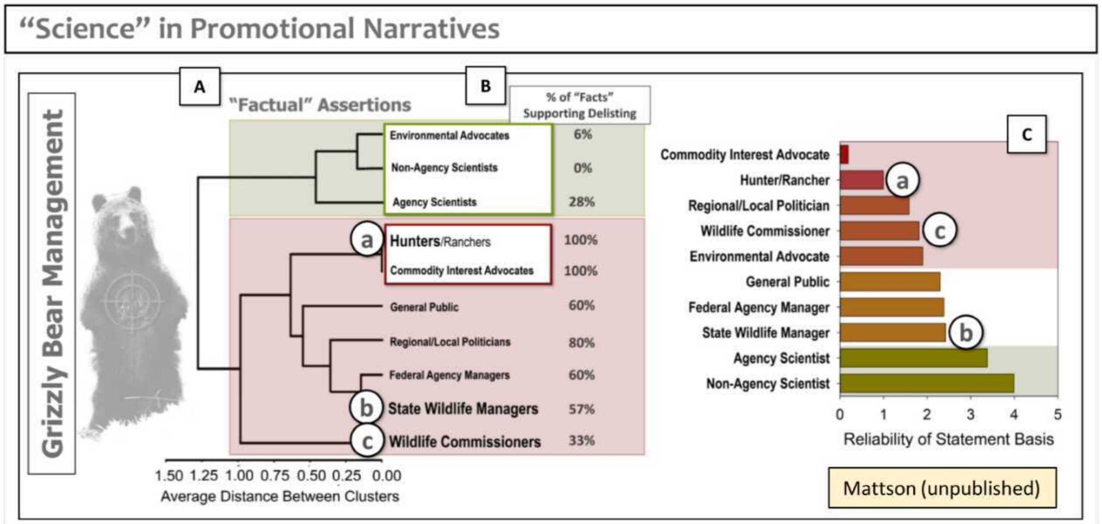

Figure 33. These graphics show the nature of "factual" statements publicly deployed by participants in debates over management of GYE grizzly bears. The graphic in (A) is a cluster diagram like the graphic in Figure 32a, but in this case clustering participants relative to whether their selectively expressed "facts" could be construed as supporting removal of ESA protections for GYE bears. Branches farther to the right represent greater similarly among participants identified at the terminus of branch limbs. The figures farthest right in (B) are percentages of "factual" statements supporting delisting. Hunters, ranchers, and people with commodity interests (a) articulated so-called facts that exclusively supported removal of ESA protections, followed by regional and local politicians, federal agency managers and the general public. Environmental advocates and non-agency scientists articulated few if any "facts" that could be construed as supporting delisting. The horizontal bars in (C) are average subjective scores for the reliability of "factual" statements expressed by discourse participants, with a score of 0-1 representing a statement that contravened published research and a score of 4-5 representing a statement that was well-supported. Hunters, ranchers, people with commodity interests, regional and local politicians, leaders of state wildlife management agencies, and environmental advocates typically expressed "facts" with little or no support from published research whereas agency and non-agency scientists tended to publicly express the most reliable "facts".

More to the point of this critique, virtually every person with significant influence over IGBST scientists through direct-line authority, indirect control over purse-strings, or political sway over agency leaders was not only advocating for removal of ESA protections for GYE grizzly bears, but also selectively using information to promote this agenda. Having worked for the USGS, the parent organization for IGBST scientists, I can testify to how concern about offending political elites with budgetary authority permeates the agency. This is more formally manifest in the accumulation of procedures to vet both research products and public statements by scientists to expunge anything that might be considered sensitive or offensive to political elites (e.g., https://www.usgs.gov/survey-manual/5005-news-release-and-media-relations-policy; https://www.usgs.gov/survey-manual/5024-fundamental-science-practices-review-approval-and-release-information-products).

Nor was the USFWS a neutral player when it came to promoting removal of ESA protections for GYE grizzly bears – in defiance of multiple authoritative legal judgments described in Section 2. The USFWS's leaders had several narratives by which they appeared to rationalize their relentless pursuit of a delisting agenda, but among several was the presumed need to free funding for other recovery efforts and save the ESA from vengeful conservative politicians (https://www.grizzlytimes.org/single-post/2016/06/23/Delisting-Grizzlies-To-Save-The-ESA). Regardless of whether these narratives had merit, they clearly influenced IGBST research through the role played by the USFWS in funding and shaping IGBST research post-1993, but especially after the litigation that culminated in 2011 (see Section 2). It is hard to imagine IGBST researchers escaping subvert or not so subvert influences on their scientific practice.

This conclusion is consistent with the results of inquiry into biased judgements by both wildlife managers and researchers regarding removal of ESA protections for GYE grizzly bears. Karns et al. (2018) found that the affiliation of scientists with government agencies vs academe "…was strongly associated with listing status recommendations; agency experts were 7.3 times more likely to recommend delisting grizzlies." Mattson et al. (2006) also found that those who identified with wildlife management agencies dismissed the idea that implementation of the ESA by agency managers was problematic. On a related note, Heeren et al. (2017) observed that judgments by managers and scientists regarding the advisability of removing ESA protections for GYE grizzly bears were, like all human decisions, more aligned with subjective identities than a rigorous examination of evidence.

Implications

In a revealing moment, a member of the IGBST recently likened development of a rule to remove ESA protections for Yellowstone grizzly bears to building a "Death Star" – a spherical space station created by the Evil Empire in the Star Wars movies to destroy planets (Koshmrl, December 6, 2023). He elaborated on how the edifice of a rule needed to be so formidable that no lawyer could successfully find a chink in the defensive armor of science and law. Perhaps without intending to, this metaphor revealed the extent to which many government employees involved in studying and managing GYE grizzly bears see science as part of a partisan bulwark rather than a source of uncertain information legitimately subject to disputation in public deliberations – and, as a corollary, see those who contest this defensive edifice and the science upon which it is built as enemies.

These sorts of "us vs them" narratives are a natural consequence of the social psychological dynamics that inevitably arise when people who identify with a collective have their shared narratives and endeavors contested. There is probably little remedy for the entrenchment of special interests arising from partisan funding and bounded perspectives, as with the IGBST, other than to enforce the imperative for transparency, meaningful exchange of perspectives, and free access to information – including scientific data – all of which is required for decision-making processes that serve the public interest in a free society (see Lasswell & McDougal [1992], Volume II, Part IV: The Structure of Decision in a Free Society).

6.3. Monopolistic Scientific Inquiry

The IGBST and U.S. Fish & Wildlife Service have assiduously maintained a monopoly over virtually all data of direct relevance to management of Yellowstone's grizzly bear population for the past 30+ years. On the face of it, perpetuation of a monopoly is prospectively problematic simply because there is only one Yellowstone grizzly bear population and only one set of collected data, which sets the stage for inflamed policy conflict if information is sequestered by a few participants with suspect motives (Fischman & Meretsky 2001; see Sections 2 and 6.2). Yet virtually none of the data collected by the IGBST has been made available to outside researchers or research teams other than those whom the Team has invited to collaborate. A monopoly such as this debars replication, disallows alternative models and hypotheses, provides ample scope for bias, and cannot be corrected by peer review (see Sections 6.1-6.2 and 6.4).

Issues

Transparency and open access to data and/or relevant systems is at the core of scientific advancement (e.g., Popper 1959, Merton 1973, Pickering 1992, Maxwell 1998, Losee 2004, and many more). There is no substitute or remedy when these conditions are lacking. In the absence of ample opportunity for others to independently check, test, replicate, contest, and advance a body of research, those who enjoy a monopoly predictably fall prey to well-documented phenomena, including confirmation bias and groupthink, especially when they are part of a closed or mostly closed research team (e.g., Oreskes 2021; Section 6.2). They can also more easily fall prey to political influence and the sway of money, especially when those involved in crafting or internally reviewing the research have an outside vested interest and are providing substantial funding (see Sections 2 and 6.2). All of this holds for the IGSBT and the science it has produced during the last two plus decades.

These intrinsic problems are further amplified by the fact that most of the science produced by the IGBST of relevance to the demography and genetic health of Yellowstone grizzly bear entails complex statistical models that perform well only if sometimes weighty assumptions are met (Section 6.1). This is intrinsically problematic because there is no one correct model for explaining a natural system, which makes model-building a vagarious and bias prone scientific undertaking. The best that scientists can corporately hope for is a range of relevant models produced by as many independent researchers as possible for use in collective deliberations (Silberzahn & Uhlmann 2015)[4].

Unfortunately, science relevant to conservation of Yellowstone's grizzly bears is the opposite of this ideal. It is a closed enterprise under IGBST and U.S. Fish & Wildlife Service auspices, privileged with fielding a few chosen models produced under predictably biasing circumstances (Sections 2 and 6.1-6.2). Perhaps even more problematic, both entities have fought to maintain monopolistic arrangements

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[4] Silberzahn & Uhlmann published a 2015 article in *Nature* reporting what happened when 29 research teams were given the same dataset and asked to determine whether a particular effect was "significant," not unlike the issue attending whether losses of whitebark pine had a significant effect on Yellowstone grizzly bears. The research teams provided essentially 29 different answers, ranging from non-significant, to slightly significant, to highly significant.

whenever they have been contested, almost invariably for disputable reasons. Perhaps most brazenly, the current leader of the IGBST claimed he could not release data collected at public expense by public servants because: "Our livelihood [i.e., career advancement] depends on producing publications…If I have to compete with other researchers…there is no point in me being a researcher". The video in which he makes this statement can be seen on Youtube.

Another notable example in which agency researchers and managers sought to restrict data access unfolded during 1992-1996. This incident was triggered by several independent researchers who discovered errors in an IGBST analysis (Eberhardt et al. 1994) that produced inflated estimates of survival and population trajectory for GYE grizzly bears (Pease 1992, Hovey & McLellan 1996). Dr. Pease consequently requested access to raw demographic data and was denied. He then repeated his request under the federal Freedom of Information Act (FOIA) and was again denied (Wilkinson 1998). These demographic data were eventually released and used for an independent analysis of GYE grizzly bear demography (Pease & Mattson 1999), but only after prolonged litigation and a failed attempt by IGBST researchers and the USFWS Recovery Coordinator at the time to have a professional organization[5] condemn the involved researchers along with the ethics of using a FOIA request to obtain government-held data (cf., Mattson 1994).

Implications

There are potentially several ways to interpret what appear to be patterns of systematic bias in public statements and behaviors by IGBST scientists. But there is little doubt about the highly problematic structural configurations of the environment within which IGBST scientists operate that virtually guarantees the production of unreliable science (Section 16; Mattson & Craighead 1994, Mattson 1996, Wilkinson 1996, Ketchum 2019). IGBST scientists consequently bear the burden of proving that they are honest brokers (cf., Pielke 2007) and that perpetuation of a monopoly on data and scientific inquiry serves the public interest—in contravention to the current consensus of social science and philosophy regarding scientific practice.

6.4. Fallible Peer Review

The IGBST operates under auspices of the US Geological Survey (USGS). In its various policy documents, the USGS makes numerous claims regarding the efficacies of peer review, including asserting that "peer review…*insures* the scientific quality of USGS information (USGS Manual, 502.4, Fundamental Science Practices) and "peer review, as cornerstone of scientific practice, *validates* and *ensures* the quality of published USGS science" (USGS Manual, 502.3, Fundamental Science Practices). It is claims such as these that apparently undergird the IGBST's defense of a monopolistic scientific enterprise. In keeping with these policy statements by USGS, the U.S. Fish & Wildlife Service and IGBST commonly claim in public

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[5] International Association for Bear Research & Management

that peer review will detect error and ensure – if not guarantee – the quality and reliability of the IGBST's science (e.g., Van Manen et al. 2013, 2023a).

Issues

Unfortunately, claims made on behalf of peer review by the U.S. Fish & Wildlife Service, USGS, and IGBST are not empirically substantiated. The corpus of scientific inquiry into efficacies of peer review has shown that error is detected at about a rate one would expect by chance, and that, if anything, peer review is about adhering to dominant paradigms and drawing support from the predictably commonplace reviewers who adhere to them as well (e.g., with the following being the first alphabetic entries in my extensive compilation of related research: Burnham 1990; Armstrong 1997; Campanario 1998a, 1998b; Bacchetti 2002; Biagioli 2002; Benos et al. 2007; and many more). Not coincidentally, the IGBST has published most of its primary research since 2004 in journals such as *Ursus* and *The Journal of Wildlife Management*, both of which could be considered bastions of dominant paradigms (see Section 6.2).

Because of empirically based concerns about peer review, there has been a corresponding groundswell criticizing the reliability of this practice in the scientific community. About the best that thoughtful defenders of peer review can say for this paradigm is something akin to what Winston Churchill said about democracy: "[it] is the worst form of government except for all those other forms that have been tried from time to time." Although defenses—and critiques—such as this still allow a constructive place for peer review, they are not a basis for putting faith in this process as guarantor of scientific quality.

Implications

Peer review too often functions as a mechanism for censorship as well as maintenance of identity and political advantage among communities of privileged researchers rather than as a corrective for error and insufficiency. In a similar vein, claims on behalf of peer review by the U.S. Fish & Wildlife Service, USGS, and IGBST bespeak a political enterprise more than an objective and empirically based assessment of what peer review can offer (see Section 6.2). As with perpetuating a scientific monopoly (Section 6.3), the burden is on IGBST scientists to somehow prove that peer review does, in fact, correct for all the bias-inducing effects configuring their arena of scientific inquiry—contrary to the best available science regarding the limitations of peer review. This burden weighs all the heavier because of the monopolistic arrangements governing scientific inquiry into the ecology and demography of Yellowstone's grizzly bears (Sections 6.2-6.3).

7. Conclusion

Scientists, like all humans, are captive to subjectivities shaped by selective attention, confirmation bias, group loyalties, and self-narratives (Section 6.2). Science is a suite of methods and practices explicitly designed to minimize the effects of individual subjectivities on the collection, analysis, interpretation, and reporting of evidence, with the intent of promoting a shared intersubjective understanding of the world. Even so, approximating the ideals of science is dependent on numerous contingencies that often defy commonplace human behaviors, including close self-scrutiny, open-mindedness, rejection of group loyalties, embrace of criticism, free sharing of information, and a willingness to reject preconceived notions…among others.

The ideal of scientific service to society is predictably betrayed to the extent that researchers deceive themselves by laying claim to objectivity and impartiality; use privileged positions to assert technocratic authority; sequester information to debar independent critical inquiry; become dependent on or vulnerable to corruptive political and financial influences; or allow ingroup loyalties to promulgate and exaggerate bias. All these phenomena clearly hold sway to some extent over IGBST scientists (Sections 2, and 6.2-6.4). A syndrome of fatally flawed research has been the predictable consequence (Sections 3-5), aided and abetted by others for whom this research serves a political purpose (Section 2). These partisans include not only managers intent on furthering their factional interests, but also a parent organization (IGBST) invested in increasing funding, minimizing offense to customers, and "enhancing [its] stature, reputation, and visibility" (https://www.usgs.gov/office-of-science-quality-and-integrity/fundamental-science-practices).

More specifically, the IGBST has fatally compromised its assessment of factors driving past and prospective future changes in demography and behavior of Yellowstone's grizzly bears in numerous ways, including: by equating omnivory with indifference to food quality (Section 3.1); misrepresenting abundance of whitebark pine seeds (Sections 3.2-3.3); failing to account for both temporal and spatial aspects of major environmental change (Sections 3.4-3.10); failing to consider the emergent effect of dietary changes on risk of death; using a suspect measure of bear density (Sections 3.11-3.12); failing to adequately account for bias introduced by increasing search effort and sightability of bears (Section 4.2); misconstruing the concepts of density-dependence and carrying capacity (Sections 4.7-4.8); underspecifying models and hypotheses (Section 6.1); and maintaining monopolistic control over scientific inquiry in a highly politicized environment (Section 6.3). These fundamental failings delegitimize most claims made in Van Manen et al. (2013), Bjornlie et al. (2014a), Costello et al. (2014), Gunther et al. (2014), Van Manen et al. (2016), and (Corradini et al. 2023). This body of research consequently offers little credible basis for judging how bear densities and environmental change have affected grizzly bear behaviors or birth and death rates in the Greater Yellowstone Ecosystem.

As problematic, IGBST researchers have relied on reporting their research results in terms of abstruse concepts such as "resilient," "omnivorous," "generalist," "carrying capacity," and "density-dependent" in lieu of credible insightful science (Sections 6.2-6.4). These obfuscations have been accompanied by surprisingly little apparent curiosity about how a complex and rapidly changing natural environment is, in fact, affecting grizzly bears in the Greater Yellowstone Ecosystem. Rather, the corpus of IGBST science and the social-political influences that produced it evince a partisan mandate to demonstrate that grizzly bears in the GYE are at carrying capacity; that bear densities, as such, are driving vital rates; and that dietary changes resulting from environmental change are inconsequential. These claims translate into support for long-standing political aspirations by state wildlife managers and the U.S. Fish & Wildlife Service to remove Endangered Species Act protection for GYE grizzly bears, execution of which has spawned intense, sustained, and corrosive litigative conflict among various interest groups, with much of this conflict focused on disagreements over science produced by the IGBST (Keiter 2022, Greenwald 2023; Section 2). The patterns described here are far removed from the ideal of reflexive scientists participating in a deliberative process that contributes to sustaining a free and democratic society and, in fact, could be described as a betrayal of the public trust (cf., Schön 1983, Susskind et al. 2007, Kitcher 2011, Oreskes 2021).

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9. Supplemental Information

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

The following list of correspondence and publications documents decision-making by the Interagency Grizzly Bear Study Team (IGBST) and US Fish & Wildlife Service (USFWS) following 2011 reversal of the 2007 USFWS rule delisting the Greater Yellowstone grizzly bear population by the U.S. Court of Appeals for the Ninth Circuit. Among other things, these documents show deep involvement of the USFWS and USFWS Recovery Coordinator in configuring, funding, and hastening IGBST research, as well as limiting focus of inquiry to the effects of whitebark pine and population density, as per Section 1 of the Technical Paper as means of providing a basis for rebutting the Ninth Circuit Court of Appeals ruling.

References under the section entitled “Correspondence” list the date followed by the author and recipient(s), concluded by the correspondence subject title.

Correspondence

1. April 11, 2011: R. Shoemaker (USFWS) to M. Haroldson (IGBST). GYE workshop.
2. September 6, 2011: C. Servheen (USFWS) to M. Haroldson (IGBST), cc C. Schwartz, S. Cain. Presentation to YES.
3. September 6, 2011: M. Haroldson (IGBST) to C. Servheen (USFWS), cc C. Schwartz, S. Cain. Presentation to YES.
4. September 7, 2011: C. Schwartz (IGBST) to M. Haroldson (IGBST), cc C. Servheen, S. Cain. Presentation to YES.
5. September 14, 2011: C. Servheen (USFWS) to C. Schwartz (IGBST), m. Haroldson (IGBST), cc S. Cain, R. Harris. Presentation to YES.
6. September 14, 2011: M. Haroldson (IGBST) to C. Servheen (USFWS), cc C. Schwartz, R. Harris, S. Cain. Presentation to YES.
7. September 14, 2011: C. Servheen (USFWS) to M. Haroldson (IGBST), cc C. Schwartz, S. Cain. Presentation to YES.
8. September 16, 2011: R. Harris to M. Haroldson (IGBST), cc C. Schwartz, S. Cain. Presentation to YES.
9. September 19, 2011: S. Cain (NPS) to C. Servheen (USFWS), C. Schwartz, K. Wilmot, M. Haroldson, R. Harris. Presentation to YES.

10. September 21, 2011: C. Servheen (USFWS) to S. Cain (NPS), C. Schwartz, K. Wilmot, M. Haroldson, R. Harris. Presentation to YES.
11. September 21, 2011: S. Cain (NPS) to C. Servheen (USFWS), C. Schwartz, K. Wilmot, M. Haroldson, R. Harris. Presentation to YES.
12. September 23, 2011: C. Servheen to S. Cain (NPS), cc C. Schwartz, K. Wilmot, M. Haroldson, R. Harris. Presentation to YES.
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15. October 9, 2011: R. Harris to M. Haroldson (IGBST), cc C. Servheen, C. Schwartz, R. Shoemaker. Completion of the demographic workshop effort and final report.
16. January 26, 2012: F. Van Manen (IGBST) *to* C. Servheen (USFWS), M. Haroldson (IGBST), R. Shoemaker (USFWS). Workshop.
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18. March 9, 2012: C. Servheen (USFWS) to Ellen Davis (USFS). 3 options for consideration.
19. March 19, 2012: G. Fazer (USFWS) to D. Ashe (USFWS). Yellowstone grizzly options for path forward.
20. March 19, 2012: D. Ashe (USFWS) to G. Fazer (USFWS), cc Siekaniec, Gregory; Gould, R W; Bean, Michael; Guertin, Stephen; Souza, Paul; Walsh, Noreen; Thabault, Michael; Sayers, Rick. Yellowstone grizzly options for path forward.
21. April 2, 2012: G. Fazer (USFWS) to D. Ashe (USFWS), cc Siekaniec, Gregory; Gould, R W; Bean, Michael; Guertin, Stephen; Souza, Paul; Walsh, Noreen; Thabault, Michael; Sayers, Rick. Yellowstone grizzly options for path forward.
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26. April 13, 2012: C. Servheen (USFWS) to M. Haroldson (IGBST). Decision for YES members.
27. April 16, 2012: S. Cain (NPS) to C. Servheen (USFWS). Option 2 action by YES.
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29. May 22, 2012: S. Guertin (USFWS) to N. Walsh (USFWS), cc M. Thabault. Outcome of today's meeting on Yellowstone strategy.
30. May 22, 2012: M. Thibault (USFWS) to C. Servheen (USFWS), cc H. Maddux. Outcome of today's meeting on Yellowstone strategy.

31. May 29, 2012: C. Servheen (USFWS) to M. Haroldson (IGBST), F. Van Manen (IGBST), cc D. Tyers. whitebark synthesis task list. Grizzly Bear WBP Straw Man (2).doc.
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34. June 25, 2012: C. Servheen (USFWS) to F. Van Manen (IGBST), M. Harolson (IGBST), cc R. Shoemaker.
35. June 25, 2012: F. Van Manen (IGBST) to C. Servheen (USFWS), cc M. Haroldson, R. Shoemaker. revisions to the CS and the recovery plan from the workshop outputs. Revisions to the CS and the recovery plan from the workshop outputs.
36. June 25, 2012: C. Servheen (USFWS) to F. Van Manen (IGBST), cc M. Haroldson. Funding.
37. June 29, 2012: F. Van Manen (IGBST) to C. Servheen (USFWS), cc M. Haroldson. Funding.
38. June 29, 2012: F. Van Manen (IGBST) to IGBST, C. Servheen (USFWS). IGBST Workshop Report-please review.
39. July 2, 2012: F. Van Manen (IGBST) to C. Servheen (USFWS). Workshop report-section 6.1.1.
40. July 6, 2012: C. Servheen (USFWS) to F. Van Manen (IGBST), M. Haroldson (IGBST), cc R. Shoemaker. Comments on the workshop draft report
41. July 6, 2012: F. Van Manen (IGBST) to C. Servheen (USFWS, cc M. Haroldson, R. Shoemaker. Comments on the workshop draft report.
42. July 6, 2012: C. Servheen (USFWS) to F. Van Manen (IGBST), cc M. Haroldson, K. Smith, D. Tyers. Funding.
43. July 6, 2012: F. Van Manen (IGBST) to C. Servheen (USFWS), K. Smith (MSU), cc M. Haroldson. Funding.
44. July 16, 2012: D. Morgan (USFWS) to M. Thabault (USFWS), C. Servheen (USFWS), cc R. Sayers. DTS Assignment – Requests the secretary work with the State of Wyoming to expedite review to delist the grizzly bear under ESA.
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49. July 24, 2012: D. Ashe (USFWS) to S. Guertin (USFWS), N. Walsh (USFWS), cc G. Fazer, C. Eustine. We okay with this? “Secretary Salazar says grizzly delisting expected by 2014.”
50. July 24, 2012: M. Thabault (USFWS) to S. Guertin (USFWS), B. Fahey (USFWS), cc N. Walsh. We okay with this?
51. July 24, 2012: C. Servheen (USFWS) to M. Thabault (USFWS). We okay with this?.
52. August 8, 2012: F. Van Manen (IGBST) to C. Servheen (USFWS), R. Shoemaker (USFWS), cc R. Harris, M. Haroldson. Demographic workshop report. Attachments: GYE monitoring mortality workshop report FINAL DRAFT (8Aug2012).docx.

53. August 13, 2012: C. Servheen (USFWS) to F. Van Manen (IGBST), M. Haroldson (IGBST). Comments on workshop document. Attachments: RShoe CS edits_GYE monitoring mortality workshop report FINAL DRAFT {8Aug2012).docx; GYE monitoring mortality workshop report FINAL DRAFT {8Aug2012) minor CS edits addede.docx; RBH minor edits 080812 {2).docx.
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Documents

55. Unknown Author (July 11, 2011). Yellowstone demographics workshop. With mark-up by C. Servheen (USFWS).
56. Unknown Author (July 12, 2011). Summary of the July 11-12 workshop to address issues of unduplicated counts and mortality limits in the GYE.
57. Interagency Grizzly Bear Study Team (December 19, 2011). Overview of Demographic and Mortality Analyses-IGBST- Winter 2011-2012 (DRAFT): Demographic review analyses.
58. Interagency Grizzly Bear Study Team (February 1, 2012). GYA demographics workshop.
59. Interagency Grizzly Bear Study Team (February 3, 2012). GYA demographics workshop.
60. Interagency Grizzly Bear Study Team (March 8, 2012). Study team meeting to discuss details regarding proposed mortality line and mortality limits and other topics, 7-8 March, 2012.
61. Bjornlie, D., et al. (April 5, 2012). Updating and Evaluating Approaches to Estimate Population Size and Sustainable Mortality Limits for the Yellowstone Grizzly Bear (Draft): Report summarizing discussion of issues and analyses during workshops at Bozeman, Montana, February 3-4, 2011; July 11-12, 2011, and February 1-2, 2012.
62. Servheen, C. (April 18, 2012). Components of the Grizzly Bear-WBP Synthesis document for FWS Straw man.
63. C. Servheen (April 18, 2012). Assigned task (+ proposed task deadline).
64. Aber, B. et al. (June 29, 2012). Updating and Evaluating Approaches to Estimate Population Size and Sustainable Mortality Limits for the Yellowstone Grizzly Bear: Report summarizing discussion of issues and analyses during workshops at Bozeman, Montana, February 3-4, 2011; July 11-12, 2011; and February 1-2, 2012. With mark-up by C. Servheen (USFWS).
65. Interagency Grizzly Bear Study Team (July 17, 2012). Grizzly bears and whitebark pine in the Greater Yellowstone Ecosystem: Project outline.
66. Interagency Grizzly Bear Study Team (July 17, 2012). Grizzly bears and whitebark pine in the Greater Yellowstone Ecosystem: Project outline. C. Servheen mark-up.
67. F. Van Manen (June 21, 2014). Q & A Interagency Grizzly Bear Study Team (IGBST) – Upper Green Allotment.

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A Critique of Science Practices and Products
by the Interagency Grizzly Bear Study Team
2006-2023

Report GBRP-2023-1
2023

The Grizzly Bear Recovery Project

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