Grizzly Bears for the Southwest

History & Prospects for Grizzly Bears in Arizona, New Mexico and Colorado

David J. Mattson, Ph.D.

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The Grizzly Bear Recovery Project

P.O. Box 2406,
Livingston,
Montana

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Abstract

For perhaps 30,000 years grizzly bears ranged throughout the mountains and riparian areas of what would eventually become the southwestern United States. But in a remarkably short 50-year period between 1860 and 1910 Anglo-Americans killed roughly 90% of the grizzly bears in 90% of the places they once lived. Most of the remaining grizzlies had been killed by the 1930s. This report provides a detailed account of natural history, relations with humans, and current and future prospects for grizzly bears of the Southwest, emphasizing the millennia prior to ascendence of Anglo-Americans.

The report's narrative is essentially chronological, starting with deep history spanning the late Pleistocene up through arrival of European colonists (Section 3.1); the period of Spanish and Mexican dominance (Section 3.2); and then the period of terminal grizzly bear extirpations that began with the political and military dominance of Anglo-Americans (Section 3.3). Section 4 examines current environmental conditions and related prospects for restoring grizzly bears to the Southwest. Section 5 completes the chronological arc by forecasting some of what the future might hold, with implications for both grizzly bears and humans.

The background provided in Section 2 offers a synopsis of grizzly bear natural history as well as a summary of foods and habitats that were likely important to grizzlies. Throughout the Holocene there was a remarkable concentration of diverse high-quality bear foods in highlands of the Southwest, notably in an arc from the San Francisco Peaks of Arizona southeast along the Coconino Plateau and Mogollon Rim to a terminus in the White, Mogollon, and Black Range Mountains in New Mexico. Additional high-quality habitat existed in the Sacramento, San Juan, Jemez, and Sangre de Cristo Mountains of New Mexico and adjacent Colorado.

Grizzlies in the Southwest survived remarkable extremes of climate and habitats for perhaps as long as 100,000 years. They also survived substantial variation in human-propagated impacts that culminated in the Crisis of 875-1425 C.E.—a period typified by episodic drought and the highest human population densities prior to recent times. In contrast to relatively benevolent attitudes among indigenous populations, there is little doubt that the terminal toll taken on grizzly bears by Anglo-Americans after 1850 C.E was driven largely by a uniquely lethal combination of intolerance and ecological dynamics entrained by the eradication or diminishment of native foods and the substitution of human foods, notably livestock, that catalyzed conflict.

More positively, the analysis presented here of current habitat productivity, fragmentation, and remoteness—as well as regulations, laws, and human attitudes—reveals ample potential for restoration of grizzlies to the Southwest, including three candidate Restoration Area Complexes: the Mogollon, San Juan, and Sangre de Cristo, capable of supporting around 620, 425, and 280 grizzlies each. Major foreseeable challenges for those wishing to restore grizzly bears to these areas include sanitation of human facilities, management of livestock depredation, education of big game hunters, coordination of management, and fostering of accommodation among rural residents. Climate change promises to compound all of these challenges, although offset to an uncertain extent by prospective increases in human tolerance.

But the evolutionary history of grizzly bears also provides grounds for optimism about prospective restoration. Grizzly bears have survived enormous environmental variation spanning hundreds of thousands of years, including many millennia in the Southwest. Grizzlies survived not only the inhospitable deeps of the Ice Ages in Asia and Beringia, but also the heat and drought of the Altithermal on this continent. It was only highly-lethal Anglo-Americans that drove them to extinction in the Southwest, which is why human attitudes—more than anything else—will likely determine prospects for restoring grizzly bears.

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1. Introduction

For perhaps 30,000 years grizzly bears ranged throughout the mountains and riparian areas of what would eventually become the southwestern United States. But no longer. In a remarkably short 50-year period between 1860 and 1910, Anglo-Americans killed roughly 90% of the grizzly bears in 90% of the places they once lived (Mattson 2021a). Most of the remaining grizzlies were finished off by the 1930s, with perhaps a handful surviving up to the 1970s in the San Juan Mountains of Colorado and the Sierra Madre Occidentale of Chihuahua, Mexico (Mattson 2021a).

More to the point, there are no grizzlies left in the Southwest to inspire modern generations of people or instruct us about how this species lived and died in a semi-arid environment noted for its vicissitudes. We are left with little more than our imaginings, most of which are informed by written accounts left by the few Europeans who took note of grizzlies during the comparatively brief time that grizzlies and Europeans interacted in the Southwest.

These accounts mostly by Anglo-Americans are noteworthy for what they both include and exclude. There is little evident curiosity about grizzlies, except to the extent that curiosity yielded insight into how to kill bears more efficiently. A reader will look in vain for any mention of natural history—whether diets, habitats, or behaviors—other than as observations incidental to the pursuit and persecution of grizzlies. Instead, the near-exclusive focus is on the courage, skill, and endurance, not only of men pursuing and killing grizzlies, but also the beloved hounds that aid and abet them (e.g., Stevens 1943, Evans 1951). The grizzlies themselves feature only to the extent that they are willey opponents, ferocious foes, or merciless depredators—attributes that serve little more than to enhance the heroic qualities of those in pursuit.

The picture of grizzly bears that emerges is incomplete, distorted, and misleading. It is also a time capsule of human perspectives that were dominant for centuries and only recently supplanted by others more benevolent and graciously inclusive of wild nature—including grizzly bears. An ethos of domination, intolerance, and eradication that led to the slaughter of predators during the 1800s and early 1900s has been slowly displaced by an ethos of moral obligation and appreciation codified in U.S. laws such as the 1974 Endangered Species Act. But, with the exception of a few surviving animals in the San Juan Mountains, grizzly bears in the Southwest had by 1975 already slipped through the safety net of the ESA and been relegated to the literary dust-bin of self-congratulatory stories crafted by men who had, by and large, devoted themselves to glorifying their deeds and eradicating predators.

The time is ripe for a corrective that comports with emergent human values and worldviews, the insights we now have into grizzly bear natural history, and a substantially changed physical environment. A useful contemporary account of grizzly bears in the Southwest moreover needs to be comprehensive and attentive to the long arc of history—in contrast to the continuing emphasis placed by a corpus of recent Southwest literature on fractious relations between grizzly bears and Anglo-Americans during the last 200 years (Petersen 1995, Bass 1995, Brown 1996, Davis 2001, Brown & Murray 2014). This report hopes to offer such a corrective.

1.a. My Motivation & Premise

I spent all or part of 19 years living, working, and recreating in the Southwest, both as a wildlife researcher and seasonal visitor. My investigations of mountain lions in the Southwest during 2002-2013 entailed field work in study areas that included the Flagstaff uplands, the North and South Kaibab Plateaus, the Grand Canyon in-between, Utah's Zion and Capital Reef National Parks, and the Nevada National Security Site. Taken together, these study areas spanned environments ranging from Mojave Desert to alpine, including piñon-juniper woodlands, ponderosa pine and mixed conifer forests, semi-desert and temperate grasslands, desert scrub, and interior chaparral. More recently, my over-winter stays along the upper Gila and Mimbres Rivers in New Mexico have allowed me to make frequent forays into the Mogollon and Black Range Mountains where grizzlies managed to survive into the 1930s (Brown 1996). From all of this I have been left with vivid impressions of not only extensive wild country, but also severe human impacts.

Of particular relevance to this report, I brought the critical eye of a grizzly bear researcher to these travels, devloped by over 20 years studying grizzlies and providing expert input for grizzly bear managers in areas straddling the spine of the Rocky Mountains from the Yukon Territories to the Greater Yellowstone Ecosystem (https://www.allgrizzly.org/david-mattson). More concretely, whether on the ground or driving roads, I found myself taking note of potential grizzly bear foods and habitats, as well as more problematic features such as livestock husbandry practices, off-road vehicles, sport hunters, and the overall human footprint. I was left with a profound curiosity about not only what life must have been like for grizzly bears prior to environmental transformations caused by Europeans, but also about prospects for restoring grizzlies to the Southwest with supplanting of the toxic human culture of the 1800s and early 1900s by the more generous and inclusive culture of the past 50 years.

I approach this report with the premise that recent changes in federal law, human culture, and regional economic and demographic patterns allow for the possibility of restoring grizzly bears to the Southwest—something that may have seemed impossible 50 years ago. The Southwest's extensive wildlands are also self-evidently home to thriving populations of black bears (*Ursus americanus*; Scheick et al. 2014, Gould et al. 2018) and replete with bear foods such as acorns, piñon pine seeds, and manzanita berries (see Section 2). Even so, I am not naïve. In this report, I look with a critical eye not only at the exigencies of history and a current situation beset with problematic human impacts, but also at a future that promises to severely challenge both wildlife and humans.

This report hopefully paints a vivid yet realistic picture of not only the rich history and promising future of grizzly bears in the Southwest, but also the trials and tribulations that grizzlies successfully navigated for millennia, which is, in itself, cause for optimism.

1.b. Geographic Scope

The geographic focus of this report is the southwestern United States, or Southwest, which is conventionally defined as being centered on the contemporary states of Arizona and New Mexico. For purposes of this report, the geographic scope for most of my analyses includes adjacent portions of Utah and Colorado, largely because core grizzly bear habitats span the arbitrary northern political boundaries of Arizona and New Mexico. My considerations of diet, habitat use, pre-European distributions, and extirpation patterns are also inclusive of northern Mexico, largely because this geographic area provides important context for understanding the history and ecological relations of grizzly bears in Arizona and New Mexico.

The 777,865-km^2 study area encompassing Arizona, New Mexico, southern Utah, and southern Colorado extends south to north from 31° 20' to 38° 07' N latitude and east to west from 103° 00' to 115° 00' W longitude, and is delimited to the east by arid grasslands, to the south and west by the Mohave, Sonoran and Chihuahuan Deserts, and to the west by the Great Basin (Figure 1a). In Arizona, elevations range from 30 m to 3860 m, in New Mexico, 915 m to 4011 m, and in Colorado, 1490 m to 4360 m.

North-central portions of the focal area consist of the deeply incised Colorado Plateau surrounded by higher elevations of the San Juan, Sangre de Cristo, and Mogollon Mountains in New Mexico and Colorado, and the Kaibab and Mogollon Plateaus and their escarpments in Arizona. The southern and eastern parts of the study area consist of broad plains or valleys broken by isolated peaks and mountain ranges such as the San Mateo, San Andreas, Sacramento, and Guadalupe Mountains in New Mexico. The large size and elevational amplitude of the study area results in a broad spectrum of climates ranging from alpine on the highest peaks to hot arid desert in the lowest plains and valleys. During the last 20 years annual precipitation and temperatures averaged about 90–200 mm and 22–24 °C in the hottest driest deserts and about 400–800 mm and 5–10 °C at the coldest wettest weather stations, excluding the highest mountains. Annual snowfall at elevations >2100 m often exceeded 250 cm.

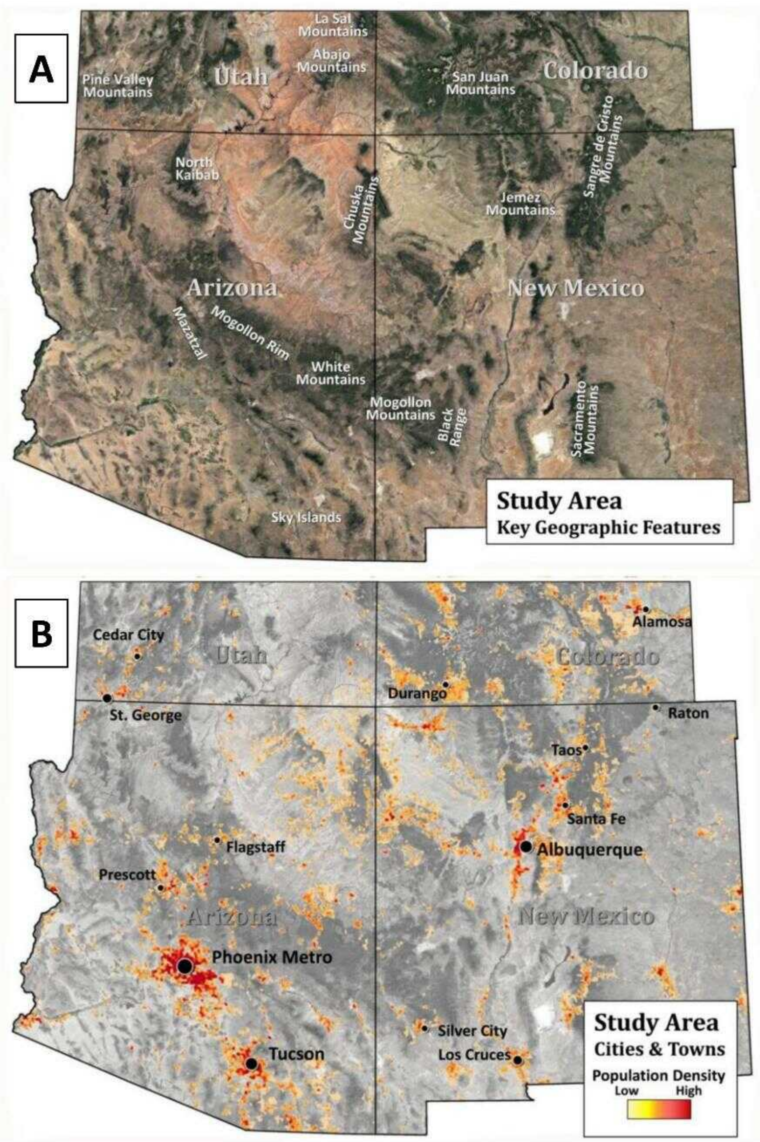


Figure 1. These maps show key human-associated and geographic features of the focal Southwest study area, including (A) major mountain ranges or other highlands of relevance to the history and current potential of grizzly bear habitat; and (B) current human densities and larger towns and cities.

As of 2020, Arizona and New Mexico had 7,152,00 and 2,118,000 residents, respectively, but with most people concentrated in large population centers such as the Phoenix (4,846,000), Tucson (1,043,000) and Albuquerque (923,600) metropolitan areas. Most areas remain relatively unpopulated (Figure 1b), largely due to the fact that 39% of Arizona, 35% of New Mexico, 65% of Utah, and 36% of Colorado are in federal ownership.

1.c. Overview of the Report

With the exception of Section 2, the structure of this report in essentially chronological, starting with deep history spanning the late Pleistocene up through arrival of European colonists (Section 3.1); the period of Spanish and Mexican dominance (Section 3.2); and then the period of terminal grizzly bear extirpations that began with the political and military ascension of Anglo-Americans (Section 3.3). Section 4 examines current environmental conditions and related prospects for restoring grizzly bears to the Southwest. Section 5 completes the chronological arc by forecasting some of what the future might hold, with implications for both grizzly bears and humans.

2. Foundations

Any useful rendering of history or current and future prospects for grizzly bear restoration necessarily starts with natural history, which is the topic of Section 2. Grizzly bear life strategies shaped by millennia of evolution provide an essential guide to identifying features of the environment that drive grizzly bear reproduction, survival, and longer-term population trajectories, which are thus the logical focus of any historical narrative or analytic exercise. Section 2 accordingly features the essentials of grizzly bear life strategies as well as habitats and foods that predictably govern the fates of grizzly bear populations.

2.a. Some Relevant Natural History

In common with other ursids, grizzly bears have a singular life history rooted in a suite of inextricably interconnected morphological, behavioral, and physiological adaptations that have been shaped by millions of years of evolution. Grizzlies are distinguished by large size, prehensile dexterity, perpetual obesity, ambulatory inefficiency, intelligence, omnivory, adaptive dietary flexibility, winter torpor, habitual denning, embryonic diapause, short gestation, and extreme altriciality of young (Stirling & Derocher 1990). Taken together, these traits define a unique niche that was shaped by both the relaxation and acceleration of selective evolutionary forces set in motion during the Eocene, over 40-million years ago (Jiangzuo & Flynn 2020, Hassanin et al. 2021).

Use of dens allows female grizzlies to not only succumb to winter torpor, but also produce altricial young that otherwise would not survive a threatening external world (Ramsay & Dunbrack 1986). Winter torpor passed in the shelter of a den moreover allows grizzlies to escape rigors of winter that are accentuated by both their dependence on vegetal foods as well as their comparative inefficiency as predators (Fowler et al. 2021). At the same time, omnivory allows for the accumulation of adipose reserves needed to sustain winter torpor as well as the adaptive exploitation of various animal and vegetal foods rich in fat and digestible energy (Rode & Robbins 2000, Robbins et al. 2012, Erlenbach et al. 2014).

Omnivory has engendered other advantages. It allowed grizzlies, as a species, to escape evolutionary constraints on body size and grow large (Fowler et al. 2021). Large size not only conveys energetic efficiencies, but also comparative invulnerability to most—but not all—predation. Substantial absolute and comparative reserves of body fat furthermore allow grizzlies to survive the vicissitudes of annually variable environments better than most other large mammals (Millar & Hickling 1990)—which facilitates occupancy of and extraction of foods from widely varied environments subject to extreme weather, including the Gobi Desert (Luvsamjamba et al. 2016), Tibetan Plateau (Ai-Chun et al. 2006), and Himalayas (Aryal et al. 2012).

Without the need to escape predators or chase down and kill prey, grizzlies can survive the ambulatory inefficiencies of dexterous forelimbs and paws (Shine et al. 2015, 2017; Pagano et al. 2018). As a pay-off, dexterity allows them to grapple with, manipulate, and extract foods that would otherwise be unavailable—including roots and fossorial rodents (Iwaniuk et al. 2000). Efficient extraction of subterranean foods is further aided by their exceptionally long blunt claws and stout forelimbs powered by a large suprascapular muscle mass comprising the grizzlies' characteristic hump (Erdbrink 1953, Davis 1964). This ability to access subterranean foods differentiates grizzlies from all other extant bear species, and facilitates their occupancy of comparatively arid open environments (Ferguson & McLoughlin 2000, Mowat & Heard 2006).

But large body size comes with a price. Unlike most other bear species, including sun bears and American and Asiatic black bears, adolescent and adult grizzlies can't climb trees, and so lack access to the security provided by an arboreal escape—even if only from predatory conspecifics (Herrero 1972, 2002). Large body size also engenders a low reproductive rate—amongst the lowest of any terrestrial mammal (Jones et al. 2009). As a consequence, persistence of grizzly bear populations depends on exceptionally high survival rates among adolescent and adult grizzlies, in excess of 90% per annum for adult females (Garshelis et al. 2005, Schwartz et al. 2006, Mace et al. 2012).

Much of the grizzly bear life strategy was plausibly shaped by the exigencies and opportunities of Pleistocene environments, especially the open arid environments of various glacial maxima. Grizzly bears took form as a species in Eurasia and rapidly diversified between 900,000 and 300,000 years ago (Doronina et al. 2015)—an epoch typified by extreme cold and aridity punctuated by more clement periods (Elderfield et al. 2012, McClymont et al. 2013). Occupancy of open variable environments coinhabited by potential predators such as simitar-toothed cats (*Homotherium latidens*), steppe lions (*Panthera spelaea*), and cave hyenas (*Crocuta crocuta spelaea*; Kurtén 2009) was likely the genesis of an accelerated increase not only in grizzly bear body size, but also aggressive behavior (Herrero 1973). There is little doubt that body sizes of brown bears peaked during the coldest epochs of the Pleistocene (Marciszak et al. 2015, 2019), although a link to aggressive behavior defies definitive testing. Even so, as a baseline, grizzlies tend to be more defensively aggressive compared to not only American or Asiatic black bears, but also polar bears (Herrero 2002)—although the latter tends to be more overtly predatory (Wilder et al. 2017).

The upshot is a distinctive species known for its fortitude, versatility, problem-solving abilities, and aggressive defense of offspring and personal space (Mattson 2021b). Yet grizzly bear populations are acutely vulnerable to evolutionarily novel predators—notably humans—that negate this complex web of adaptations by targeting the species' least elastic trait: survival of adults and adolescents (McLellan et al. 1999, Benn & Herrero 2002, Schwartz et al. 2006). Rapid and widespread extirpations of grizzly bear populations in the United States and Europe (Mattson & Merrill 2002, Albrecht et al. 2017), as well as challenges conserving the species where it remains threatened, is testimony to this simple fact.

One further aspect of natural history is worth highlighting of relevance to explaining extirpations of grizzly bears in the Southwest, especially with arrival of Anglo-Americans (see Section 3.3). Despite being a centerpiece of grizzly bear life history, the onset and duration of denning and winter torpor are highly variable among populations. Not only do these temporal dimensions differ among males and gravid and non-gravid females, but also with latitude, climate, and availability of winter foods (Fowler et al. 2019, González-Bernardo et al. 2020).

Onset is earlier and of longer duration farther north as well as for gravid females in all locations—although delayed at higher latitudes where abundant late-spawning salmonids or other late-season high-quality foods are available (Pigeon et al. 2016, Fowler et al. 2019).

Generalized relationships based on latitude suggest that onset of denning for grizzlies in the Southwest occurred sometime between early and late December, roughly 1-½ to 2 months later than in the U.S. northern Rockies, and lasted roughly 100-120 days, approximately 2-½ to 3 months less than for grizzlies 10º latitude farther north (Fowler et al. 2019). More to the point, this abbreviated denning period would have increased the exposure of grizzlies to Europeans bent of eradicating them, potentially further exacerbated if livestock carrion or calves were available and inducing bears to remain active longer than they otherwise might have been—for males even to the extent of forgoing denning altogether (e.g., Gunther & Smith [2004], Nores et al. [2010], as has been documented for black bears in southerly latitudes [e.g., Hellgren et al. 1987, Doan-Crider et al. 1996]).

2.b. Geographic Frame

Even though individual grizzly bears can survive in depauperate environments, grizzly bear populations are manifestly sensitive to variations in habitat productivity. Population-averaged rate of body mass increase, ages of sexual maturity, interbirth intervals, and asymptotic body sizes are all affected by aggregate habitat productivity (Kingsley et al. 1983, Bartareau et al. 2011; Hilderbrand et al. 2018, 2019; Cameron et al. 2020). As a consequence, population densities can vary by orders-of-magnitude, even in interior regions where grizzlies rely exclusively on terrestrial as opposed to marine foods (Mowat et al. 2013, Mattson 2021a).

These effects of productivity are directly relevant to framing any useful analysis of history or prospects for restoration of grizzly bears in the Southwest. Geospatial configurations of productive habitat define areas that have disproportionately shaped the fates of Holocene grizzly bear populations, and serve as well to identify areas where human have likely had their greatest impacts. Of contemporary relevance, the juxtapose of productive habitat with remote areas subject to legal protections predictably configures prospects for restoring grizzly bears to the Southwest perhaps more than any other landscape feature. But productivity, in the abstract, also throws into relief the importance of specifying elements that more concretely define this notion, notably, distributions of specific bear foods rich in digestible energy and nutrients.

As a corollary, in addition to highly productive habitats, there are also areas that are too barren or too hot and dry for grizzly bears to survive. This is clearly relevant to the Southwest given that the Mojave and Sonoran Deserts are, year-round, the hottest environments in North America (PRISM Climate Group). The Mojave Desert is also among the least productive (https://gisgeography.com/ndvi-normalized-difference-vegetation-index/). This matters to grizzly bears because sustained high ambient temperatures can limit where they live or when they can be active, which they can only partially offset by shifting to predominantly nocturnal activity or by bathing in standing water (McLellan & McLellan 2015, Luvsamjamba et al. 2016, Pigeon et al. 2016, Ansari & Ghoddousi 2018, Johnson et al. 2018, Rogers et al. 2021). If night-time temperatures are high and free water limited, there is little prospect that grizzlies would be able to adequately thermoregulate and thus survive.

The map in Figure 2 shows the approximate pre-European distribution of grizzly bears in the Southwest, inclusive of Mexico—essentially a binary map of where grizzlies occurred based on documented observations, modeled habitat relations, and the extent of broad-scale ecoregions productive enough and cool enough to have supported grizzly bear populations (see the figure caption for sources). This map, although coarse-grained, attends to habitat productivity as well as thermal limits, and offers a more realistic representation of grizzly bear distributions compared to blob maps used by the U.S. Fish & Wildlife Service up through the 2000s (U.S. Fish & Wildlife Service 1982, 1993) and, as such, offers a broad-scale geospatial frame for accounts of history as well as assessments of future prospects.

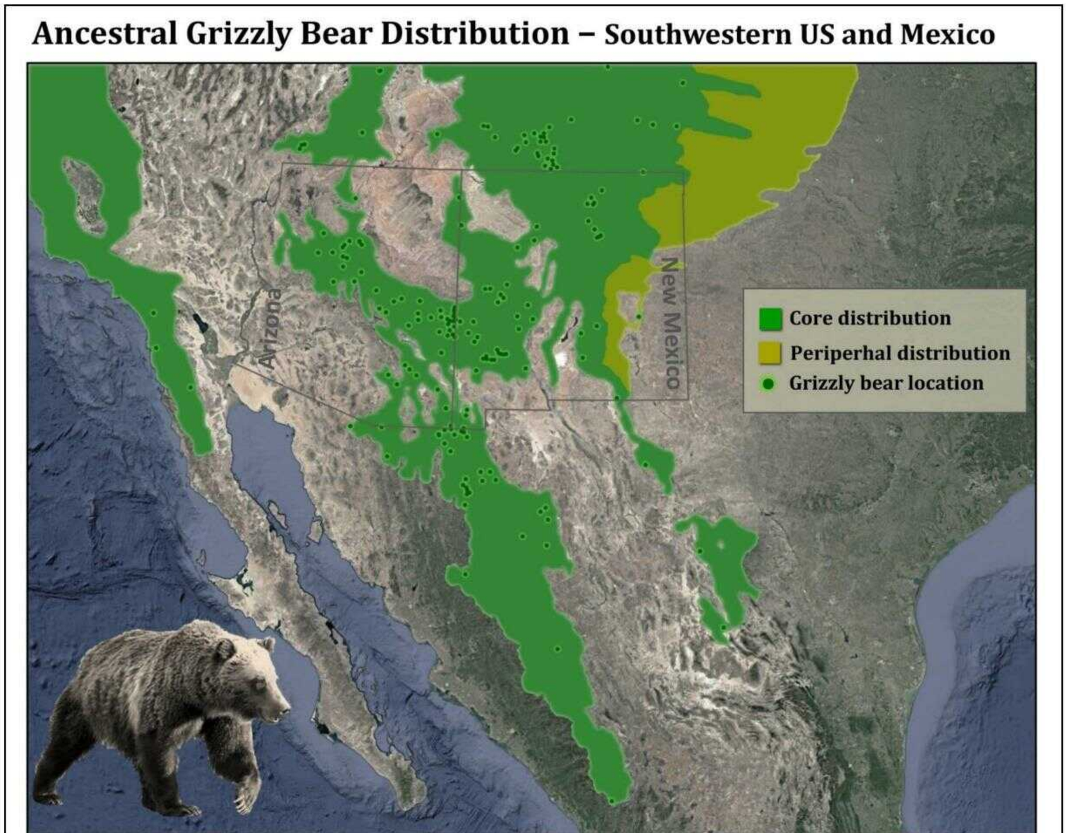


Figure 2. This map shows the approximate distribution of grizzly bears at the time of first contact with Europeans in what was to become the southwestern United States and northern Mexico. Green denotes grizzly bear strongholds and, lighter yellow-green, areas where grizzlies would have been present but largely restricted to linear west-east trending riparian zones along major rivers. Dark-green dots denote encounters with grizzly bears documented by literate Europeans, exclusive of California. This distribution map was constructed based on documented bear locations together with coarse-grained maps of ecoregions and distributions of known high-quality bear foods such as bison (*Bision bison*). Mattson (2021) provides a comprehensive list of sources for grizzly bear locations. My primary regional sources were Bailey (1905, 1931), Barnes (1927), Brown (1996, 2009), Cary (1911), Dasmann (1969), Davis (2001), Gallo-Reynoso et al. (2008), Goldman (1951), Leopold (1959), Pedersen (1995), Trevino & Jonkel (1986), and Warren (1910), augmented by maps of grizzly bear distributions from Mattson (2021), the predicted distribution of grizzlies in Mexico by Ceballos et al. (2006) and the predicted Pleistocene distribution from Kantelis (2017) and Luna-Aranguré et al. (2019). My sources for ecoregion maps are listed in Mattson (2021), augmented by Brown (1994), Commission for Environmental Cooperation (2005), and U.S. Environmental Protection Agency (2007, 2016). The reconstructed distribution of grizzly bears in Mexico corresponds with the Western Sierra Madre and Western Sierra Madre Piedmont Ecoregions. To the east, the reconstructed distribution corresponds with portions of the Eastern Sierra Madre and Tamaulipas-Texas Semiarid Plain Ecoregions occupied by black bears (*Ursus americanus*), but inclusive of historical grizzly bear locations.

The maps in Figure 3 offer a finer-resolution geospatial depiction of suitable grizzly bear habitat based on environmental conditions (Figure 3a) and historical grizzly bear distributions (Figure 3b) for the U.S. portion of the Southwest. The map in 3a shows in pink and burgundy areas that are likely too hot and arid to have supported grizzlies, along with intrinsic habitat productivity shown in shades of green. Productivity is represented by the Normalized Difference Vegetation Index (NDVI), which is highly correlated with documented grizzly bear locations in the Southwest as well as indices of wetness and greenness derived from Landsat imagery (Mattson & Merrill 2021a). The latter have consistently performed well in models of fine-scale habitat selection by grizzlies as well as broad-scale patterns of population density (Mace et al. 1996; McLoughlin et al. 2002; Nielsen et al. 2002; Boyce & Waller 2003; Apps et al. 2004; Mattson & Merrill 2004, 2021b).

The map in 3b integrates information from 3a with documented observations of grizzlies (red triangles) to produce a more detailed, albeit somewhat speculative, reconstruction of pre-European grizzly bear distributions, differentiating areas that likely supported source (i.e., core) versus sink (i.e., peripheral) populations. According to this rendering, the Great Plains of Colorado and New Mexico were probably only marginally suitable for grizzly bears, largely contingent on the availability of bison carrion (see below and Mattson [1997] and Green et al. [1997]).

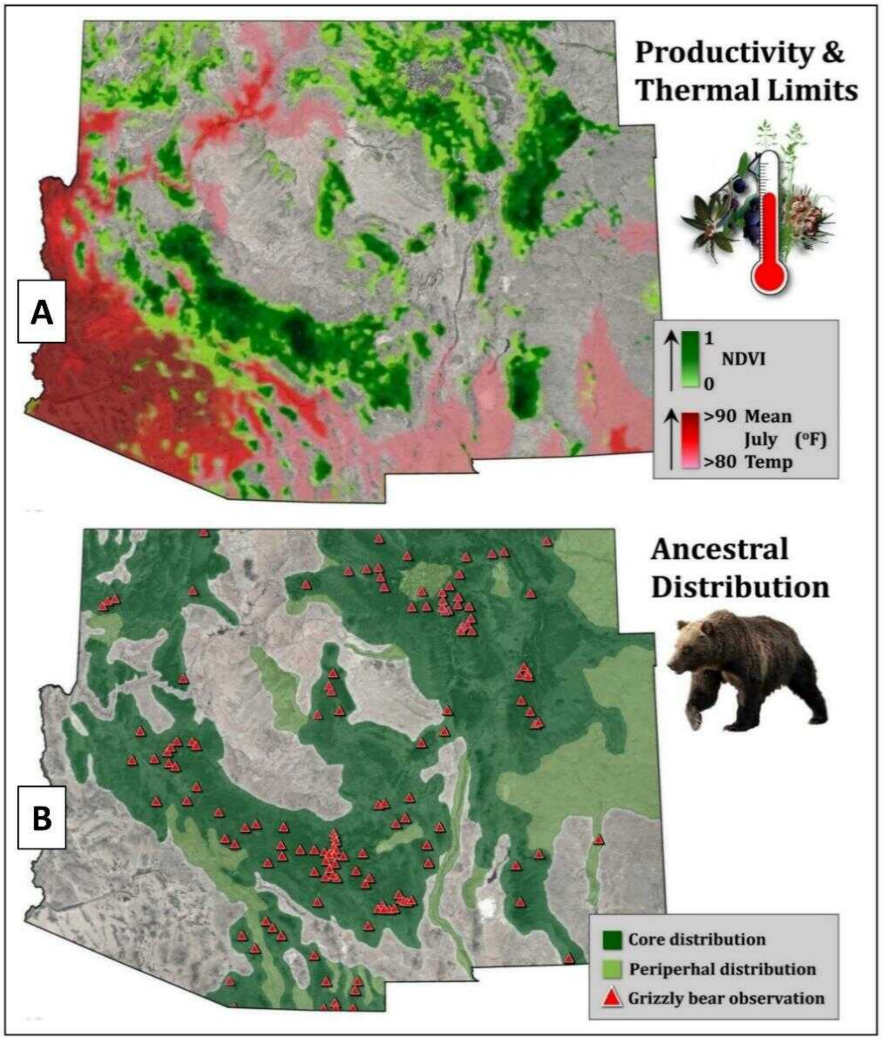


Figure 3. The map in (A) shows features of the biophysical environment that likely configured where grizzly bears lived in the Southwest during most of the Holocene. Shades of green in (A) positively correlate with values of the Normalized Difference Vegetation Index (NDVI), truncated to exclude vales <0.5 (2015 average; map by Abraham Parrish [2020]), whereas shades of red positively correlate with increasing average July temperatures (from PRISM Climate Group, 30-year normal, 1981-2010). NDVI has a strong positive correlation with locations of historical bear observations (see Figure 26), whereas average July temperatures >80°F (27°C) likely imposed limits on where grizzly bears could adequately thermoregulate (see Mattson & Merrill [2021a]). The map in (B) provides a fine-grained look at where most grizzly bears probably lived in the Southwest at the time of first contact with Europeans. Darker green denotes areas that likely served as source habitats, whereas lighter green denotes areas where grizzly bears were likely present but reliant on an influx of dispersers for persistence. This reconstruction of grizzly bears distributions integrated information on intrinsic productivity and thermal limits from (A) with observations of grizzly bears documented by Europeans (the red triangles in [B], from Mattson & Merrill [2021a]) and distributions of higher-quality bears foods—including bison—shown in Figures 6 through 10.

Of relevance to what follows, the maps in Figure 3 define the geospatial bounds within which foods, habitats, and human-propagated impacts likely dictated fates of grizzly bear populations, not only with the advent of European colonists, but also during preceding millennia of the Holocene.

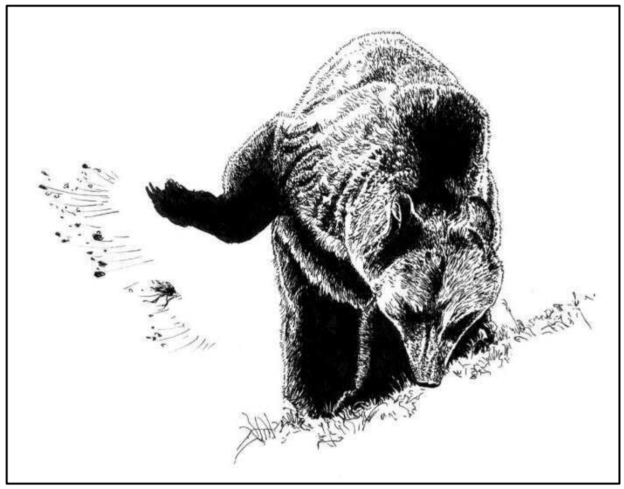
2.c. Diets & Habitats

Grizzly bear diets are foundational to any useful understanding of history and future prospects for restoration, principally because diets dictate the energetic and nutritional lives of bears and, through that, reproductive success and demographic trajectories. Moreover, diets indirectly configure mortality risk for grizzlies to the extent that acquisition of key foods exposes them to predators, notably humans and, in the case of adolescents and females, adult male grizzlies. The first are potentially lethal to all bears whereas the second are potentially lethal to cubs and yearlings.

Unfortunately, we know comparatively little about grizzly bear diets in the Southwest based on direct evidence. As I noted before, European observers expressed little interest in the natural history of grizzlies and, moreover, had no apparent expertise in identifying plant foods or any smaller animals other than big game that might have been consumed by grizzlies. For reasons presumably related to the construction of narratives that legitimized the persecution of predators, cattle featured prominently—certainly disproportionately—as a component of grizzly bear diets documented by early Europeans (see Section 3.3). People who are interested in developing a replete picture of grizzly bear diets, habitats, and foraging behaviors in the Southwest are seemingly left with little to inform such an endeavor.

But there is ample evidence from black bear research in the Southwest that can be judiciously extrapolated to grizzly bears. Black and grizzly bears are omnivores that share numerous life history traits. Despite the fact that black bears are smaller, more fecund, and less aggressive, there are substantial commonalities of diet and foraging behaviors, especially in interior regions of North America where there is a dearth of large herbivores (Mattson et al. 2005). In fact, in regions where both species rely heavily on fruit and herbaceous foods, black and grizzly bear diets can be compositionally indistinguishable.

However, there are two notable provisos. Grizzly bears are clearly better adapted than black bears to exploiting subterranean foods such as roots and fossorial rodents (see Section 2.1). Unlike black bears, grizzly and brown bears in places as far flung as central Asia, the Yellowstone ecosystem, the Canadian arctic, and the Rocky Mountains consume substantial amounts of roots and rodents, including marmots (*Marmota himalayana*), pikas (*Ochotonia curzoniae*), ground squirrels (*Urocitellus parryii*), pocket gophers (Thomomys talpoides), biscuitroot (*Lomatium cous*), yampa roots (*Perideridia gairdneri*), and sweetvetch roots (*Hedysarum* spp.; Holcroft & Herrero 1984; Mattson 1997b, 2000, 2004; Ai-Chun et al. 2006; Aryal et al. 2012; Barker et al. 2015).



More to the point, black bear diets offer little insight into subterranean foods that grizzly bears might have exploited in the Southwest. But traditional diets of humans—also a large-bodied omnivore—prospectively fill this knowledge gap given that people have routinely used tools and fire to overcome innate morphologic limitations to exploit subterranean foods. A review of traditional human diets in the Southwest and adjacent Mexico reveals a host of roots from species that grizzly bears likely exploited as well, including wild relatives of the domesticated potato (*Solanum* spp.), various members of the carrot (e.g., *Cymopterus* spp.) and pea families (*Pomaria jamesii*, *Dalea purpurea*, *Hoffmannseggia glauca* and *Astragalus ceramicus*), plus sego lily (*Calochortus nutallii*; for sources, see the caption of Figure 11, below).

In addition to this difference organized around fossorial foods, anywhere that bears of both species have access to meat from large herbivores, grizzly bears consume far more of it and, among grizzlies, adult males consume most of all (Mattson 1997a, Jacoby et al. 1999, Hobson et al. 2000, McLellan 2011, Fortin et al. 2013, Merkle et al. 2017). This conspicuous exception likely arises from the fact that larger-bodied grizzly bears are better able to both prey on large herbivores and dominate any carcasses they might find, compounded by their comparative inefficiencies relative to black bears when foraging on lower-density patches of both fruit and herbaceous forage (Welch et al. 1997, Rode et al. 2001, Mattson et al. 2005).

Of final relevance here, consumption of meat also plays a prominent role in configuring mortality risk for grizzly bears, whether from humans or from adult male grizzlies. Concentrated sources of meat that aggregate bears predictably lead to increased risk of infanticide perpetrated by adult males (Mattson et al. 1992, Olson 1993), which is presumably why many female bears accompanied by dependent offspring forego foraging opportunities that bring them near adult males exploiting large-bodied carrion or concentrations of spawning salmonids

(Reinhart & Mattson 1990, Mattson & Reinhart 1995, Ben-David et al. 2004, Gunther & Smith 2004, Rode et al. 2006, Steyaert et al. 2013). Perhaps more self-evidently, exploitation of meat from livestock or ungulates killed by big game hunters often leads to the death of involved grizzlies, either because humans act in self-defense or in retaliation (Johnson & Griffel 1982, Jorgensen 1983, Knight & Judd 1983, Anderson & Moody 2002, Gunther et al. 2004, Haroldson et al. 2004, Wells et al. 2019)—with clear implications for understanding the history as well as future prospects of grizzly bears in the Southwest (e.g., Brown 1996).

2.c.i. Black Bear Diets in the Southwest

My first step in approximating diets of Southwest grizzly bears entailed assembling and summarizing results of all the dietary studies I could find for black bears in an area stretching from central Colorado and Utah south to the limits of black bear distribution in Mexico. Figure 4 shows a summary from 15 studies that provided results based on analysis of fecal matter, one of which corrected for differential passage of foods through the gut (Hewitt & Robbins 1996), plus one study that reported results based on remains found in the alimentary tract of dead bears (see the caption of Figure 4 for sources).

Because sample sizes and methods varied substantially among studies (for example, *n* ranged from 18 to 859 scats), I generalized compositional results to an index, where 1 = incidental, 2 = common, and 3 = abundant for each diet item. Because diet composition also varied substantially from north to south, I stratified results according to whether they were from northerly latitudes (six studies from southern Utah and Colorado, plus one high-elevation study from northern New Mexico); Mexico and the U.S.-Mexico borderlands (six studies); or from central New Mexico and Arizona (four studies). I then summarized for each region the relative dietary contributions of different genera, species, and functional food groups (i.e., grazed foods, fleshy fruits, mast, invertebrates, and vertebrates) expressed as the weighted percent relative importance of each, shown in the pie diagrams in Figure 4a-4c. I also estimated general latitudinal trends for dietary groups comprised of genera or species that tended to discriminate among regions (Figure 4d-4f). My approach using relative dietary importance mitigated to some extent for differences among study methods as well as differences in digestibilities of diet items (see Section 2.c.ii), although the comparative contributions of vertebrates probably remain substantially under-represented.

Broadly speaking, the contributions of functional food groups did not vary substantially from south to north, with the proviso that vertebrates and fleshy fruits tended to be more prominent in the north, and mast from oaks (*Quercus* spp.) and junipers (*Juniperus* spp.) more prominent at mid-latitudes. However, there were substantial dietary trends at the level of species and genera. From south to north succulent portions of desert-dwelling monocots (*Yucca*, *Dasilyrion*, and *Nolinia* spp.) were replaced by grasses and sedges (i.e., graminoids) among grazed foods. Likewise, among fruits and masts, genera typical of Mexico (*Diospyros*, *Chlococca*, and *Berberis* spp.) and desert regions of the Southwest (*Opunita* spp.) were replaced by species and genera characteristic of higher latitudes (*Prunus virginiana*, *Amelanchier alnifolia*, and *Ribes* spp.). Among invertebrates, wasps, bees (Vespidae) and other arthropods were supplanted by species of ant (Fromicidae) farther north.

There are several implications of these patterns for bear diets in general and prospective grizzly bear diets in particular. As might be expected from theory and laboratory studies (Rode & Robbins 2000, Erlenbach et al. 2014), bears throughout the Southwest seemed to balance nutrients, as evident in broadly similar representations of functional dietary groups in population-averaged diets. Even so, dietary composition at the level of ingested genera and species varied enormously in reflection of broad-scale differences in climate and related flora and fauna. By implication, the comparative composition and importance of specific habitats also varied, albeit within the probable constraints dictated by overall environmental productivity (see Section 2.b).

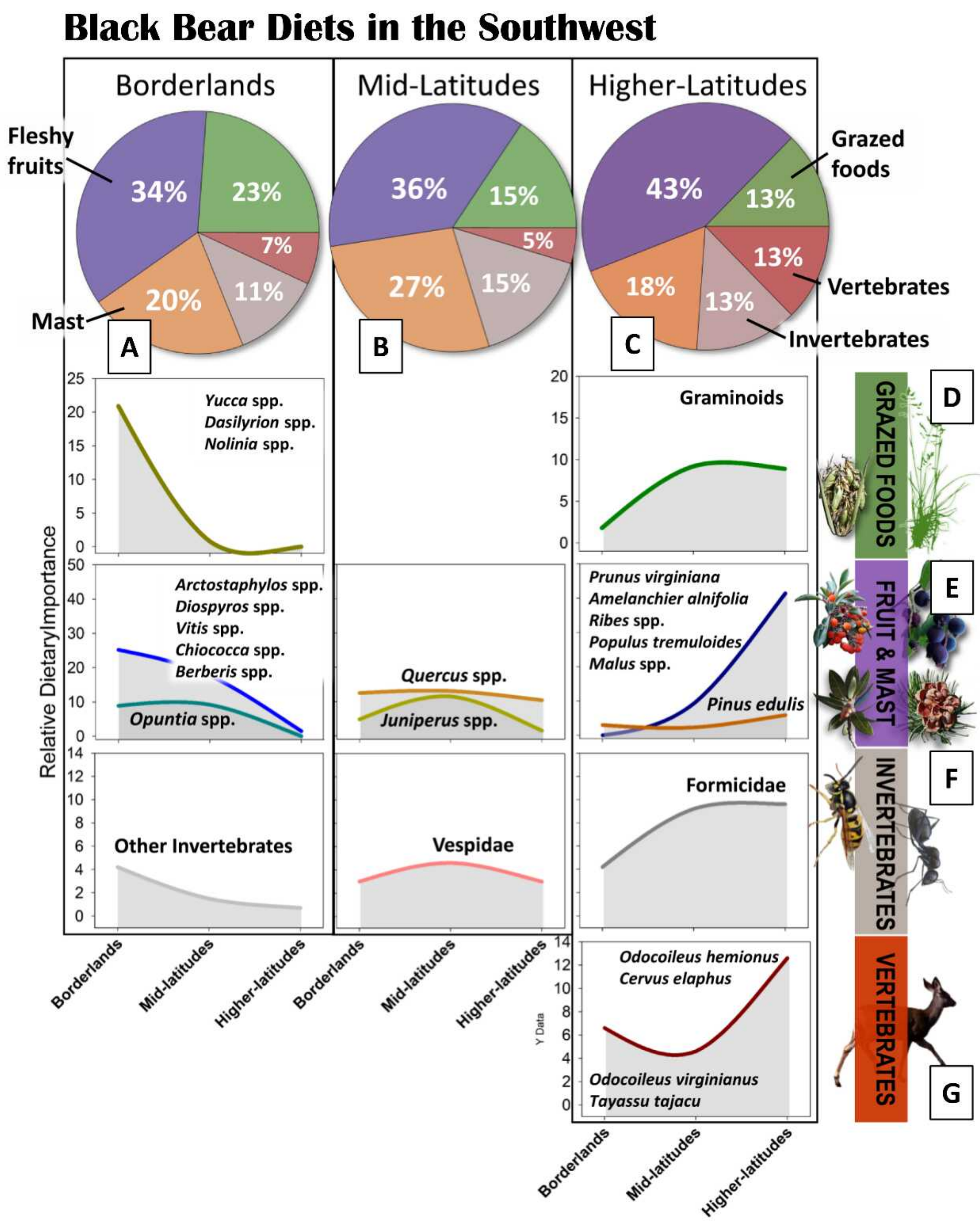


Figure 4. This graphic presents a synthesis of information regarding the composition of black bear diets in the Southwest and adjacent Mexico as well as how that composition broadly varies from north to south (A, B, C) in terms of grazed foods (D), species of fruits and mast (E), and species of invertebrates (F) and vertebrates (G). The pie diagrams at top show proportional composition of feces averaged from multiple bear studies differentiated by whether they were on the borderlands of Mexico and the U.S., at higher-latitudes in southern Colorado and Utah, or at mid-latitudes in between (Baldwin & Bender 2009; Berry 1996; Costello et al. 2001; Doan-Crider 1995, 2003; Doan-Crider & Hewitt 2009; Fuchs et al. 1997; Guntly 2016; Hellgren 1993; Heward et al. 2004; Juárez-Casillas & Varas 2013; Martínez Muñoz et al. 2014; McClinton et al. 1992; Sierra Corona et al. 2005; Tredick 2016). Trend lines in the x-y graphics below each pie diagram depict changes in relative consumption of different food groups from south to north (left to right), with those foods most commonly consumed in a given region aligned below the corresponding pie diagram. Predominant genera or species of foods are labeled in each x-y graph; e.g., species or genera more common in the borderlands vs. higher latitudes vs. mid-latitudes centered on New Mexico and Arizona.

On the one hand, black and grizzly bears can clearly adapt to dramatically different environments, while on the other hand being constrained by life strategies that dictate balancing certain nutrients as well as seasonally ingesting digestible calories so as to maximize accumulation of adipose reserves in the case of females, and optimize growth in both lean body mass and adiposity in the case of males (Mattson 2000, Costello et al. 2016). More specific to this analysis, grizzly bears likely consumed all of the genera and species listed in Figures 4 and 5, plus additional species exploited to obtain roots and underground caches of food made by rodents (e.g., pocket gophers; Mattson [2004]). Grizzlies moreover almost certainly ate more meat, especially from elk and bison during pre-European times (e.g., Green et al. [1997], and Mattson [1997a]), and from livestock such as cattle and sheep after herds multiplied with the arrival of Anglo-Americans (see Section 3.3).

2.c.ii. Nutritional Characteristics of Foods

An often-repeated misconception holds that, because grizzly bears are omnivores, they are relatively unaffected by the composition and quality of their diets, with consequently few effects of dietary differences on population density and demography. This claim has been and continues to be falsified by virtually everything we know about grizzly bear populations and individuals. As I note in Section 2.b., effects of diet on the condition and reproductive success of individual bears have been amply demonstrated, together with orders-of-magnitude variation in population densities driven by broad-scale differences in habitat productivity.

More to the point, any useful understanding of historical grizzly bear habitat relations and foraging behaviors in the Southwest is necessarily rooted in understanding the nutritional characteristics of bear foods, notably concentrations of lipids and digestible energy and protein (Erhlenbach et al. 2014), as well as characteristics that affect foraging efficiencies, including size, clustering, and ease of extraction (Holcroft & Herrero 1984, Mattson 1997b, Welch et al. 1997, Hamer 1999, Rode et al. 2001). In service of this purpose, I summarized all the analyses I could find of nutritional characteristics for likely grizzly bear foods in the Southwest, featuring foods documented in diets of black bears (as per Section 2.c.i; see Appendix A for sources), with the notable proviso that I could find little information on prospective root foods largely because ethnobotanical and wildlife researchers have tended to neglect this functional food group.

The graphics in Figure 5 summarize key nutritional characteristics for bear foods of the Southwest, differentiated by whether they are fleshy fruits, hard mast (e.g., acorns, pine seeds, and juniper berries), fibrous grazed foods, or vertebrate and invertebrate animal foods. The values for each parameter for each food are proportional to the vertical distance of each dot and line from the x-axis. The length of vertical brackets around each dot are proportional to the standard deviation of estimates from different sources. Foods are further differentiated by colors denoting those characteristic of higher latitudes (in purple), U.S.-Mexico borderlands (dusky green), and latitudes in between (in gray). Raw values are given in Appendix B.

The nutritional characteristics of Southwest bear foods comprising different functional groups are similar to characteristics of bear foods in the same functional categories farther north (e.g., Mattson et al. 2004). Fleshy fruits are typified by moderate concentrations of digestible energy, but low concentrations of lipids and digestible protein. By contrast, mast has higher concentrations of lipids, comparably low concentrations of digestible protein, and highly variable concentrations of digestible energy. Of the mast-producing species, pine seeds (*Pinus edulis* and *P. monophyla*) are richest in lipids and digestible energy, but disadvantaged by small size. Of the animal foods, invertebrates (i.e., Vespidae and Formicidae) offer less digestible protein and energy than do vertebrates, and are also further disadvantaged by very small size. Finally, although some grazed foods offer moderate concentrations of digestible protein (notably, clover, dandelions, and graminoids), most provide only small amounts of digestible energy, and none more than trace amounts of lipids.

There are several notable provisos to these conclusions and general patterns. First, root foods, which do not appear in these tables, are unique in providing concentrations of starch, which are a prominent source of digestible energy for foraging grizzly bears (Mattson et al. 2004). Also, although Figure 5c provides information on the mass of individual food “packets,” a number of other factors affect foraging efficiencies, including the energetic costs of extracting roots (Holcroft & Herrero 1985, Mattson 1997b, Hamer 1999); the density, clustering and vertical presentation of mast and fleshy fruits (Welch et al. 1997); the physical architecture and density of grazed foods (Rode et al. 2001, Mattson et al. 2004); and whether vertebrates are obtained as carrion or through outright predation and, if the latter, how easily and with what risk. Animals as small and agile as mule deer (*Odocoileus hemionus*) are difficult for grizzlies to capture, and, in the face of competition from coyotes (*Canis latrans*) offer typically little reward as carrion, whereas animals as large as bison are difficult to kill outright, but offer a large reward for scavenging bears (Green et al. 1997, Mattson 1997a).

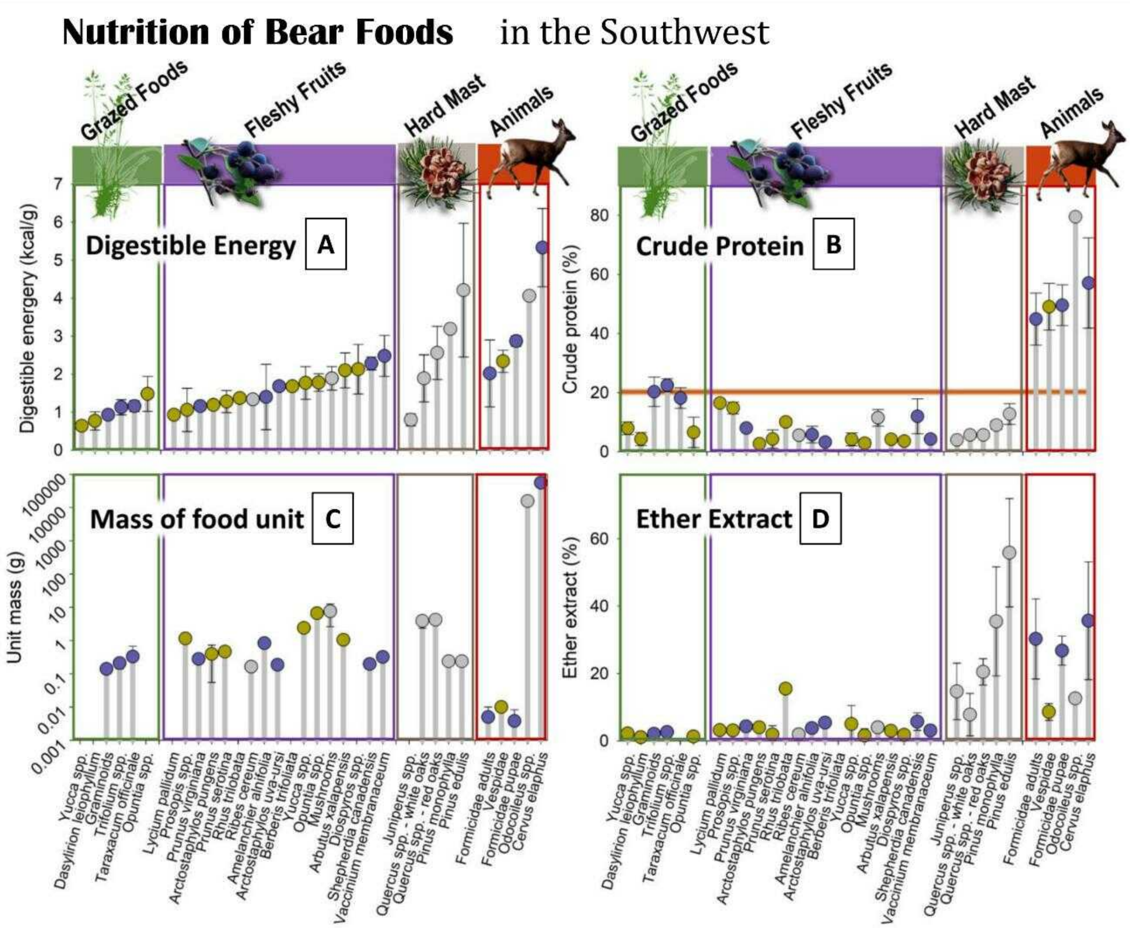


Figure 5. These graphics summarize key nutritional characteristics of foods likely consumed by grizzly bears in the Southwest prior to their extirpation, including digestible energy per gram of oven-dried food (A), percent crude protein (B), percent ether extract (i.e., lipids; D), and mass of discrete items comprising the focal food (C; e.g., size of individual fruits or seeds, characteristic bites of grazed foods, or individual invertebrates or vertebrates; on a log scale). The height of each dot above the bottom horizontal axis in each diagram is proportional to energy content, nutrient content, or food item size. The vertical brackets above and below each dot are proportional to the standard deviation of estimates from different sources, all of which are are listed in Appendix A. Food-specific values and methods for estimating digestible energy are given in Appendix B. Dots colored purple, green, and gray denote foods characteristic of higher latitudes, the US-Mexico borderlands, and areas in-between, respectively. This list of foods is based on documented occurrences in regional black bear diets (see Figure 3 plus Auger et al. [2004], Bender et al. [2007], Coop et al. [2005], Hatch et al. [2019], Jones et al. [2016], Laufenberg et al. [2018], Lomas & Bender [2007], López-González et al. [2009], Lundgren et al. [2022], Mattson & Arundel [2013], McCutchen [1996], Quintana [2016], Seid [2004], and Smith [1983]) or known consumption by indigenous people prior to loss of traditional life-ways (Castetter 1935, Driver 1952, Janetski 1999, Jordan et al. 2006, Jordan 2008, Kindscher et al. 2018, Kirkpatrick & Ford 1977, Laferrière et al. 1991, Melo-Ruíz et al. 2017, Mitchell 2016, Moerman 2010, Smith et al. 2001, Smith & McNees 2005, Teufel 1996, Wolfe et al. 1985, Yanovsky 1936).

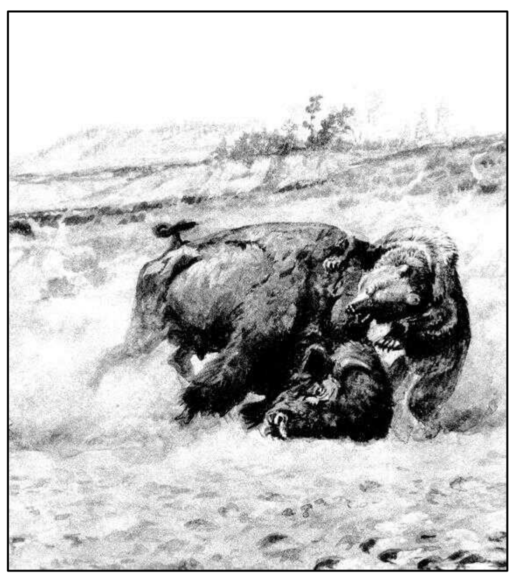
2.c.iii. Implications for Grizzly Bear Diets and Behavior

Although information on the nutritional and energetic characteristics of known and probable foods is relevant to judging where, when and how grizzly bears foraged in the Southwest, it is not a definitive basis for reckoning which foods and habitats were critical to their existence. Other research on population-level responses to functionally similar foods prospectively augments information on basic nutrition to provide a better reckoning of what foods might have governed the fates of grizzly bears in the Southwest—including research on black bears in the region as well as grizzly bears elsewhere.

Perhaps most important, there is a consensus regarding the effects of hard mast and fleshy fruits on the reproductive success of both black and grizzly bear females. There are a number of publications showing the effects of variation in crops of oak acorns and beech nuts on production of cubs at both an individual and population level for black bears in eastern North America, including Minnesota (Rogers 1976), the Appalachians (Eiler et al. 1989, Clark et al. 2005), Maine (McLaughlin et al. 1994), and Massachusetts (Elowe & Dodge 1989). LeCount (1982), Costello et al. (2003), and Doan-Crider (2003) show the same for the Southwest and northern Mexico, consistent with widespread selection by black bears for vegetation with abundant oak trees or shrubs (LeCount 1990, Cunningham et al. 2003, Onorato et al. 2003, Harding & Black 2004, Sierra Corona et al. 2005). More specific to grizzly and brown bears, there is a well-documented effect of variation in production and consumption of seeds from whitebark pine (*Pinus albicaulis*) on reproductive success of grizzlies in the Yellowstone ecosystem (Mattson et al. 1992, Pease & Mattson 1999, Mattson 2000, Schwartz et al. 2006), plus one study documenting the effects of variation in availability of berries from Ericaceous shrubs on reproductive success of female brown bears in Scandinavia (Hertel et al. 2018).

These effects comport with the life strategy of female bears and documented foraging efficiencies of smaller (i.e., female and adolescent) versus larger (i.e., adult male) bears of both species (e.g., Welch et al. 1997, Rode et al. 2001). More so than males, females depend upon accumulation of body fat to ensure reproductive success (Farley & Robbins 1995, Dahle et al. 2006, Robbins et al. 2012, Heldstab et al. 2017), and there are no foods better than those high in fat content to promote accumulation of adipose reserves (Erhlenbach et al. 2014). Not surprisingly, if available, females tend to eat smaller-sized and higher-fat-content foods, documented perhaps most definitively for adult female grizzly bears in Yellowstone that historically ate roughly twice as many high-fat-content whitebark pine seeds as did adult males (Mattson 2000). By contrast, adult males tend to eat greater amounts of protein-rich foods, notably meat from ungulates (Jacoby et al. 1999; Mattson 1997a, 2000; Hobson et al. 2000; McLellan 2011; Costello et al. 2016; Hatch et al. 2019).

Yet grizzlies are not equally likely to exploit all types of ungulates. Even though some black bears are known to frequently prey on mule deer fawns (Smith 1983, Pojar & Bowden 2004, Lomas & Bender 2007), this phenomenon has only been rarely documented for larger-bodied grizzly bears, even where mule and white-tailed deer (*Odocoileus virginianus*) are abundant—and despite the fact that grizzlies, like black bears, routinely prey on elk calves (French & French 1990, Gunther 1990, Hamer & Herrero 1991, Mattson 1997a, Guntley 2006, Fortin et al. 2013, Quintana 2016). Additionally, unlike black bears, some grizzlies—especially adult males—are formidable predators on fully-grown elk and moose (Schleyer 1983, Mattson 1997a), although ungulates as large as adult bison are only rarely prey because of the entailed risks for a predatory bear, and are instead a rich source of carrion once they die from other causes (Green et al. 1997, Mattson 1997a).



As I noted above, despite the fact that terrestrial vertebrates can provide much of, if not most, energy and nutrients ingested by grizzly bears (Mattson 1997a, Jacoby et al. 1999, Mowat & Heard 2006, Fortin et al. 2013, Schwartz et al. 2014), grizzlies are not indifferent to the costs and benefits of preying on or scavenging different types of ungulates. By-and-large, deer are either too agile to be grizzly bear prey, or too small to provide much meat for a bear competing with other scavengers. Adult elk can be prey year-round for grizzlies that have learned the requisite predatory skills (Schleyer 1983, Mattson 1997a), but are more commonly a source of spring carrion for scavenging bears on winter ranges (Green et al. 1997). As in the Yellowstone ecosystem, bison on the high plains of Colorado and New Mexico were probably only rarely outright prey, but rather an important source of carrion for scavenging grizzlies during spring on bison winter ranges and during and after the rut in areas where bison mated (Green et al. 1997, Mattson 1997a).

All of this having been said, foods that are nutritionally and energetically less beneficial also play a key role in the grizzly bear life strategy, largely because they offer alternatives during seasons and years when richer foods are scarce, or because they offer a means of balancing ingestion of different nutrients to achieve a dietary optimum (Felicetti et al. 2003, Coogan et al. 2014, Erlenbach et al. 2014, Costello et al. 2016). Roots, foliage, rodents, and invertebrates are notable examples, with the proviso that exploitation of these less-rewarding foods by grizzlies entails a high degree of choice regarding when and where they are consumed (Holcroft & Herrero 1985; Welch et al. 1997; Hamer 1999; Mattson 1997b, 2000, 2001, 2002, 2004; Rode et al. 2001; Fortin et al. 2013).

2.c.iv. Geospatial Distributions of Key Grizzly Bear Foods

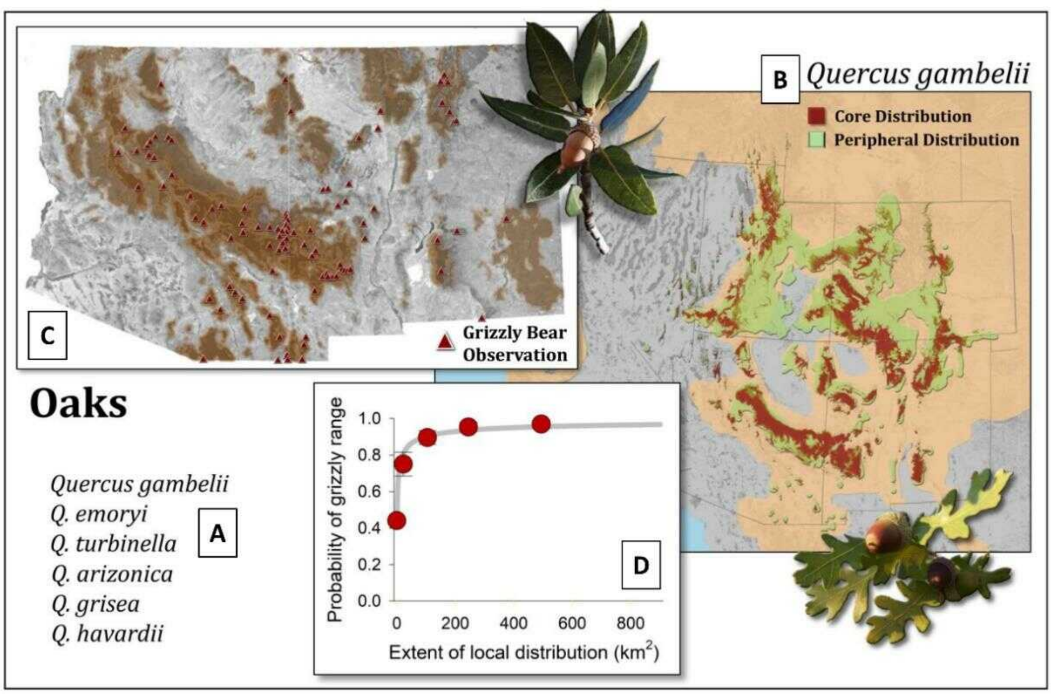


Figure 6. These graphics show the distributions of oak species that produce acorns known to be consumed by humans and/or black bears (*Ursus americanus*; listed in [A]) as well as by pre-European grizzly bears in the western United States and adjacent Mexico. The map in (B) shows the distribution of Gambel oak (*Quercus gambelii*) based on modeled climatic relations (shown in shades of green and dark reddish-brown, adapted from Rehfeldt et al. [2006]) in relation to the pre-European distribution of grizzly bears (shown in tan, from Mattson & Merrill [2002]). Gambel oak is a particularly importance source of food for black bears in the Southwest (e.g., Costello et al 2001, Heward et al. 2004, Guntley 2016). The map in (C) shows the cumulative distribution of all oaks listed in (A) in Arizona and New Mexico, with darker shades of brown denoting greater overlap of distributions (from Thomas et al. [2012]). Documented grizzly bear locations are shown as red triangles. The graphic in (D) shows the strong geospatial relation between pre-European distributions of grizzly bears (y-axis) and all oaks (x-axis) in the western United States (adapted from Mattson & Merrill [2002]). This association of pre-European grizzly bears with oaks is the strongest of any documented for a habitat or food resource in the contiguous U.S. (Mattson & Merrill 2002).

The figures in this section show the composition and distributions of prospective grizzly bear foods in Arizona and New Mexico which, in toto, provide a refined geospatial picture of foods that likely defined the Holocene distributions and histories of grizzly bears in the Southwest. Each figure features a functional food group, with additional differentiations of piñon pines from oaks, and elk from bison.

Oaks and Acorns—Figure 6 features oaks that produce acorn likely consumed by grizzly bears, including a map showing the cumulative distributions of six species of acorn-producing oaks (Figures 6a and 6c), as well as a map showing the total southwestern distribution of Gambel oak (*Quercus gambelii*; Figure 6b), which is known to be a key source of food for black bears (LeCount 1990, Doan-Crider 1995, Costello et al. 2003, Heward et al. 2004, Sierra Cornona et al. 2005, Guntly 2016). The greatest diversity and abundance of oaks occurs in arc stretching from the Mogollon and Black Range Mountains in the southeast northwest along the Mogollon Rim.

Visually, the positive geospatial association between documented grizzly bear locations and distributions of oaks in the Southwest is striking (Figure 6c), confirmed by the statistically positive west-wide association between oaks and historical grizzly bear distributions in the United States (Mattson & Merrill 2002). These positive associations comport with the documented importance of oak acorns—especially those of Gambel oak—to reproductive success, fine-scale patterns of habitat selection, and distributions of black bears in the Southwest (Section 2.c.iii), with straight-forward implications for grizzly bears. The only exception to this generally positive association pertains to shinnery oak (*Quercus harvardii*), which in the Southwest is restricted to portions of southeastern New Mexico that are likely too hot and unproductive to have supported populations of grizzlies (Figure 3a).

Although acorns are indisputably an important part of contemporary black bear diets in the Southwest, and likely played a prominent role in grizzly bear diets as well, acorns, like most mast, can vary substantially in abundance from one year to the next. Among the oaks that have been monitored, Gambel oak is the most reliably productive (only 9-13% of crops are failures, with 2-4 years between good crops; Costello et al. [2001], Guntley [2016]) and scrub oak (*Quercus turbinella*) the least (58-68% failed crops with 5-6 years between good crops; Parmenter et al. [2018]). Production of acorns by wavy-leaf (*Q. undulata*) and gray (*Q. grisea*) oaks falls in between these extremes (13-38% failed crops and 4-8 years between good crops; Costello et al. [2001]). Among other factors, the reliability of production by Gambel oak likely explains its dietary importance for bears.

Different species of oak also produce acorns with varying amounts of tannins that affect both palatability and digestibility of proteins (Robbins et al. 1987)—a factor known as "sweetness." Emory (*Quercus emoryi*), Gambel, and wavy-leaf oaks are commonly referred to as "sweet" whereas Arizona white oak is commonly referred to as "bitter" (Driver 1969, Mason 1992). The former can be eaten by humans with little preparation to neutralize tannins whereas the latter can't. Even so, the effects of tannins on digestibility of proteins can be offset in species that produce salivary proteins capable of binding with tannins, as has been documented for black bears (Robbins et al. 1991). Grizzlies likely share this trait with black bears given their phylogenetic relatedness and the conservative nature of traits that facilitate omnivory (e.g., Altmann 2009, Chubaty et al. 2014).

Fleshy Fruits—Figure 7 features a wide variety of species that produce fleshy fruits eaten by bears. The greatest diversity and abundance of these species is concentrated in an arc running northwest from the Mogollon Highlands along the Mogollon Rim in a distribution that closely matches that of oaks (Figure 7a). Dietarily, some of the most important fruit in this area is produced by various species of serviceberry (*Amelanchier* spp.) and manzanita, most prominently pointleaf manzanita (*Arctostaphylos pungens*). Farther south into Mexico, fruits from species such as agarita (*Berberis trifoliata*), persimmon (*Diospyros texana*), and Texas madrone (*Arbutus xalapensis*) are more important parts of bear diets (Section 2.c.i).

As in the case of oaks, documented grizzly bear locations have a striking positive geospatial association with distributions of fruit-producing shrubs in the Southwest, with the notable exception of one species—skunkbush (*Rhus trilobata*). Even though black bears are known to eat berries of this species, most skunkbush is distributed in semi-arid regions such as the Little Colorado River basin that are, overall, comparatively unproductive for bears.

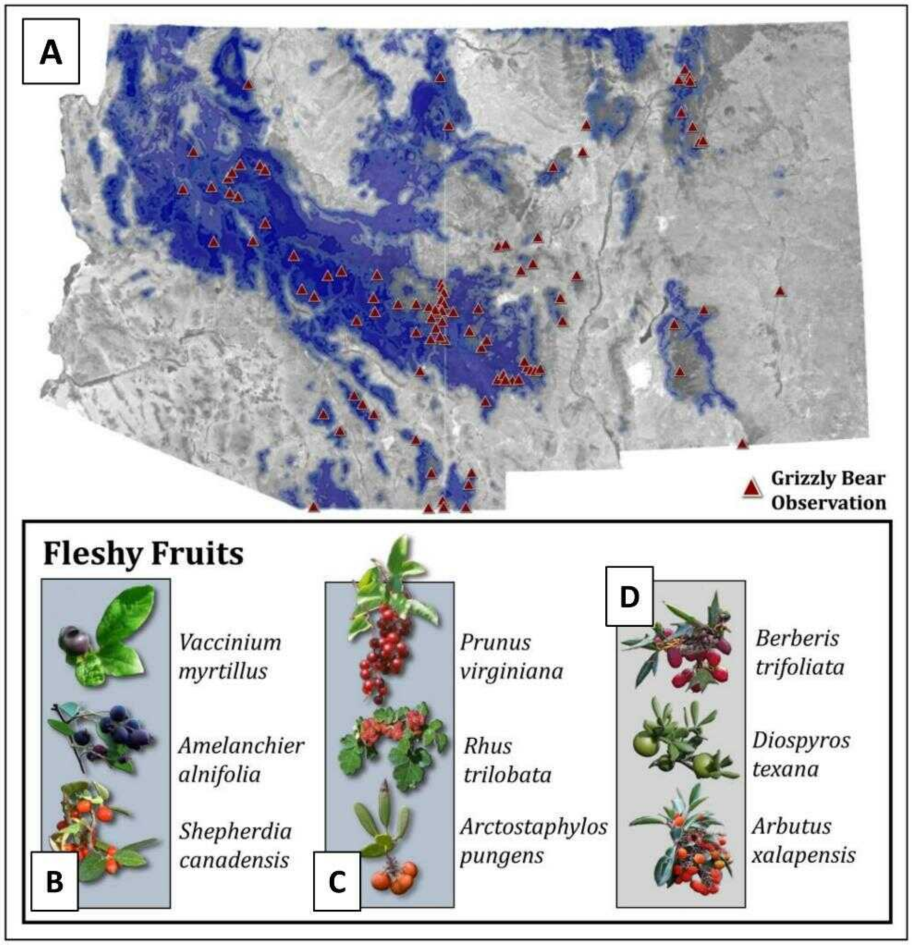


Figure 7. These graphics show the composition and cumulative distribution of species that produce fleshy fruits known to be consumed by black bears (*Ursus americanus*) and also likely consumed by grizzly bears (see Figure 4 for sources). Areas shaded progressively darker blue in (A) denote areas of greater cumulative overlap of fruit-producing species, with documented locations of grizzly bear (red triangles) superimposed on top. The species listed in (B) are distributed at higher latitudes, notably in the San Juan, Sangre de Cristo and Chuska Mountains, whereas the species in (C) are distributed and known to be consumed by bears at comparatively lower elevations and latitudes. Documented consumption by bears of the species listed in (D) occurs almost solely in Mexico, far southern Texas, and the borderlands area of Mexico, New Mexico, and Arizona. Distributions of species in (B) and (C) are from Thomas et al. (2012). Distributions of species in (D) are based on generalizations of locations documented in Wildflower Search (https://wildflowersearch.org/).

Piñon Pine Seeds—Figure 8 features piñon pines, including the cumulative distribution of piñon pines in the Southwest (Figure 8b) as well as, more broadly, distributions of piñon pines in western North America (Figure 8c). The distribution of Southwestern piñon pines overlaps almost wholly with areas of maximum diversity and abundance for both oaks and berry-producing shrubs, with commensurate contributions to the overall productivity of these areas. Even so, the apparently limited contributions of pine seeds to most bear diets and related absence of documented effects on female reproduction suggest that in these areas of overlap acorns and fleshy fruits are of primary importance, with pine seeds serving primarily as a back-up or augmentative food (Costello et al. 2001). This limited contribution is consistent with the extent to which pine seed crops are judged to fail—36-94% of years, depending on the species and location, with an average 8 years between good crops (Costello et al. 2001, Redmond et al. 2012, Guntley 2016, Khuu 2017, Parmenter et al. 2018), which is roughly twice the failure rate of most oak acorn crops.

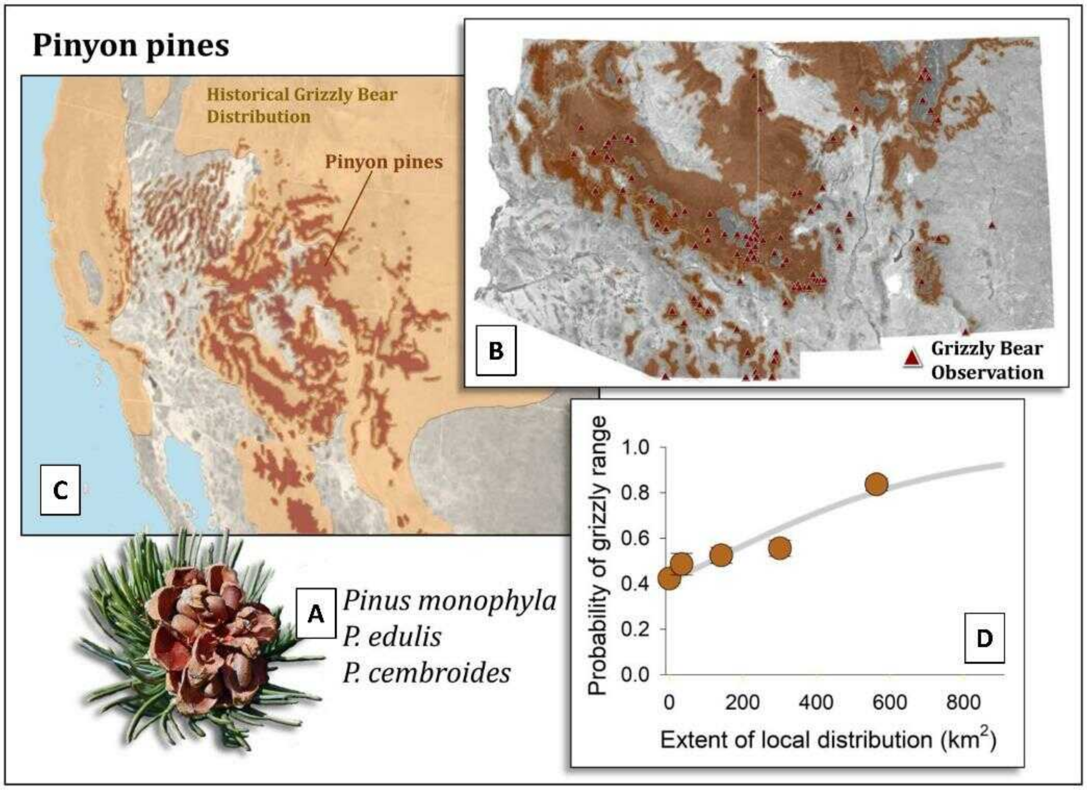


Figure 8. These graphics show the distributions of piñon pines (A; *Pinus monophyla, P. edulis*, and *P. cembroides*) and pre-European grizzly bears in the western United States and adjacent Mexico. The map in (B) shows the distribution of piñon pines in Arizona and New Mexico based on known locations and modeled climatic relations (Rehfeldt et al. 2006, Thomas et al. 2012, Cole et al. 2013), together with documented locations of grizzly bears shown as red triangles. The map in (C) shows the joint pre-European distribution of all piñon pines and grizzly bears for the western United States and northern Mexico, with distributions of piñon pines shown in dark brown (from Farjon et al. [1997] and Cole et al. [2013]) and the distribution of grizzly bears shown in tan (from Mattson & Merrill [2002]). The statistically significant and moderately strong geospatial relation between the distribution of grizzly bears (y-axis) and piñon pines (x-axis) is shown in (D), adapted from Mattson & Merrill (2002). The main area of non-overlap between piñon pines and historical grizzly bear distribution occurred in the Great Basin where piñon pines and grizzly bear habitat are restricted to the flanks of lineated south-north trending mountain ranges surrounded by dry sagebrush- (*Artemisia* sp.) and saltbrush- (*Atriplex* sp.) dominated basins.

Overall, in contrast to oaks and berry-producing shrubs, piñon pines probably made a more limited contribution to historical grizzly bear diets in the Southwest, albeit allowing for the likelihood that pine seeds could have been dietarily important at certain times and in certain places. This conclusion is consistent with the modest geospatial association of documented grizzly bear locations with piñon pines (Figure 8b), as well as, in contrast to oaks (Figure 6d), a weaker although significant positive correlation with west-wide grizzly bear distributions (Mattson & Merrill 2002; Figures 8c and 8d).

Wapiti—From the time of European arrival up through the late 1800s wapiti likely had a limited distribution in the Southwest centered on the White, Mogollon, Sangre de Cristo, and Jimenez Mountains (Figure 9a). These areas coincided with comparatively productive higher-elevation habitats where free water was available from naturally-occurring fluvial and lacustrine sources (Truett 1996, Davis 2001). Wapiti were slaughtered by Europeans during the 1800s to the point of extirpation by 1900. Restoration efforts followed soon after in the early 1900s and intensified during subsequent decades. Since then, wapiti distributions have steadily increased to the point where they far exceed historical bounds, especially in Arizona (Figure 9a). This increase is plausibly attributable to the widespread construction of water sources to provision livestock and wildlife with water—in the case of stock tanks as an unintended side effect (Figure 9b; Truett 1996, Davis 2011, Mattson & Holton 2022).

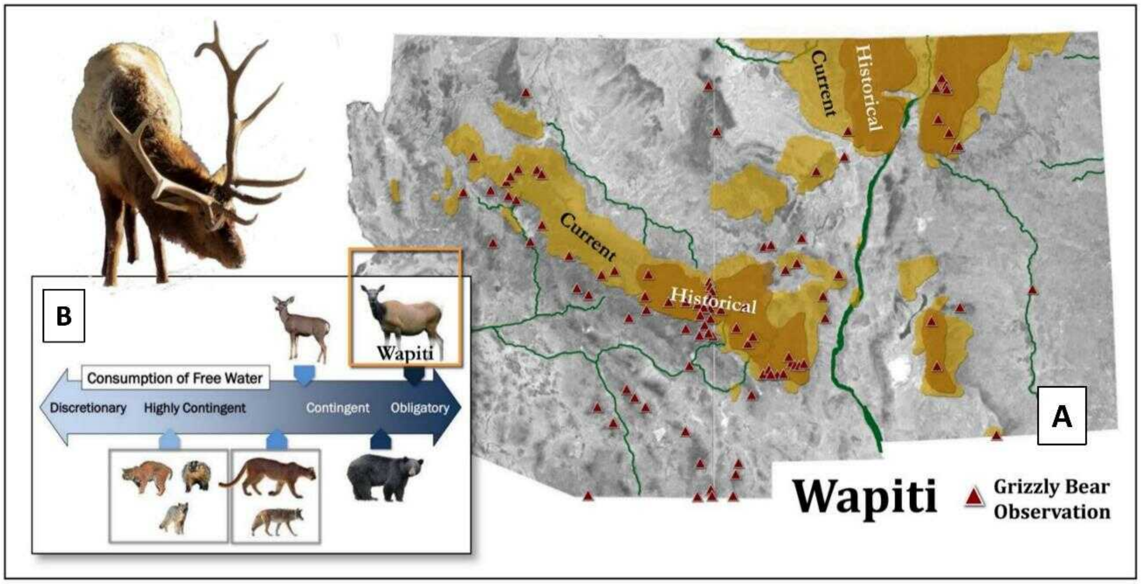


Figure 9. The map in (A) shows the historical and current distributions of wapiti (or elk; *Cervus elaphus canadensis*) in Arizona and New Mexico. Approximate pre-European distributions are shown in darker tan (from Truett [1996]), whereas more extensive current distributions are shown in light tan (from Arizona Game & Fish Department [1988] and Rocky Mountain Elk Foundation [2019]). Documented grizzly bear locations are shown as red triangles. The limited historical and more extensive current distributions of wapiti can be explained by the availability of perennial free water (Truett 1996, Davis 2001). Prior to the 1880s perennial free water was not widely available in the Southwest other than in the Mogollon, White, Sangre de Cristo, Jemez, and Sacramento Mountains plus lower-elevation rivers fed by these highlands. Larger-bodied herbivorous mammals such as wapiti are predictably more dependent on free water compared to omnivores, carnivores, and small herbivores (Mattson & Holton 2022), consistent with the greater documented water-dependence of wapiti compared to mule deer (*Odocoileus hemionus*; Parker & Robbins [1984]). The graphic in (B) shows the probable degree to which different mammals native to the Southwest are dependent on free water, with wapiti and black bear being more dependent than any other ('obligatory' versus 'contingent' or 'discretionary'). It is thus likely that the recent expansion of wapiti distribution is linked to the widespread construction of not only reservoirs to benefit livestock, but also numerous devices specifically designed to provision wildlife with water (as per Rosenstock et al. [1999] and Arizona Game & Fish Department [2012]).

Of relevance to grizzly bears, they undoubtedly exploited wapiti where available, which largely coincided with areas that likely also produced the greatest amounts of fleshy fruits and acorns (Figures 6c and 7a). The extirpation of wapiti in these historical ranges probably contributed both directly and indirectly to the demise of grizzlies, not only by depriving them of a high-quality food, but also by amplifying the switch to preying on livestock that had already been triggered by dramatic increases in numbers of cattle (Section 3.3). More positively, unlike with bison, wapiti constitute a bear food that has increased in abundance, perhaps substantially, in contrast to a historical baseline that probably existed throughout the Holocene.

Bison—With the exception of the Great Plains in eastern Colorado and New Mexico, bison were probably never very abundant in the Southwest during the Holocene. This dearth has led some to even speculate that bison never occurred in areas west of the Plains. However, recent compilations of historical and paleontological records make clear that bison did occur, albeit at probably low densities, in the scattered semi-desert and temperate grasslands of Arizona and western New Mexico (Figure 10a; Truett 1996, List et al. 2007, Harris 2013, Wolff 2013, Martin et al. 2017). Even so, bison were almost certainly much more abundant throughout most of the Holocene on the Great Plains farther east (e.g., Bailey 1931), with the notable proviso that bison probably disappeared from parts of the southern Plains during the hottest driest periods of the Altithermal (Lohse et al. 2014a, 2014b).

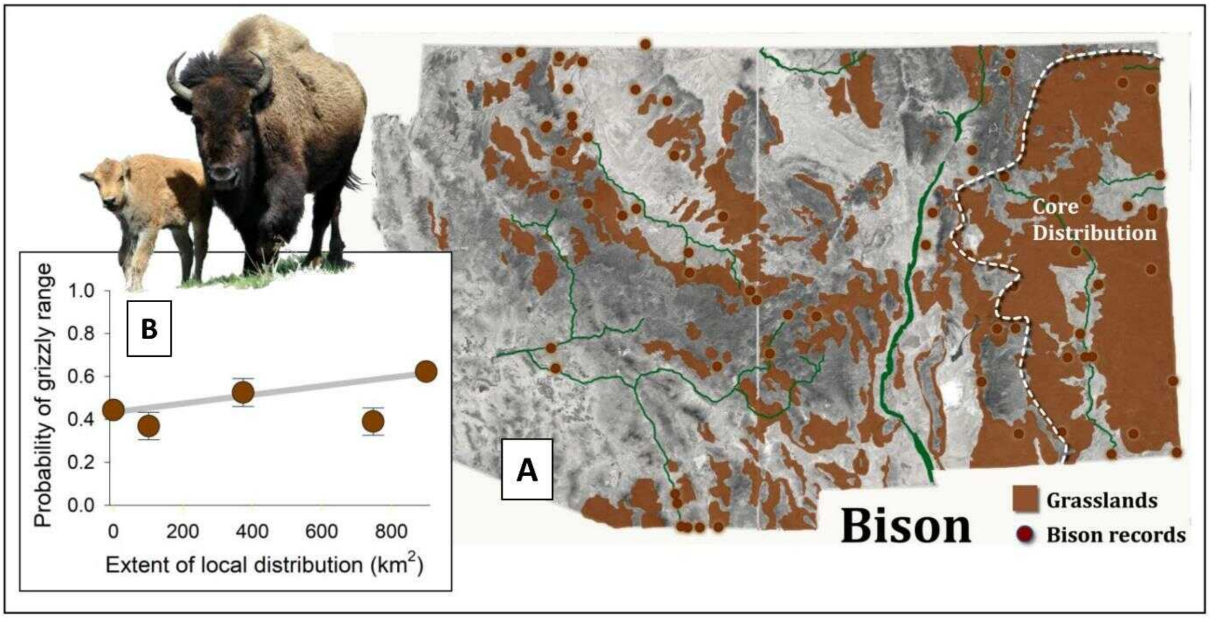


Figure 10. The map in (A) shows the documented Holocene and late-Pleistocene distribution of bison (*Bison bison*) in New Mexico and Arizona overlain on top of the approximate extent of semi-desert and temperate grasslands, shown in dark brown. Site-specific historical or paleontological records of bison are shown as dark red-brown dots (from Truett [1996], List et al. [2007], Harris [2013], Wolff [2013], and Martin et al. [2017]). The area east of the white dashed line in New Mexico was described by Bailey (1931) as being the core of bison distribution in New Mexico, coincident with the distribution of short-grass prairie dominated by grazing-adapted C^4 plants of the genus *Bouteloua.* The inset x-y graph in (B) shows the weak positive association between pre-European distributions of bison and grizzly bears in what was to become the western United States (adapted from Mattson & Merrill [2002]). Despite this weak West-wide association, the eastern-most distributions of bison and grizzly bears coincided almost exactly on the Great Plains (Mattson et al. 2005).

As evident by the contemporary behavior of grizzly bears in the Yellowstone ecosystem (Green et al. 1997, Mattson 1997a), bison were likely exploited by grizzlies wherever they were available in the Southwest, most often as carrion, and, along with fleshy fruits produced by shrubs in riparian areas, almost certainly as a staple of the few grizzlies living on the Great Plains in New Mexico and Colorado (e.g., Dodge 1981, Gowans 1986, Clark & Casey 1992, Burroughs 1995, Mattson et al. 2005, Flores 2016, Mattson 2021a). Extirpations of bison on the Great Plains during the late 1800s no doubt contributed to the early demise of grizzly bears in this ecosystem, although there is no evidence that the distribution of grizzlies in Arizona and western New Mexico was affected by the availability of bison occupying the semi-arid and temperate grasslands (Figure 10a), with the corollary that grizzlies likely existed at only very low densities on the southern Great Plains (Mattson & Merrill 2002). Overall, despite the fact that availability of bison likely defined the eastward distribution of grizzlies on the central and northern Plains, the west-wide association of grizzly bears with bison was very weak (Mattson & Merrill 2002).

Roots—Although roots are an intrinsically limited or at least highly-contingent source of energy for grizzly bears (Section 2.c.ii), at times and places they can be of major dietary importance, especially in colder and drier environments. *Hedysarum* spp. in Canada and *Rheum nanum* in Mongolia are noteworthy examples (e.g., Hamer & Herrero 1987, McLellan & Hovey 1995, MacHutchon & Wellwood 2003, Munro et al. 2006, Qin et al. 2020). Apropos, most prospective grizzly bear root foods in the Southwest are located in drier parts of the region, notably in the northern plains and upper Rio Grande drainage of New Mexico, and drainages of the Little Colorado River in Arizona (e.g., Figures 11a, 11b, and 11c). Wild relatives of the potato, of the genus *Solanum* (Figure 11d), are more common to the south, especially in southeastern Arizona.

The geospatial correlation between documented grizzly bear locations and root foods is correspondingly relatively poor in the Southwest (Figure 11a), although roots probably comprised an important part of grizzly

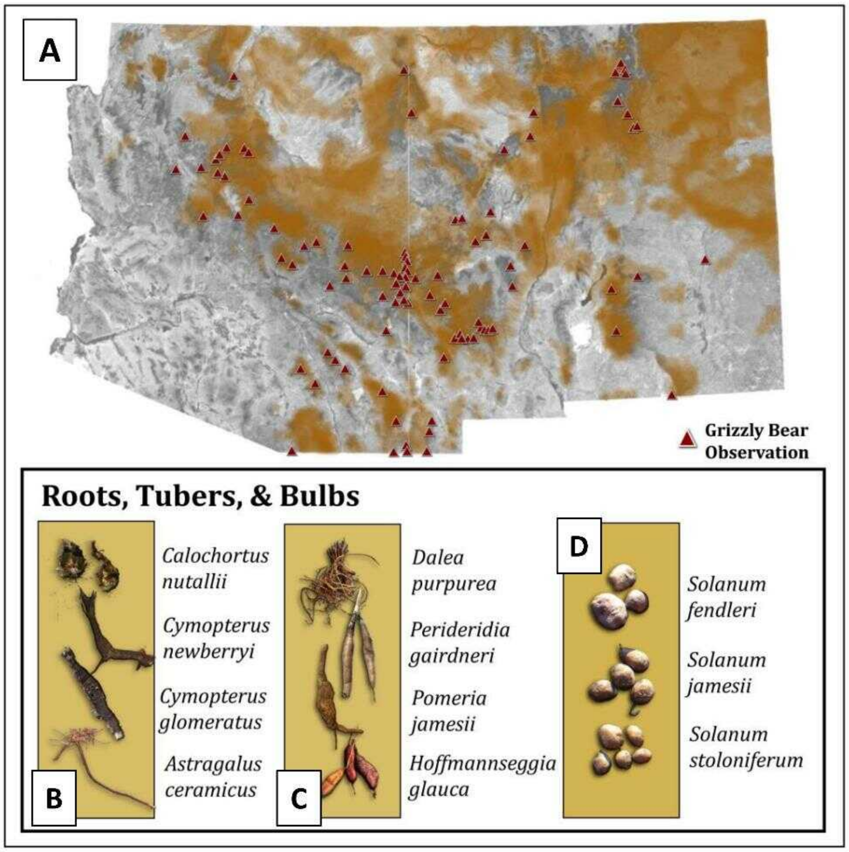


Figure 11. These graphics show the distribution and composition of plants that produced roots likely exploited by grizzly bears prior to extirpations by Europeans, with documented locations of grizzly bears overlain as red triangles. Cumulative distributions of root foods are shown in shades of brown in (A), with darker shades denoting greater overlap of species distributions. All distribution maps for individual species were derived and generalized from documented locations of each species listed in (B-D) in Wildflower Search (https://wildflowersearch.org/). Focal distributions of root foods listed in (B) are in the west and northwest, in (C) in the north and northeast, and in (D) comprised of ancestral species of potato. I identified root foods that were once likely exploited by grizzly bears based on documented use by humans in the ethnobotanical literature, notably Castetter (1935), Yanovsky (1936), Krochmal et al. (1954), Colton (1974), Plog (1981), Wolfe et al. (1985), Smith et al. (2001), Smith & McNees (2005), Moerman (2010), Mitchell (2016), and Kindscher et al. (2018), Girgin et al. (2020). The geospatial correlation between grizzly bear locations and root foods, largely concentrated in semi-arid areas, is manifestly poor.

bear rations during periods or seasons when higher-quality foods were scarce. Roots could have also been dietarily more important for smaller or more subordinate bears, as is the case with grizzlies in the Yellowstone ecosystem (Mattson 2000), with the potential to play an important role as fallback foods for grizzlies should they be restored to the Southwest.

Arid-Land Foods—In common with people, black bears are known to consume fruits of several arid-land species in the Southwest, most prominently of yuccas (*Yucca* spp.) and prickly pear (*Opuntia* spp.; Section 2.c.i). On the basis of nutritional characteristics alone, fruits of these genera are well-endowed, and would seem to offer bears a significant reward for their investment (Section 2.c.ii). However, representatives of these two genera are concentrated in hotter drier regions that would have been in all other respects inhospitable to grizzly bears (Figures 12a and 12b), consistent with the poor association between documented grizzly bear locations and fruit-producing yucca and prickly pear. Nonetheless, like roots, fruits of these arid-land species would have likely been important fallback foods for grizzlies, as well as important to grizzlies that ventured seasonally or longer term into hotter drier lowlands.

2.c.v. Synopsis of Geospatial Distributions

There is a remarkable concentration of diverse high-quality bear foods in highlands of the Southwest, notably in an arc from the San Francisco Peaks of Arizona southeast along the Coconino Plateau and Mogollon Rim to a terminus in the White, Mogollon, and Black Range Mountains in New Mexico—plus in the Sacramento, San Juan, Jemez, and Sangre de Cristo Mountains of New Mexico and adjacent Colorado. The constellation of food-producing species in these highlands includes wapiti, oaks, berry-producing shrubs, and piñon pines, and of these notably Gambel oak, manzanita, chokecherry (*Prunus virginiana*), various species of serviceberry, and

Colorado (or two-needle) piñon (*Pinus edulis*). In addition, roots and fruits from yucca and prickly pear offer subsistence for bears on warmer-drier sites and at lower surrounding elevations.

This diverse assemblage of higher-quality plus lower-quality fallback or alternative foods would have made highlands of the Southwest a productive environment for grizzly bears during most of the Holocene. Bison would have furthermore allowed grizzlies to survive on the Great Plains, albeit at low densities, necessarily concentrated along riparian corridors offering water and thermal cover. Of particular relevance here, although bison have been extirpated in the region, ample bear foods continue to be available throughout highlands of the Southwest, with the prospect of supporting restored populations of grizzly bears (Mattson & Merrill 2021a).

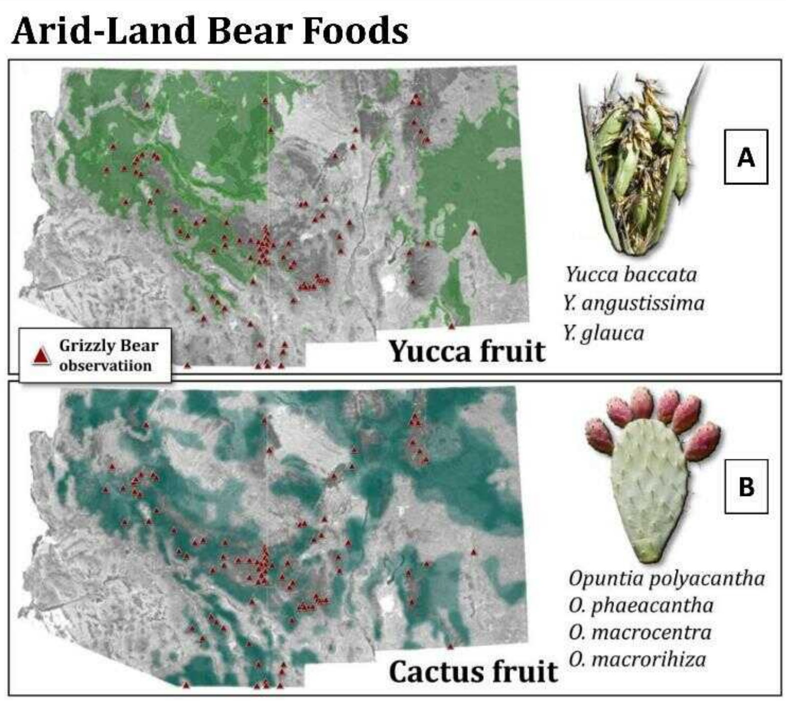


Figure 12. These maps show the distribution of several bear foods with a focal distribution in semi-arid to arid regions of the Southwest, together with documented locations of grizzly bears overlain as red triangles. Areas with greater overlap of different species of *Yucca* or *Opuntia* are shown in progressively darker shades of green (A) or turquoise (B). The top map (A) shows combined distributions of species of *Yucca* that were likely consumed as either fruits or succulent foliage by grizzly bears (from Thomas et al. 2012). The bottom map (B) shows combined distributions of species of *Opuntia* (prickly pear) that produce fruits that were likely consumed by grizzlies, with distributions approximated from documented occurrences in Wildflower Search (https://wildflowersearch.org/). The geospatial correlation between grizzly bear locations and distributions of arid-land *Yucca* and *Opuntia* is manifestly poor. I identified species of *Yucca* and *Opuntia* that were once likely exploited by grizzly bears based on documented use by humans in the ethnobotanical literature, notably Castetter (1935), Yanovsky (1936), Castetter & Bell (1941), Kirkpatrick & Ford (1977), Wolfe et al. (1985), Teufel (1996), Jordan (2008), Moerman (2010), Mitchell (2016), and Kindscher et al. (2018).

Box 1. This box describes a phenomenon that is often over-looked and under-appreciated: consumption of seeds from southwestern white pine by bears, with implications for understanding the past as well as potential future diets of grizzly bears in the Southwest. Red squirrels serve as fascinating and critical intermediaries in the exploitation of this resource by bears.

Bears & Southwestern White Pines (*Pinus strobiformis*)

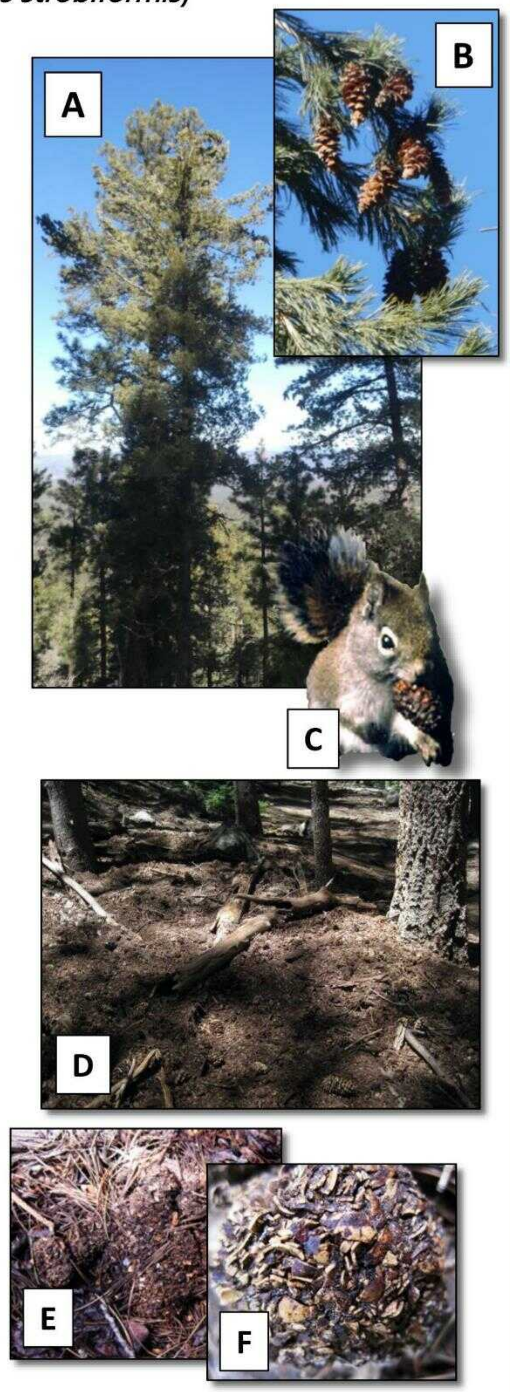
Southwestern white pine (*Pinus strobiformis* [A]) is a taxonomically ill-defined native of northern Mexico and the southwestern United States that hybridizes with limber pine (*P. flexilis*) at the northern limits of its distribution in New Mexico (Menon et al. 2018). Regardless of fuzzy taxonomic boundaries, trees of this genetic group share a tendency to produce large cones (B) with large wingless seeds ranging in average size from around 0.1 to 0.35 g. Seed mass varies primarily as a function of precipitation and the presence of competitors such as Douglas-fir (*Psuedotsuga menziesii;* Leal-Sáenz et al. 2020).

These large seeds attract numerous seed predators, of which red squirrels (*Tamiasciurus hudsonicus* [C]) are the most prominent (Samano & Tomback 2003). Southwestern white pines not only produce ideal squirrel food, but also grow under conditions that are ideal for sustaining high densities of red squirrels, notably diverse stands of conifers in well-watered higher-elevation mountains (Mattson & Reinhart 1997).

When southwestern white pine cones are abundant, squirrels harvest large quantities of them to cache in "middens" (D) consisting of the spongy residuum of cones harvested by previous generations of squirrels. Squirrels intend cached cones to be the source of meals during privations of winter or other mast shortages. However, these same cones unintentionally constitute a potentially valuable source of fat-rich food for bears.

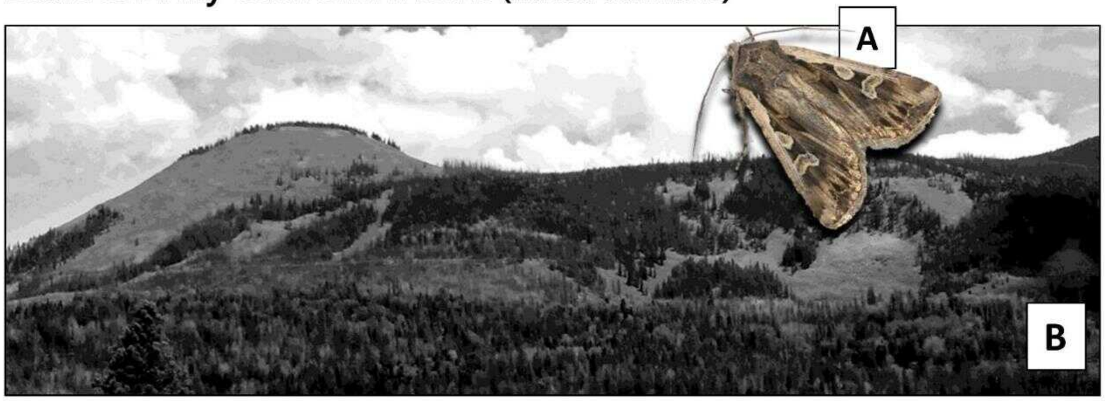
Thanks to the labors of squirrels harvesting and caching southwestern white pine cones, bears merely need to seek out middens, excavate the concentrations of cones within (as per in D), and then extract enclosed seeds (Mattson et al. 2001). Bears are so fastidious that the fecal residuum of these meals (E) consists almost entirely of seed coats (F). Cone scales and cores are comparatively rare.

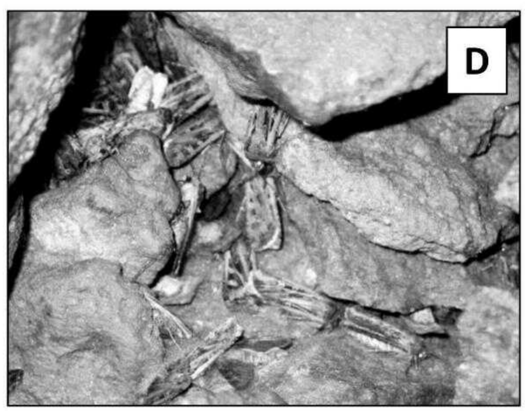
Although consumption of white pine seeds is not documented in historical accounts, contemporary observations of black bears eating both piñon pine and white pine seeds suggest that *Pinus strobiformis* and *P. flexilis* may have been important sources of food for grizzly bears foraging at higher elevations of the Southwest (Mattson & Arundel 2013).



Box 2. This box describes the first documented consumption of army cutworm moths by bears in the Southwest (Coop et al. 2005), with implications for understanding the past as well as potential future diets of grizzly bears in this region.

Bears & Army Cutworm Moths (*Euxoa auxiliaris*)





Consumption of army cutworm moths (*Euxoa auxiliaris* [A]) by bears is a well-documented phenomenon in the Rocky Mountains of Montana and Wyoming. Virtually all this exploitation occurs at high elevations between mid-July and mid-September on rock-covered slopes, also known as talus or scree. Adult cutworm moths congregate in alpine environs during late summer to feed on nectar of tundra flowers and, in the process, increase adipose reserves from c. 40% at the time of arrival to near 70% by the time they depart on long-distance migrations to lower-elevation agricultural lands. The high fat content of moths makes them one of the calorically-richest foods available to bears. Bears need to only flip back rocks under which masses of moths are congregated during day-light hours, and then lick the moths up with their tongue.[1]

Consumption of moths by bears in the southern Rocky Mountains was not known to occur until recently documented by Coop et al (2005) on talus slopes near the top of Redondo Peak in the Jemez Mountains of New Mexico (B). The observed behaviors of both bears and moths were nearly identical to that observed in the northern Rocky Mountains (C & D). Although additional moth sites have not yet been documented in the southern Rockies, this recent discovery leaves open the possibility, not only that additional sites might exist, but also that both black and grizzly bears fed on army cutworm moths in high-elevation areas of Arizona, New Mexico, and Colorado prior to widespread extirpations of the late-1800s and early-1900s.

[1]For in-depth information on consumption of army cutworm moths by bears see: https://www.mostlynaturalgrizzlies.org/army-cutworm-moths

3. History

Grizzly bears have lived at mid-latitudes of North America perhaps as long as 130,000 to 70,000 years, including all of the Last Glacial Maximum and much of the Holocene. The following sections feature the history of grizzly bears in the Southwest during these many millennia—a period typified by extreme changes in the natural and human environments that challenged the abilities of grizzlies to adapt and survive. The history concludes with the rapid extirpation of grizzly bears by Anglo-Americans. Never before during its evolutionary history had grizzly bears encountered such a relentless predator willing to deploy all available methods to achieve its extirpation—with tragic consequences for grizzly bears in much of the area that was to become the United States.

3.a. Before Europeans

3.a.i. Pleistocene Arrivals and Distributions

Fossil remains of grizzly bears are intrinsically rare, not only because grizzlies typically exist at low densities, but also because they rarely die under circumstances conducive to preservation of their remains. This paucity of fossils in the paleontological records stands in stark contrast to species such as cave bears (*Ursus spelaeus* and *U. deningeri*) that occupied caves, often died over-winter, and were thus preserved in their thousands during the course of millennia (e.g., Kurtén 1976). Even so, researchers have been able to accumulate enough direct as well as circumstantial evidence during the last 25 years to allow for a judicious reconstruction of deep history for grizzly bears at mid-latitudes in North America, including the area that was to become the southwestern United States.

At one time grizzly bears were thought to have arrived at mid-latitudes in North America a mere 12-13,000 years ago, after terminal melt of the ice sheets had exposed an ice-free corridor from eastern Beringia south along the east slope of the Rocky Mountains (Kurtén and Anderson 1980). This changed when the remains of a grizzly bear dated to roughly 35,000 years ago were discovered near Edmonton, Alberta, well south of Beringia (Matheus et al. 2004). Subsequent genomic research reinforced the conclusion that grizzlies must have dispersed south well before 35,000 years ago (Miller et al. 2006), with recent research suggesting that the first dispersal event had occurred between 70,000 and 130,000 years ago, ten times earlier than was thought in the 1970s (Salis et al. 2021). More to the point, grizzly bears have occupied mid-latitudes of North America for a long time, including well before the Last Glacial Maximum.

From this it is reasonable to assume that grizzly bears would have in theory been able to colonize and occupy much if not all suitable habitat at mid-latitudes. Absent fossilized remains, the best representation of this habitat for the late Pleistocene has been offered by researchers using modeled relationships that produce remarkably consistent results (Kantelis 2017, Luna-Arnaguré et al. 2020). The maps in Figure 13 show the extent of intrinsically suitable habitat in green, along with the handful of grizzly bear fossils dated from the late Pleistocene and early Holocene, shown as orange bear-shaped symbols.

Although the modeled habitat is extensive, there are several noteworthy reasons to suspect that ancient grizzly bears would not have populated this entire area, most prominently because potential predators likely imposed constraints on where grizzlies could live, in what numbers. Up through the early Holocene until their ultimate extinctions, the most prominent of these predators would have been giant short-faced bears (*Arctodus simus*), American lions (*Panthera atrox*), scimitar-toothed cats (*Homotherium serum*), and saber-tooted cats (*Smilodon fatalis*; Kurtén and Anderson 1980). All could have likely killed an adult grizzly. Short-faced bears were formidable scavengers as well, and would have competed with grizzlies for carrion from large herbivores (Matheus 1995). The toll exacted by short-faced bears could have great enough to cause local extirpations of grizzlies—as probably happened in eastern Beringian between 25,000 and 35,000 years ago (Barnes et al. 2002, Salis et al. 2021). Newly-arrived humans sporting high-technology Clovis-pointed and later Folsom-pointed weapons could have also posed a mortal threat to grizzlies (e.g., Mattson et al. 2005)—consistent with the lack of spatial overlap between grizzly bears and fluted points shown in Figure 13b. Grizzly bears—although present—may have lived a furtive existence during the late Pleistocene and early Holocene trying to avoid potential predators while seeking out low-risk foods.

Of more direct relevance to this report, grizzly bears likely occupied the Southwest for many thousands of years prior to the arrival of Europeans, including all of the last Ice Age and subsequent early Holocene. However, it is unclear in what numbers. More certainly, their densities were probably quite low. Unlike during most of the Holocene, grizzlies would not have been able to dominate carcasses of large herbivores in the face of competition from the many larger carnivores. Instead, grizzlies probably derived most of their diet from vegetal foods as well as excavated fossorial rodents such as pocket gophers (*Thomomys* spp.) and ground squirrels (*Urocitellus* and *Spermophilus*). Roots may have played a particularly important dietary role especially in the drier colder climates of the Last Glacial Maximum (see Section 2 and below).

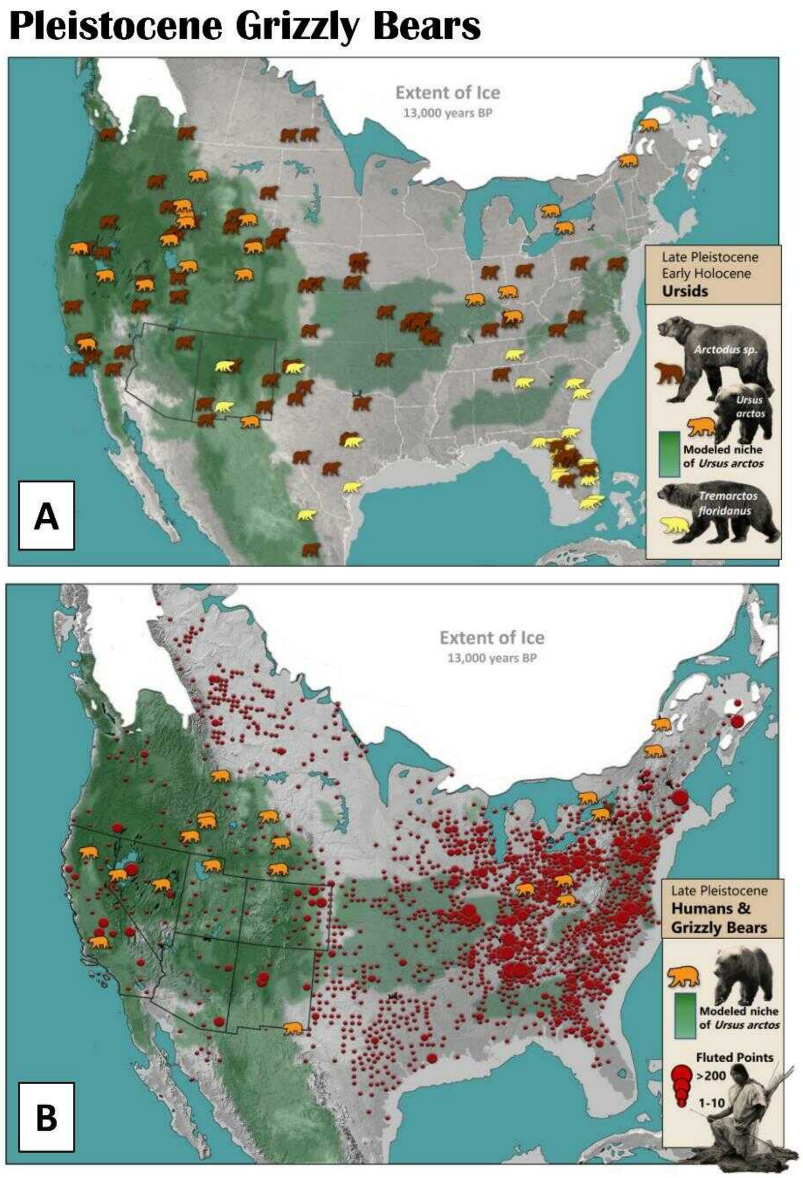


Figure 13. The maps above show features of the late Pleistocene environment that configured the distribution of grizzly bears at a time when continental ice sheets were rapidly melting and large-bodied carnivores as well as humans were competitors and potential predators. The green shaded area in both maps is the result of merging modeled Pleistocene niches of grizzly bears from Kantelis (2017) and Luna-Aranguré et al. (2020). The areas in white were covered by ice sheets *circa* 13,000 years before present (from Dyke 2004, Dalton et al. 2020). Map (A) shows paleontological records of large-bodied ursids during the late Pleistocene and early Holocene, including giant short-faced bears (*Arctodus pristinus* and *A. simus*; burgundy symbols), Florida cave bears (*Tremarctos floridanus*; yellow symbols), and grizzly bears (orange symbols; from Kurtén & Anderson [1980], Richards et al. [1996], Ferrusquía-Villafranca et al. [2010], Mychajliw et al. [2020], and Neotoma Paleoecology Database). The map in (B) shows grizzly bear locations and all documented finds of Clovis and Clovis-like points ("fluted points"). Finds of fluted points are shown as red dots, with larger dots denoting progressively larger concentrations of points (from the Paleoindian Database of the Americas [PIDB]).

3.a.ii. Late Pleistocene-Early Holocene Climate and Vegetation

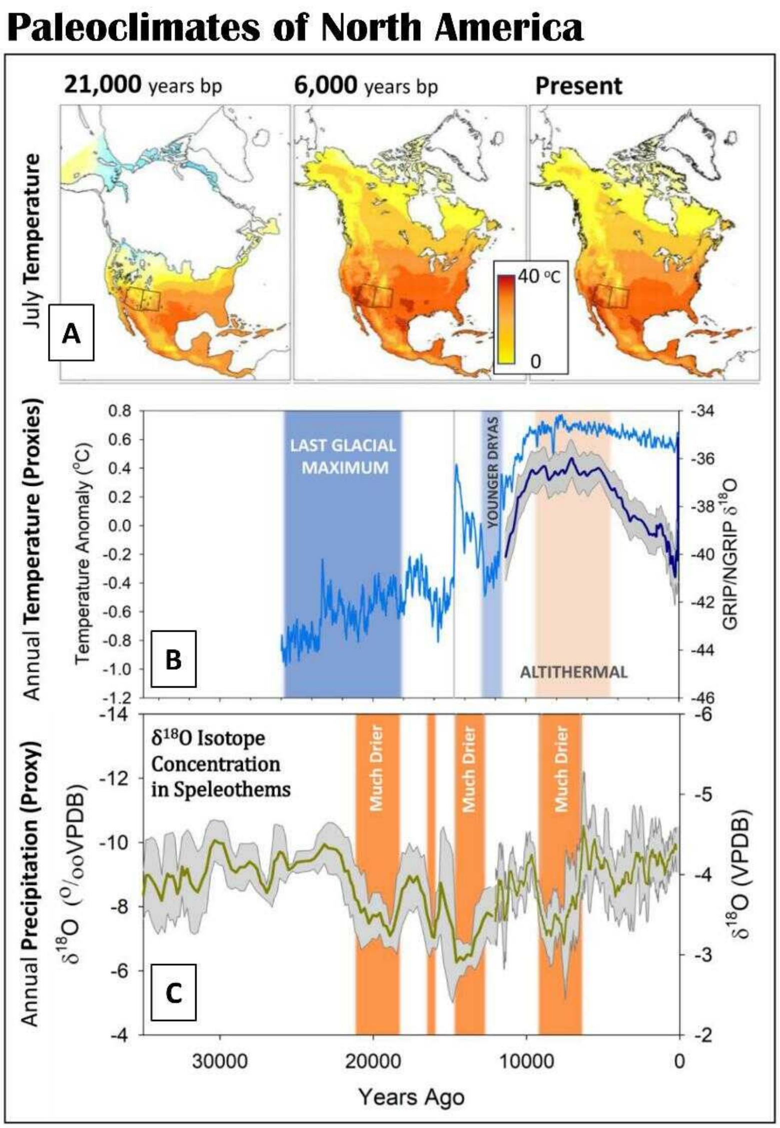


Figure 14. The maps in (A) and figures in (B0 and (C) above show reconstructed paleoclimates spanning the Last Glacial Maximum, roughly 19,000-26,500 years ago, farthest left, through the Altithermal, roughly 9,000-5,000 years ago, up through the present, farthest right. The maps at top show modeled average July temperatures, centered on the Last Glacial Maximum, Altithermal, and near present (Bartlein et al. 1998). Comparatively warmer temperatures are shown in darker shades of yellow-orange. White denotes areas covered by ice sheets (from Dyke 2004). Borders of the current states of Arizona and New Mexico are also shown. The graph in (B) represents a compilation of temperature reconstructions, including the NGRIP $\delta^{18}O$ record in bright blue (Centre for Ice and Climate) and a compilation of more direct estimates of temperature deviations for the Holocene in darker blue (Marcott et al. 2013). The graph in (C) uses a proxy ($\delta^{18}O$ isotope concentrations from cave speleotherms) to show reconstructed annual precipitation in the Southwest (from Polyak et al. [2004], Asmerom et al. [2007], and Hudson et al. [2019]). The dusky green line shows a 100-year moving average of $\delta^{18}O$ values and the gray band around it the standard deviation of measures within each interval. Periods of much drier conditions, corresponding to higher $\delta^{18}O$ values, are shown in orange.

Apropos the last point, above, Figure 14 shows simulations and proxies of summer temperatures and precipitation spanning the last Ice Age up through the present, including the Last Glacial Maximum (LGM) and Altithermal. The LGM lasted from roughly 30,000 to 19,000 years ago, and the Altithermal from 9,000 to 5,000 years ago. Not surprisingly, the climate of the Southwest was much colder during the LGM (Figure 14a; Bartlein et al. [1998]), consistent with a major depression of temperatures globally (Figure 14b). However, with the exception of the last part of the LGM, the Southwest was likely wetter during much of the last Ice Age (e.g., Wagner et al. 2010; Figure 14d), largely because of a compressed and accelerated westerly jet stream roughly centered on the region (Asmerom et al. 2010, Oster et al. 2015, Wang et al. 2018). As a consequence, cover of conifer woodlands was likely greater that it is today (Shao et al. 2018), comprised of junipers as well as five-needled and piñon pines. Temperatures were hotter during the Altithermal (Figure 14b), but varied from a drier earlier period to a wetter one that transitioned to the late Holocene (Figure 14d).

Of relevance to grizzlies, they endured these vicissitudes, probably in mid-latitude refugia, unlike virtually all other megafauna in North America, which went extinct largely between 11,000 and 8,000 years ago, after the Younger

Dryas and before onset of the Altithermal (Stewart et al. 2021). The climatic whip-lash of the last 30,000 years included dramatic warming and wetting after the dry bitter-cold end of the LGM, then a severe 2-½ millennia-long drought that preceded a brief return of cold temperatures during the Younger Dryas, roughly 13,000 to 11,500 years ago, and, after a respite, the hot and dry conditions that marked the first half of the Altithermal, roughly 9,000 to 6,500 years ago. But grizzlies survived these changes to become the last of the large terrestrial carnivores left standing.

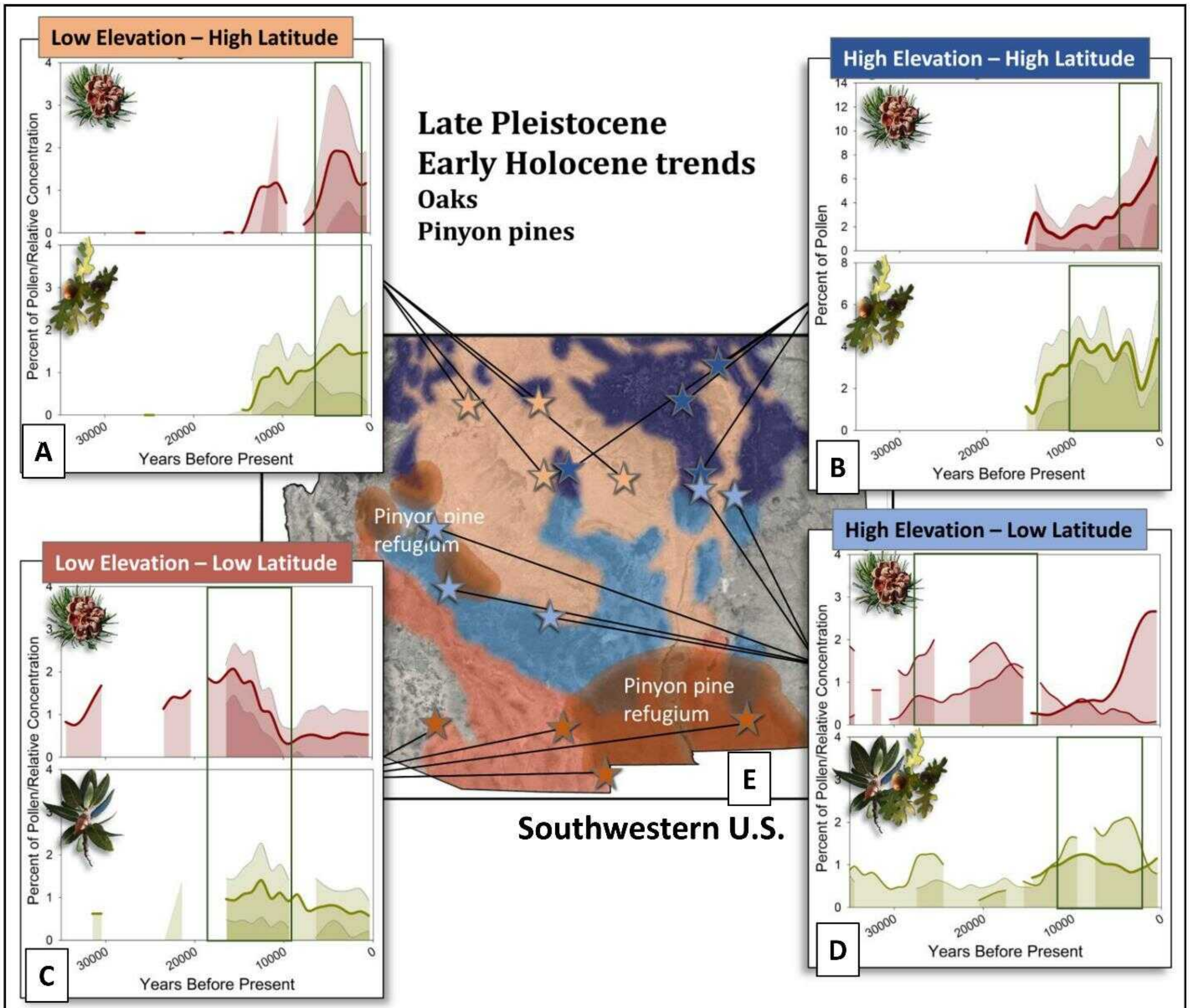


Figure 15. The quartet of graphics shown above summarize results of numerous paleontological studies from the Southwest. Each shows trends in relative amounts of pollen from piñon pines (in burgundy) and oaks (*Quercus* sp., in green), from the last ice age up to the present, with study sites differentiated by four permutations of elevation and latitude. Higher latitudes or elevations correspond with intrinsically colder climates. Study site locations are shown as stars in map (E), with each of the four zones shown in different colors (dark blue, the coldest, and dark orange, the warmest). For zones where basic trends in composition were approximately the same among sites, results are summarized by a mean trend line and one standard deviation above and below (for Low Elevation-High Latitude [A], Low Elevation-Low Latitude [B], and High Elevation-High Latitude [C]). Results from the two sites with comparable data for the High Elevation-Low Latitude zone (D) were different enough to warrant being shown separately. The theorized Pleistocene refugium for piñon pines is also shown in (E) in a dark shade of orange (from Duran et al. [2012]). Sources of paleontological data are: Anderson & Van Devender (1991), Anderson (1993), Anderson et al. (2000, 2008a, 2008b, 2009), Betancourt (1984), Betancourt (1993, 2001), Cisneros-Dozal et al. (2010, 2014), Holmgren et al (2003, 2006), Jiménez-Moreno et al. (2008, 2010), Louderback et al. (2020), and Paklaian (2017).

Even though extreme climates would have created direct challenges for grizzlies, the main effects of climate change would have been indirect, propagated through changes in vegetation and foods—which were substantial in the Southwest. Figure 15 summarizes much of the paleontological research in the region focused on variation in abundance of flora during the past 35,000 years, differentiating study sites at high- and low-elevations, and among those, sites that were at high- or low-latitudes. High-elevation high-latitude sites were largely concentrated in the Rocky Mountains of southern Colorado and northern New Mexico (Figure 15b), whereas low-elevation low-latitude sites were concentrated in desert regions of southern Arizona and New Mexico (Figure 15c). The results summarized in Figure 15 feature trends in abundance of oaks and piñon pines, not only because they produce foods that are often heavily used by bears, but also because, of all the potential bear foods, they are the only ones routinely documented in regional paleontological studies. Even so, they are indicative of the substantial changes in vegetation that occurred during the late Pleistocene into the Holocene that would have affected grizzly bears.

One of the most prominent trends was a dramatic increase in both oaks and piñon pines that occurred at high latitudes 14,000 to 13,000 years ago, irrespective of elevation (Figures 15a and 15b). This period coincided with the dry and comparatively warm conditions that post-dated the Late Pleistocene and predated the Younger Dryas (Figure 14). Of relevance to higher-elevations, it would have also come after terminal melt of the mountain ice caps and glaciers that capped the Rocky Mountains during much of the Pleistocene (Pierce 2003), which would have allowed colonization of newly ice-free areas in addition to areas that were previously too cold for most oaks and piñon pines. Prior to the arrival of these warmer-climate species, limber pine (*Pinus flexilis*) was relatively abundant at lower elevations of northerly latitudes (Anderson 1993, Coats et al. 2008), and potentially a food source for both bears and humans before a switch to consumption of piñon pine seeds between 15,000 and 10,000 years ago (Rhode & Madsen 1998).

Farther south, the trends are a bit muddier, although at low altitude-low elevation sites peak abundance of both oaks and piñon pines occurred between roughly 19,000 and 10,000 years ago, prior to a dramatic decline in the abundance of especially piñon pines (Figure 15c) with onset of the hot dry Altithermal (Figure 14). These trends are consistent with the occurrence of an area in southern New Mexico and southeastern Arizona that is thought to have been a Pleistocene refugium for piñon pines (Duran et al. 2012). These patterns further suggest that portions of the current Sonoran and Chihuahuan Desert could have supported grizzlies during the late Pleistocene through the early Holocene. Trends in sites elsewhere (Figure 15d) suggest that piñon pines might have been most abundant during the LGM, and oaks most abundant from the Younger Dryas up through about 2,000 years ago—although trends are mixed, if not contradictory, depending upon the site.

In toto, trends in climate and abundance of mast-producing species suggest that the Southwest was probably a productive environment for grizzly bears during the few-thousand-year interval between the Younger Dryas and Altithermal, and then for 5,000 years after the Altithermal when precipitation increased and temperatures declined. By contrast, the last third of the LGM was probably inhospitable for grizzlies in the Southwest and the first half of the Altithermal challenging, at best. Bison were furthermore probably absent from much of the southern plains during the latter half of the Altithermal (Dillehay 1974), during a warmer but wetter period that likely allowed for encroachment of woody vegetation to the detriment of productivity for bison (Huebner 1991, Lohse et al. 2014a).

3.a.iii. Living With Indigenous Peoples

Figure 16 reiterates information in Figure 2, primarily to emphasize where grizzly bears likely occurred during more clement conditions of the last 2,000 years—up until the arrival of Anglo-Americans. Although climate and vegetation were not static during the last two millennia, variations in both were much less dramatic than those that typified the previous 24,000 years (Figures 14 and 15). It is probably safe to assume that the areas shaded green in Figure 16 are those that configured the fates of grizzly bear populations in the Southwest throughout recent millennia.

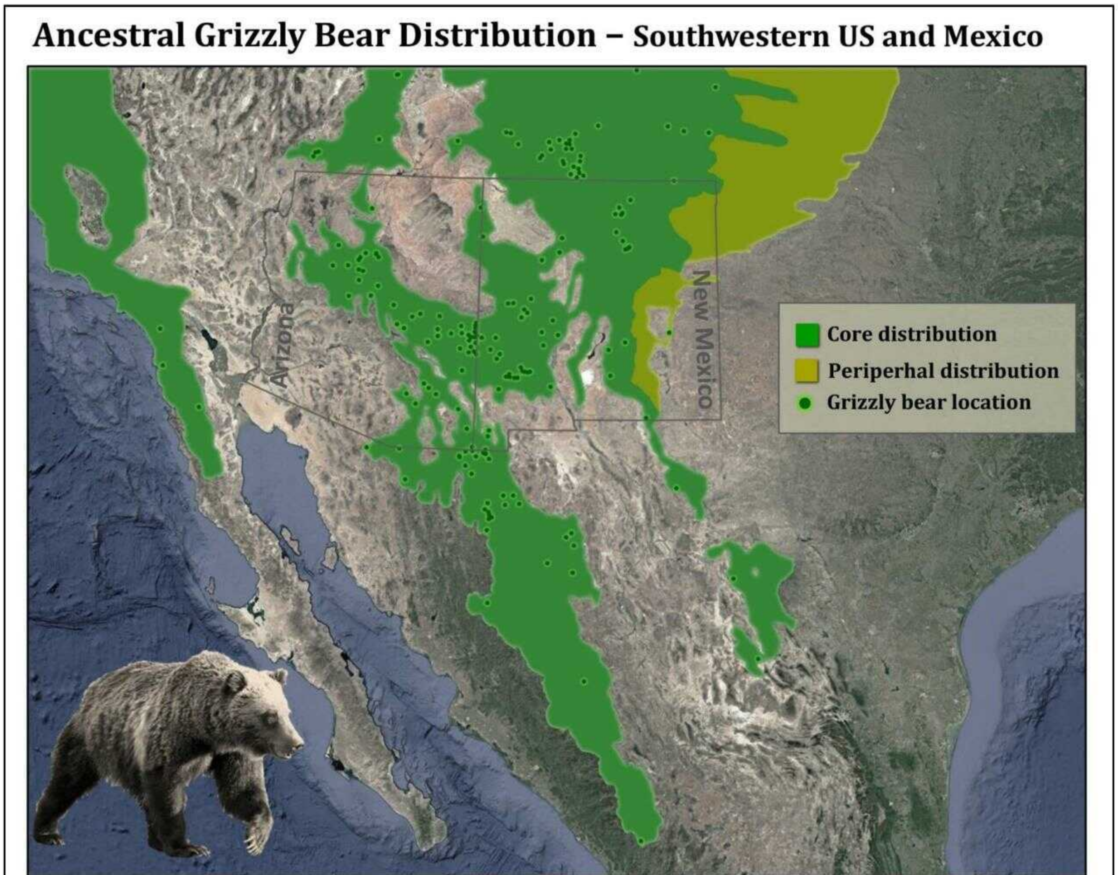


Figure 16. This map reiterates the information in Figure 2, specifically the approximate distribution of grizzly bears at the time of first contact with Europeans in what was to become the southwestern United States and northern Mexico. Green denotes grizzly bear strongholds and, lighter yellow-green, areas where grizzlies would have been present but largely restricted to linear west-east trending riparian zones along major rivers. Dark-green dots denote encounters with grizzly bears documented by literate Europeans, exclusive of California.

With that proviso, although the biophysical environment was not subject to wide-amplitude fluctuations of the Late Pleistocene and early Holocene, the same cannot be said about human impacts. Various reconstructions of pre-European human populations in the Southwest show a dramatic increase beginning around 600 C.E. (Current Era), or roughly 1,400 years ago (Figure 17c). Populations peaked between 900 and 1200-1500 C.E. before catastrophically declining—the timing depending on the region. There is little doubt that the dramatic increase in human populations was linked to widespread adoption of agriculture and subsequent dependence of people on cultivated crops. Although maize was likely present in the Southwest over 4,000 years ago (Wills 1988, Merrill et al. 2009, Da Fonseca et al. 2015), agriculture did not reach ascendence until more productive cultivars and a perfected system of maize, squash, beans, and turkey production was developed (Wills 1988; Kohler et al. 2008, 2014), which varied from around 1,800 years ago at higher latitudes and elevations (Chisholm & Matson 1994, Diehl 1996, Martin 1999, Schollmeyer & Turner 2004) to nearer 1,000 years ago in southern Arizona and New Mexico (Gilman 1995, Hard et al. 1996).

But dependence on agriculture did not obviate impacts of high human densities on natural foods. Ample evidence suggests that agriculturalist continued to exploit wild plant and animal foods (Kaplan 1963, Wills 1988, Herring et al. 2014, Sullivan et al. 2015, Crabtree et al. 2017b, Martinez 2021, Pavlik et al. 2021), with apparent resulting depletion of larger mammals and subsequent reliance on small mammals such as lagomorphs (*Lepus* and *Sylvilagus*) for wild game in many areas (Cannon 2000, 2003; Muir & Driver 2002; Schollmeyer 2011, 2018).

This spill-over effect of high human population densities on the natural environment would have likely impacted grizzly bears, especially given that humans and bears—both large-bodied omnivores—compete for the same foods.

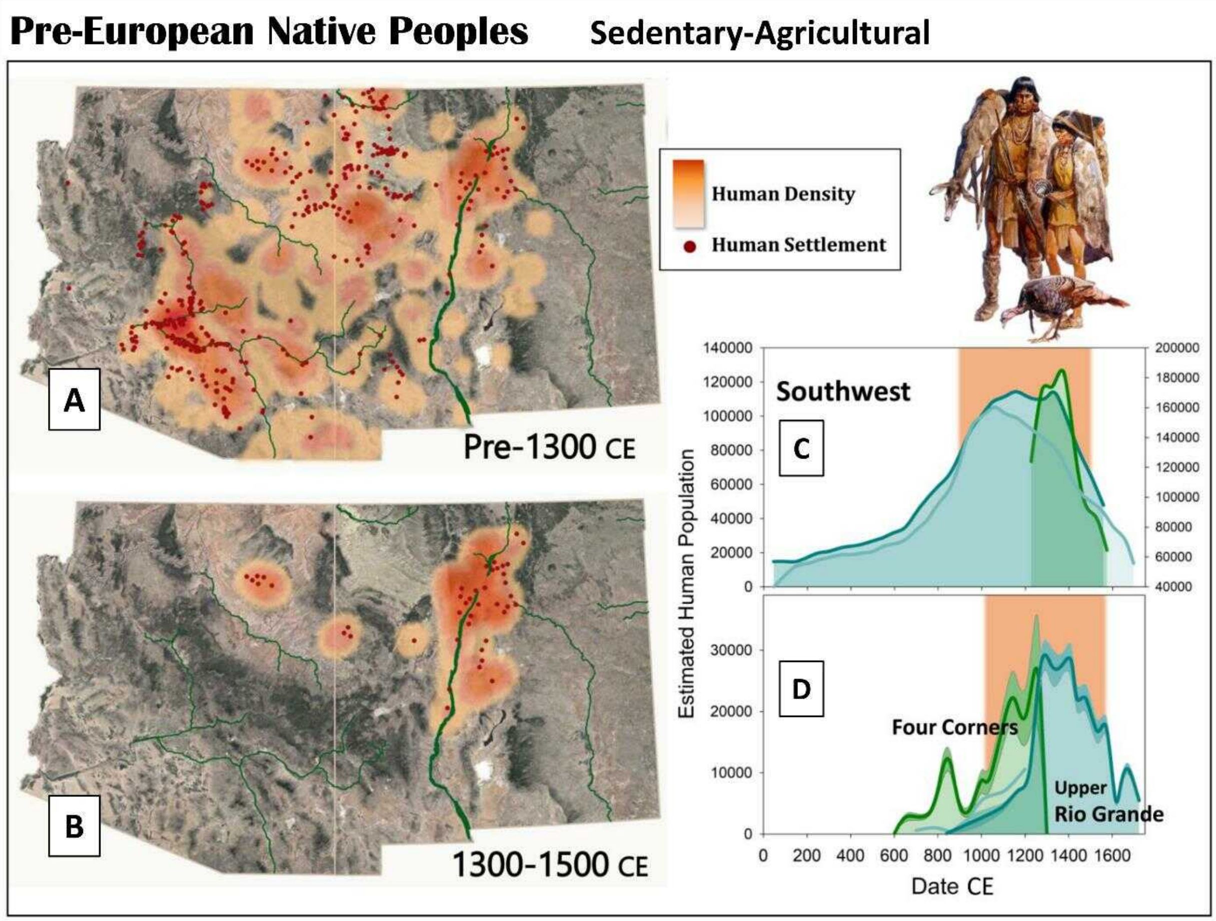


Figure 17. The maps in (A) and (B) show relative densities of humans in the Southwest during the pre-European (pre-Coronado) period back to roughly 1000 CE (Current Era), with darker shades of orange denoting progressively higher estimated densities (from Hill et al. [2004]). These density maps roughly correlate with distributions of larger permanent settlements, shown as red dots for (A) prior to 1300 CE and for (B) 1300-1500 CE, prior to first contact with Spaniards (from Wilcox [1999], Bayman [2001], Hill et al. [2004], and Ortman [2016]). The graphics in (C) and (D) show estimated sizes of human populations in the Southwest, with different-colored lines representing estimates from different sources, and vertical orange-shaded areas denoting the period of peak estimated population sizes. Estimates in (C) are for the entire Southwest (from Hill et al. [2004]) whereas estimates in (D) are for subregions centered on the current four corners of Utah, Colorado, Arizona and New Mexico (in green) and on the upper Rio Grande River drainage in modern-day New Mexico (blue; from Schwindt et al. [2016], Cooper [2020] and Robinson et al. [2021]). Pre-European populations in the Southwest peaked between roughly 1200 and 1400 CE, although a major population redistribution from the Four Corners region to the Upper Rio Grande occurred around 1300 CE, coincident with the collapse of settlements centered on Mesa Verde in modern-day southwestern Colorado and the demise of major Hohokam and Sinagua settlements in southern Arizona.

The potential geospatial extent of major human impacts is vividly illustrated in Figure 17a. This map shows human densities (shades of orange) and associated larger permanent settlements (red dots) at the time of peak human populations, pre-1300 C.E. (see figure caption for sources). Much of the area that was intrinsically most productive for grizzly bears would have been within the bounds of this human footprint. It is difficult to estimate the magnitude of impacts, but it would likely have been non-trivial.

Human population declines began at different times in different places, with some areas affected more than others partly because of population migrations and displacements. Abandonment of Chaco great houses in northwestern New Mexico occurred around 1250 C.E. (Stuart 2014), of Mesa Verde in southwestern Colorado around 150 years later, circa 1300 C.E. (Kohler et al. 2013), and of Hohokam settlements in southern Arizona around 1450 C.E. (McClelland 2015). All but Hohokam abandonments were roughly correlated with a great drought that occurred during the late 1200s C.E. (Figure 18a), potentially exacerbated by a history of environmental degradation around major settlements (Kohler et al. 2013, Stuart 2014). Much of the population in the Four Corners area was apparently displaced to settlements in the Upper Rio Grande (the Pueblo IV culture), off-setting some of the regional population declines (Figure 17c). The net spatial effect is shown in Figure 17b, notably a marked decline in the human footprint, especially in areas encompassing the Mogollon Rim and Mountains, although with perpetuation of likely human impacts on grizzly bear habitat in the Jemez and southern Sangre de Cristo Mountains of northern New Mexico.

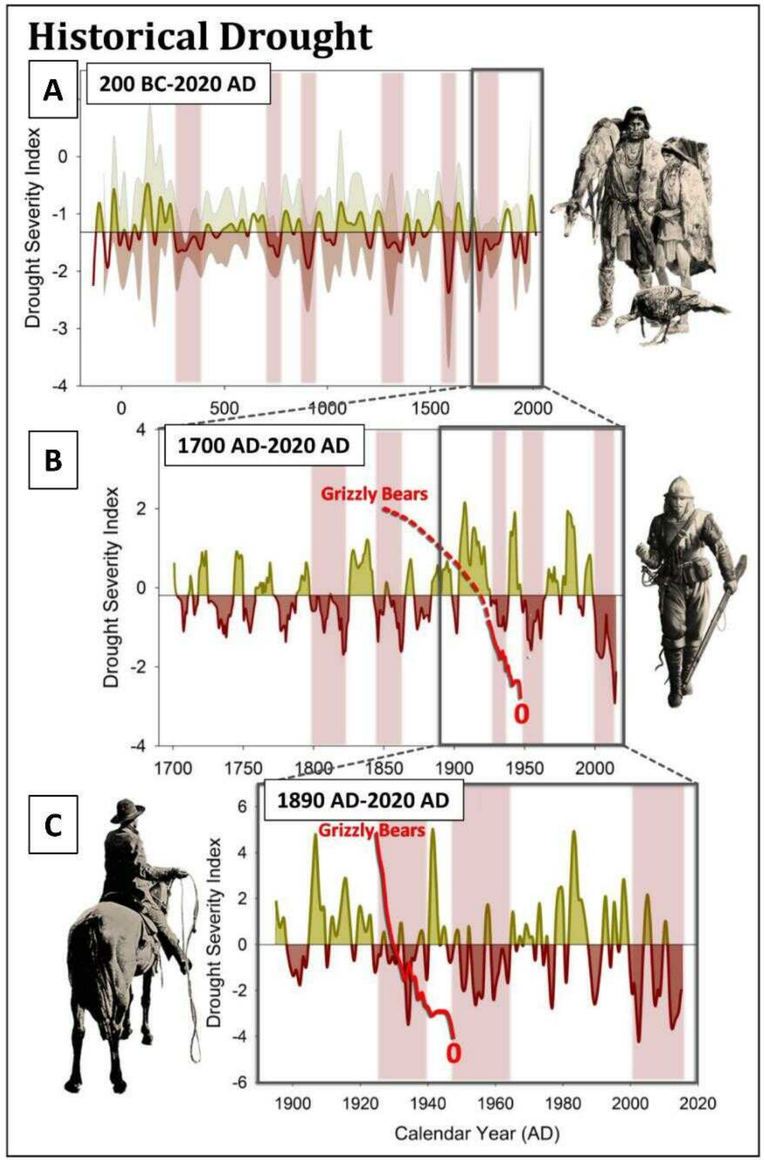


Figure 18. These graphics show histories of drought in the Southwest based on modeled reconstructions (A & B) and recorded weather (C). Periods of drought are shown as burgundy-shaded deviations of trend lines below long-term averages, standardized for each time frame. Comparatively wet periods are shown as green-shaded positive deviation. Periods of sustained severe drought are denoted by vertical burgundy-shaded bars. The terminal decline of grizzly bear populations in Arizona and New Mexico is shown as a red line (from Figure 22). (A) Shows water-year Palmer Drought Severity Index (PDSI) smoothed with a 25-year spline, modeled from growth of Rocky Mountain junipers (*Juniperus scopulorum*) in west-central New Mexico (Oliver 2017). (B) Shows summer PDSI smoothed with a 10-year spline, modeled from regional tree-ring chronologies (Fye et al. 2003). (C) Shows the 9-year weighted running average of PDSI for the Southwest based on weather station instrument records (U.S. Environmental Protection Agency 2016).

Even though exploitation competition with humans for shared foods likely occurred prior to arrival of Europeans—especially between 900 and 1500 C.E.—that does not necessarily imply that humans were a significant direct source of mortality for grizzly bears. In fact, archeological information and traditional knowledge suggest that newly arrived Athapascans (e.g., Navaho and Apache) as well as long-established

Ancestral Puebloans only rarely killed bears, and when they did so it was primarily for ceremonial purposes or self-defense (Hallowell 1926, Rockwell 1991, Pavlik 1997, Hill 2000, Berres et al. 2004). Furthermore, tradition holds that among Navajo and Puebloans killing and eating bears was considered tantamount to cannibalism (Miller 1982, Pavlik 1997). More to the point, this sort of evidence suggests that prior to the arrival of Anglo-Americans, humans did not often kill grizzly bears, and so were probably not a significant additive source of mortality—in contrast to the probable effects of bear-hunting traditions among indigenous people in boreal regions (Hallowell 1926, Nelson 1983, Rockwell 1991).

3.b. Early European Period

3.b.i. The Period of Spanish and Mexican Control

Although Coronado's 1540-1542 C.E. expedition into the Southwest was preceded by a handful of Spanish emissaries, the expedition itself forever changed the region's human history (Flint 2008). Spanish settlement of the region by Oñate did not occur until 1595, over 50 years later, but subsequent imposition of Spanish control over indigenous Puebloans was rapid and thorough (Spicer 1962), primed by the effects of drought and cold temperatures (White 2014; Figures 18a and 20a). The journals of Spaniards such as Fray Alonso de Benavides vividly illustrate the nature and magnitude of Spanish dominance and exploitation (Morrow 1996). One side-effect of colonization was widespread displacement of indigenous people (Schroeder 1968, Kulisheck 2003), but colonization itself was preceded by catastrophic population declines caused by diseases such as smallpox, typhus, and measles that had spread among native populations soon after first contact with Europeans (Liebmann et al. 2016). Subsequent outbreaks of these European diseases together with a number of severe droughts during the 1600s and 1700s (Figure 20b) continued to depress indigenous populations (e.g., Stodder & Martin 1992, Fenn 2001).

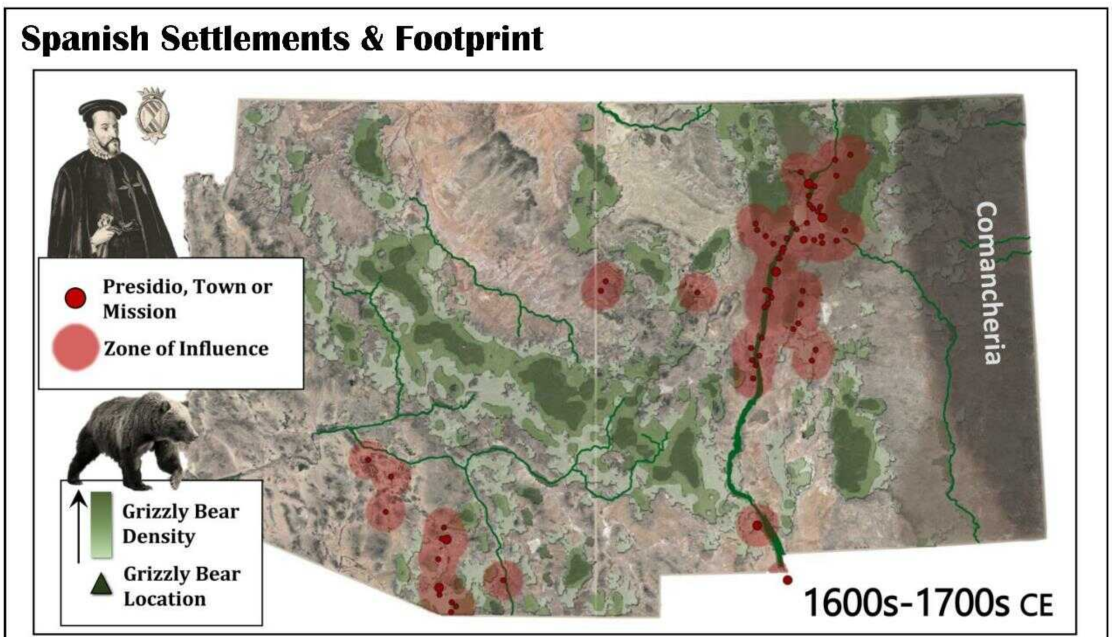


Figure 19. The map in this figure shows in shades of red the distribution of major impacts attributable to Spanish colonists in the Southwest during 1600 to 1800 CE (Current Era) relative to the estimated distribution of grizzly bears during this same period in shades of green. Major Spanish presidios, towns, or missions are shown as red dots, each with a zone of influence that approximates the distances residents would have frequently travelled away from these settlements (from Williams [1986] and Southwest Missions Research Center http://southwestmissions.org/maps/). The distribution of grizzlies is represented by densities estimated from intrinsic habitat productivity, with darker green denoting higher estimated densities (Mattson & Merrill 2021a). The area controlled by the Comanche (i.e., "Comancheria") during this period is also shown (from Hämäläinen [2008]). Areas with the highest estimated potential to support grizzly bears probably remained largely unaffected by direct impacts from both the Spanish and Comanche throughout this 200-year period.

Interestingly, for reasons seemingly related to culture, a rigid hierarchical system, the agendas of conquest, and lack of weapons and empowerment among mestizos as well as lower-class creoles and Spaniards (Spicer 1962, Kessell 2003), the footprint of Spanish impacts was little more than that of pre-European Puebloans during the two centuries prior to colonization (compare Figure 19 to Figure 17b). Geospatially, these impacts were largely restricted to areas along the upper Rio Grande River in New Mexico and Santa Cruz River in Arizona. This spatial confinement together with early dramatic declines in indigenous populations likely resulted in a reduction of human impacts on grizzly bears in areas of Spanish and Mexican control throughout the 1600s and 1700s, especially compared to during the pre-European period of 900-1450 C.E. (see Section 3.a.iii), leaving much of the best grizzly bear habitat unaffected (Figure 19).

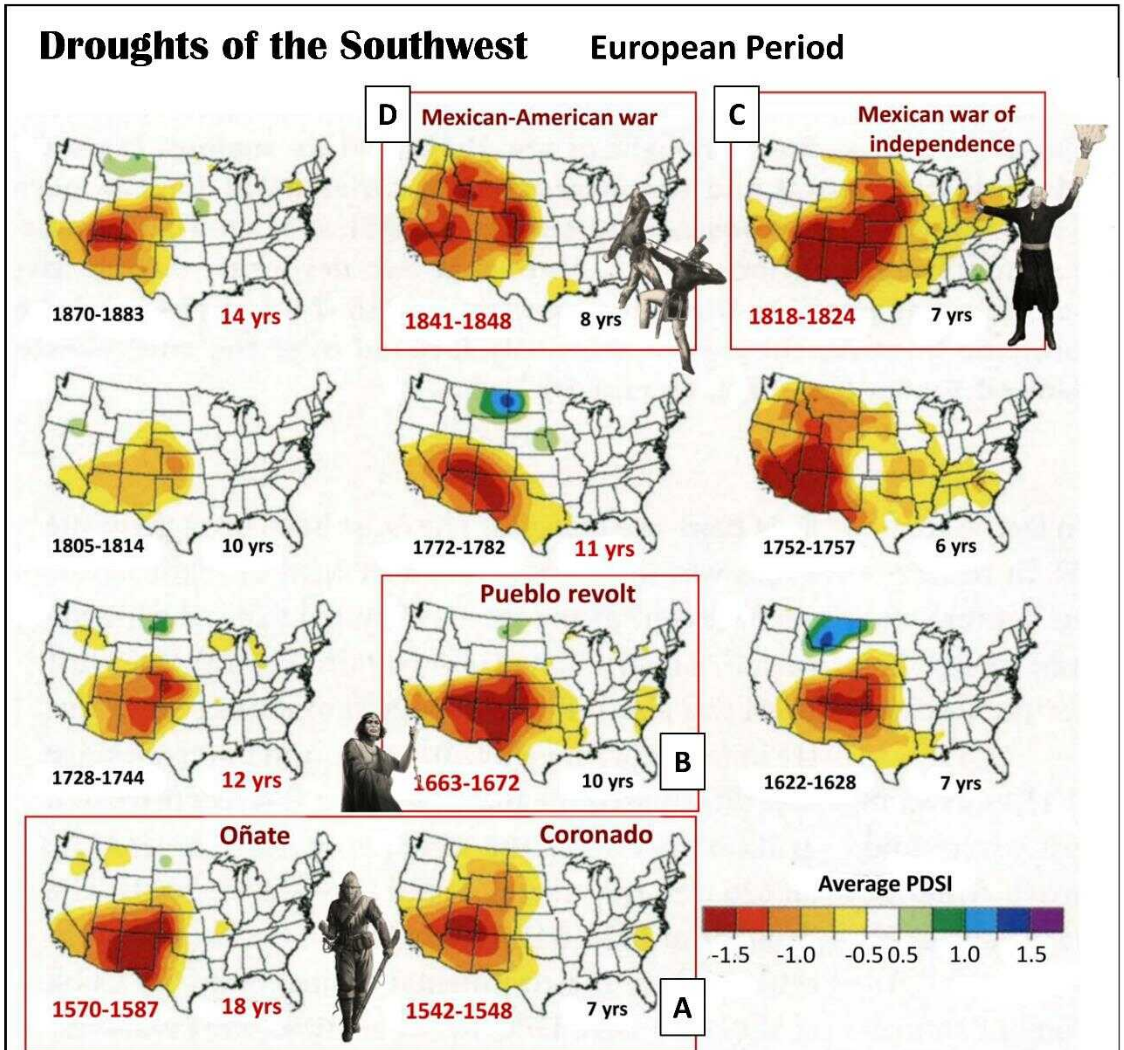


Figure 20. The maps above show the severity of various notable droughts centered on or substantially affecting the Southwest during the period 1500-1900 CE (adapted from Fye et al. [2003]). Drought severity is represented in terms of the Palmer Drought Severity Index (PDSI), with darker shades of orange denoting greater drought severity. The dates and durations of each drought are shown below each map. Historical events correlated with different drought periods are also shown, including the period of Spanish exploration and conquest (A; Coronado and Oñate), the Pueblo Revolt (B), the Mexican Wars of Independence (C), and the Mexican-American War (D). Details of these historical episodes can be found in Flint (2008), Simmons (1993), Roberts (2008), Henderson (2010), and Eisenhower (1989). Notably, none of these works contain any significant reference to environment factors such as drought that might have influenced or even driven these human upheavals.

3.b.ii. The Comanche

A major proviso to this general point holds for areas dominated by non-sedentary or nomadic indigenous people during the equestrian period, notably the Comanche. Horses captured from the Spanish spread and multiplied among indigenous people in the Rocky Mountains and on the Great Plains shortly after the Pueblo revolt of 1680 (Haines 1938, Worcester 1944). This proliferation of horses was accompanied by increased trade with French and Anglo-American merchants that placed firearms in the hands of equestrian natives (Hämäläinen 2008).

Of particular relevance to the fate of grizzly bears on the southern Great Plains, this period coincided with movement of the Comanche out onto the high-elevation grasslands of Colorado, New Mexico, Oklahoma, and Texas, followed shortly by their ascendence to political, military, and commercial dominance (Hämäläinen 2003, 2008; Figure 19). Soon after, well-armed and mounted Comanche proceeded to heavily harvest bison herds, primarily for hides and meat used in trade with Europeans and Puebloans (Isenberg 2000, Hämäläinen 2001). The skills used to efficiently hunt bison mirrored a revolution in warfare that featured a widespread transition among Indians on the Great Plains from armored phalanxes to highly mobile, well-armed, and dispersed warriors (Secoy 1992).

Figure 21. This map shows in green were grizzly bears likely persisted as of *circa* 1920 in the southwestern United States and northern Mexico, superimposed on where grizzlies were likely distributed at the time of first contact with Europeans (in yellow, from Figure 16). Where known, years of extirpation for relict populations are given in Current Era (C.E.) dates. The reconstructed 1920s distribution and known dates of extirpation are from Merriam (1922), Barnes (1927), Bailey (1935), Grinnell et al. (1937), Durrant (1952), Trevino & Jonkel (1986), Brown (1996), Gallo-Reynosa et al. (2008), Mattson (2021), and Denver Museum of Nature & Science.

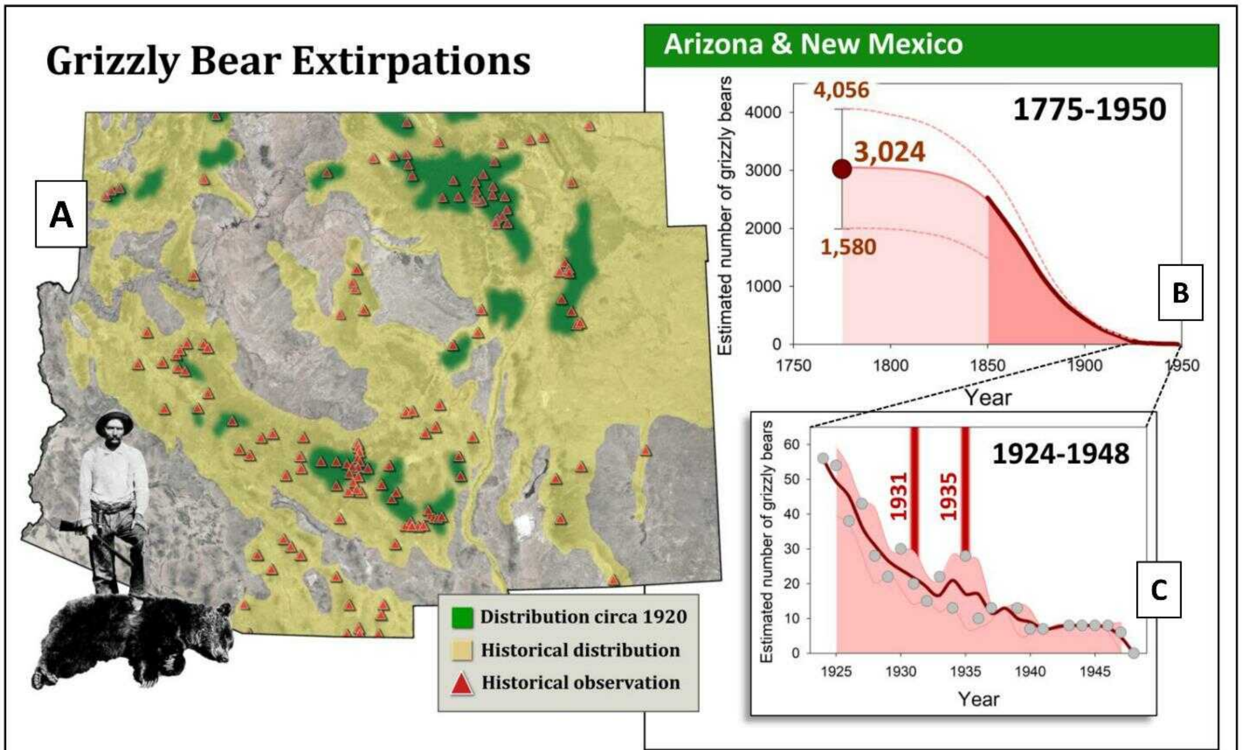


Figure 22. The map in (A) and graphics in (B) and (C), above, summarize temporal and spatial dimensions of grizzly bear extirpations in Arizona, New Mexico, southern Utah and Colorado between 1800 and the 1970s. Map (A) shows the distribution of grizzly bears during the early 1800s in dusky yellow (from Figure 3b) and the approximate distribution of grizzly bears *circa* 1920 in green (from Cary [1911], Merriam [1922], Warren [1942], Durrant [1952], and Brown [1996], and National Museum of Natural History, Division of Mammals Collection). Observations of grizzly bears documented by Europeans are shown in (A) as red triangles (from Cary [1911], Merriam [1922], Warren [1942], Durrant [1952], Armstrong [1972], Hoffmeister [1986], Petersen [1995], Brown [1996], Mattson [2021], and National Museum of Natural History, Division of Mammals Collection). The graphs in (B) and (C) show the approximate trajectory of grizzly bear population declines in Arizona and New Mexico—in (B) for 1775 to 1950 and in (C) for terminal extirpations during 1924-1948 (from Brown [1996]). Beginning population size *circa* 1775 is averaged from estimates in Mattson (2021) and Merrill & Mattson (2021b), with 1 SD for these estimates shown by the vertical uncertainty interval. The dark red line in (C) is a moving 3-year average of annual estimated population sizes made by the U.S. Forest Service, shown as gray dots. The vertical bars and associated dates in (C) denote when grizzly bears were last known to be alive in Arizona (1931 CE) and New Mexico (1935 CE). Population sizes after these dates were based on professional estimates made by Fores Service personnel using undisclosed evidence and criteria.

The impacts of this revolution in Comanche life-ways on grizzly bears were probably stark. Mounted warriors with guns could have cornered or run down and killed grizzly bears with comparative ease in open environments and lineated riparian areas typical of the high plains. Unlike in the case of the Puebloan and Apachean peoples (Section 3.c.iii), Comanche would have probably had little compunction doing this (Rockwell 1991). A likely increase in human-caused mortality combined with early reductions in bison herds plausibly explains the commensurately early extirpation of grizzly bears on the southern Great Plains, including eastern New Mexico and southeastern Colorado—prior to dominance of the region by Anglo-Americans (Mattson & Merrill 2002, Mattson 2021a). As with impacts attributable to high human densities during 900-1450 C.E. in the heart of the Southwest (Section 3.c.iii), impacts attributable to the Comanche reflect a generalizable proposition that indigenous people affected grizzly bear populations and distributions well before, in addition to well after, arrival of Europeans (e.g., Mattson et al. 2005).

3.c. Anglo-Americans & Extirpations

Although the Mexican-American war of 1846-1848 caused much suffering and distress among Mexicans and Hispanic residents of the Southwest (Eisenhower 1989), it marked the onset of an absolute catastrophe for grizzly bears. Anglo-Americans had insinuated themselves into the commerce and society of New Mexico prior to the Mexican-American war (e.g., Gregg 1845, Couse 1898, Sides 2007), but their impact was comparatively minor compared to what came soon after. With the almost immediate advent of government sponsored expeditions, reports were soon filled with accounts of Anglo-Americans encountering and killing grizzly bears (e.g., Baird 1859). The prominent place given these encounters in official narratives is in stark contrast to an absence of the same in Spanish and Mexican documents. Whatever the cultural, social, and material reasons for this difference, the ensuing slaughter of grizzlies during the next 90 years is an indisputable fact at odds with anything that came before. The end result was extirpation of grizzlies in the Southwest. The last known grizzly bear was killed in the southern San Juan Mountains of Colorado in 1979.

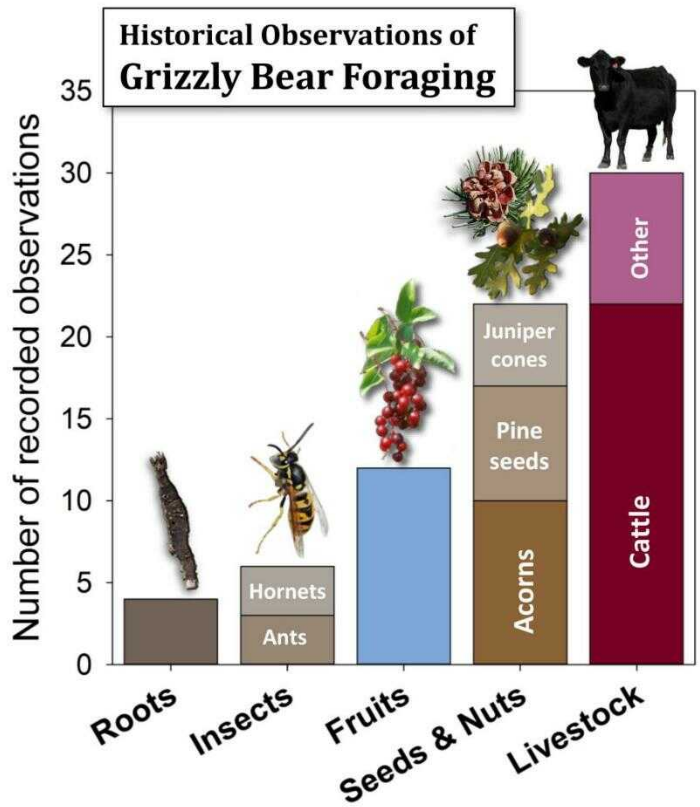


Figure 23. This bar graph shows the frequency with which literate Europeans documented consumption of different categories of foods by grizzly bears in the Southwest, with bar height proportional to absolute frequency. Hard mast (i.e., seeds and nuts) is differentiated by observed consumption of acorns, piñon pine seeds, and juniper cones (i.e., "juniper berries"). Documented observations rarely if ever differentiated the species of fruit or root foods consumed by grizzlies, which were consequently lumped into broad categories. Most observations are from Stevens (1943), French (1997), O'Bagy Davis (2003; by Nat Straw), and Dobie (2012; by Ben Lilly), with numerous other incidental observations from historical summaries by Davis (2001), and Brown (1996, 2009). These observations are heavily biased towards exploitation of cattle by grizzlies given that most historical records focus on the heroic pursuit of "stock killers" by hunters and related justifications for unrelenting slaughter of predators.

The somewhat speculative terminal trajectory of grizzly bear populations in the Southwest is shown for the period 1775-1950 C.E. in Figure 22b, and for the final phase of extirpations in Figure 22c. Data for the latter figure are taken from Brown (1996), who provides perhaps the most comprehensive account of the final days of grizzlies in the Southwest. The main point of these figures is that steepest declines began about 1850 with advent of Anglo-American dominance, whereas the period of 1924-1948 offered little more than a glimpse of the grizzlies' final days. Most losses had probably already occurred by 1900, roughly 30-40 years before final extirpations in most areas barring the San Juan Mountains in Colorado and the Sierra Madre Orientale in Chihuahua, Mexico.

The maps in Figures 21a and 22b illustrate the magnitude of losses by around 1920. Remnant populations of grizzlies are shown in green, the original Holocene distribution in yellow (from Figure 16), with losses by 1920 amounting to roughly 90% of all grizzlies in 90% of the areas they once lived (Mattson 2021a). The red triangles in Figure 22a are locations of grizzly bears documented by literate Anglo-Americans, largely during the 85 years between 1850 and 1935. The juxtapose of these locations with not only remnant grizzly bear distributions *circa* 1920, but also distributions of productive habitat (see Figure 3a), emphasizes the extent to which productive mountainous areas, replete with vegetal foods, mitigated against the local demise of grizzly bears (see Section 2.c.iv).

The rapidity of grizzly bear losses with political ascendence of Anglo-Americans begs for some sort of proximal explanation. In contrast to when Spaniards and Mexicans governed the Southwest, it is clear that the influx of well-armed Anglo-Americans rapidly took their toll. These newcomers also brought a murderous attitude informed by variations on the theme of Manifest Destiny, which both justified and motivated extirpations of any wild animals and indigenous peoples who stood in the way of thorough colonization (Slotkin 1973, 1985, 1992; Drinnan 1980). But another factor almost certainly contributed to extirpations, especially after 1880.

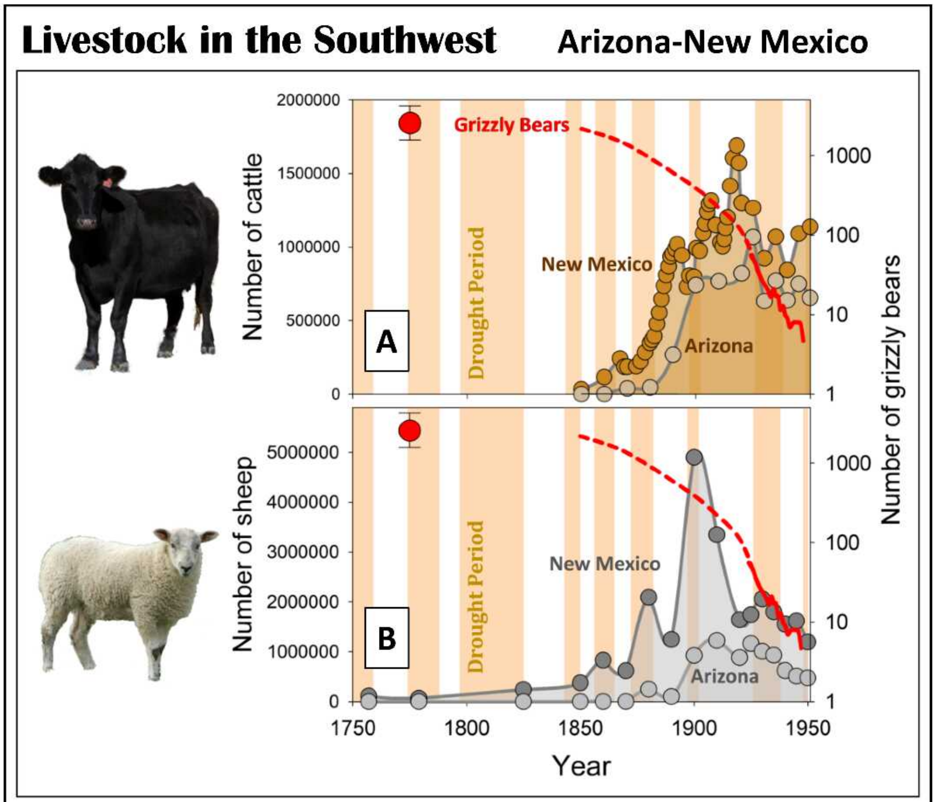


Figure 24. The graphs above show trends in numbers of cattle (A) and sheep (B) in New Mexico and Arizona during 1750-1950 CE, juxtaposed on trends in estimated size of the regional grizzly bear population and periods of drought. Cattle numbers in (A) are shown in shades of brown, sheep numbers in (B) in shades of gray, estimated numbers of grizzly bears as a red dashed or solid lines in both (from Figure 22), and drought periods as vertical orange shaded bars (from Figure 18). Data for sheep and cattle numbers are from Culbert (1941), Scurlock (1998), Wallace (2013), and U.S. Department of Agriculture Historical Census of Agriculture publications (https://www.nass.usda.gov/AgCensus/).

The establishment of large-scaling ranching in or near areas with the best grizzly bear habitat was restricted up until the 1880s by the presence of Navajo and Apache hostile to European encroachment (e.g., Basso 1983, Roessel 1983, Sweeney 1991), as well as by lack of railways to transport cattle to market (Culbert 1941, Sheridan 2012). By the 1880s these two impediments had been removed. Numbers of cattle and sheep in both Arizona and New Mexico increased dramatically (Figure 24), flooding not only low-elevation rangelands, but also mountainous areas with even a modicum of forage—all of this coincident with catastrophic declines in numbers of native wapiti and mule deer caused by unchecked hunting (Section 2.c.iv and Connolly [1981]).

With the loss of native ungulates and the overwhelming substitution of livestock, it is little surprise that depredation on cattle by grizzly bears increased dramatically during the 1880s, as evidenced by monotonous recitations of government officials charged with killing depredating predators (Ligon 1927; Bailey 1931; Brown 1996, 2009; Davis 2001). Isotopic evidence from the scant remains of grizzlies dating to this period is consistent with heavy reliance on meat, almost certainly from livestock (Jacoby et al. 1999). Government-paid professional bear killers along with ranchers with a penchant for tracking down and killing bears were unleashed on grizzlies with predictable results (e.g., Stevens 1943, Evans 2003, O'Bagy Davis 2003, Dobie 2012). Documented observations of grizzly bear feeding behavior by Anglo-Americans during this period confirms a dynamic organized around not only around depredation on cattle but also devotion to eradication of grizzlies. Figure 23 summarizes all of the observations that I could find, which are *prima facie* heavily biased towards what Anglo-Americans chose to observe and document. Predation and scavenging on cattle unequivocally dominate these observations, followed by observations of grizzlies consuming hard mast.

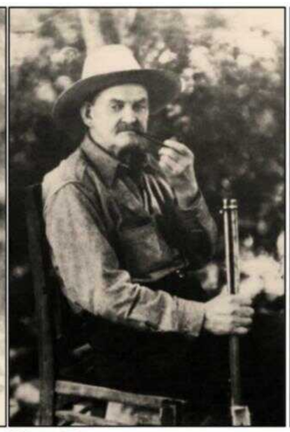
There is little doubt that the terminal toll taken on grizzly bears by Anglo-Americans after 1850 was primarily driven, not by anything intrinsically problematic to grizzly bear behaviors, but rather by intolerance and an ecological dynamic entrained by the eradication or diminishment of native foods and the substitution of human foods, notably livestock, that predictably catalyzed conflict. Although grizzly bears were able to survive as much as 100,000 years of exposure to extreme changes in climates and environments in the Southwest, they were not able to survive less than 100 years of exposure to Anglo-Americans driven by the ethos of Manifest Destiny.

Box 3. This box offers a thumbnail description of four famous men who hunted grizzly bears in the Southwest, each emblematic of distinctive personalities, worldviews, circumstances, and personal evolution that manifest in their persecution of grizzlies, ranging from the unrepentant and merciless Ben Lilly farthest left to the enlightened and evolved Aldo Leopold farthest right. Sources include Dobie (2012), O'Bagy Davis (2003), Stevens (1943), and Meine (1988).

Famous Bear Hunters of the Southwest

Ben Lilly
1856-1936

Ben Lilly was remarkable for a number of reasons. He was consummately skilled at not only killing bears, but other wildlife as well. He combined exceptional physical stamina with a noteworthy lack of empathy for animals and people, augmented by a self-referential Christian morality that manifest primarily as a devotion to resting on Sundays and abstinence from alcohol. He was unrepentantly devoted to killing bears until his final days. He used hounds and horses as needed, but more often relied on his own feet for hunting. He lived in the Southwest from 1911 until his death in 1936.

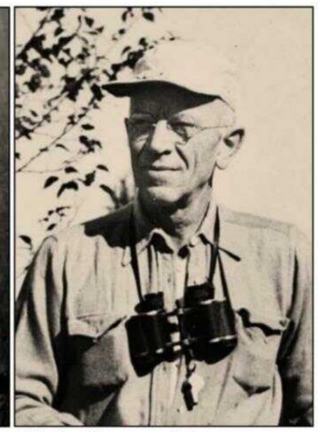


Nat Straw
1856-1941

Nat Straw was a contemporary of Ben Lilly's who specialized in using traps to capture bears and mountain lions. He was a solitary man who avoided towns, but was at the same time a good-natured conversationalist who, although honest, was inclined to tell tall tales. Unlike Lilly, Nat was tidy, well-kept, a good cook, and not particularly religious. However, in common with Lilly, he remained an unrepentant killer of bears until the end of his life. Nat lived in the Southwest from 1876 until his death during 1941 in Cliff, New Mexico.

Montague Stevens
1859-1953

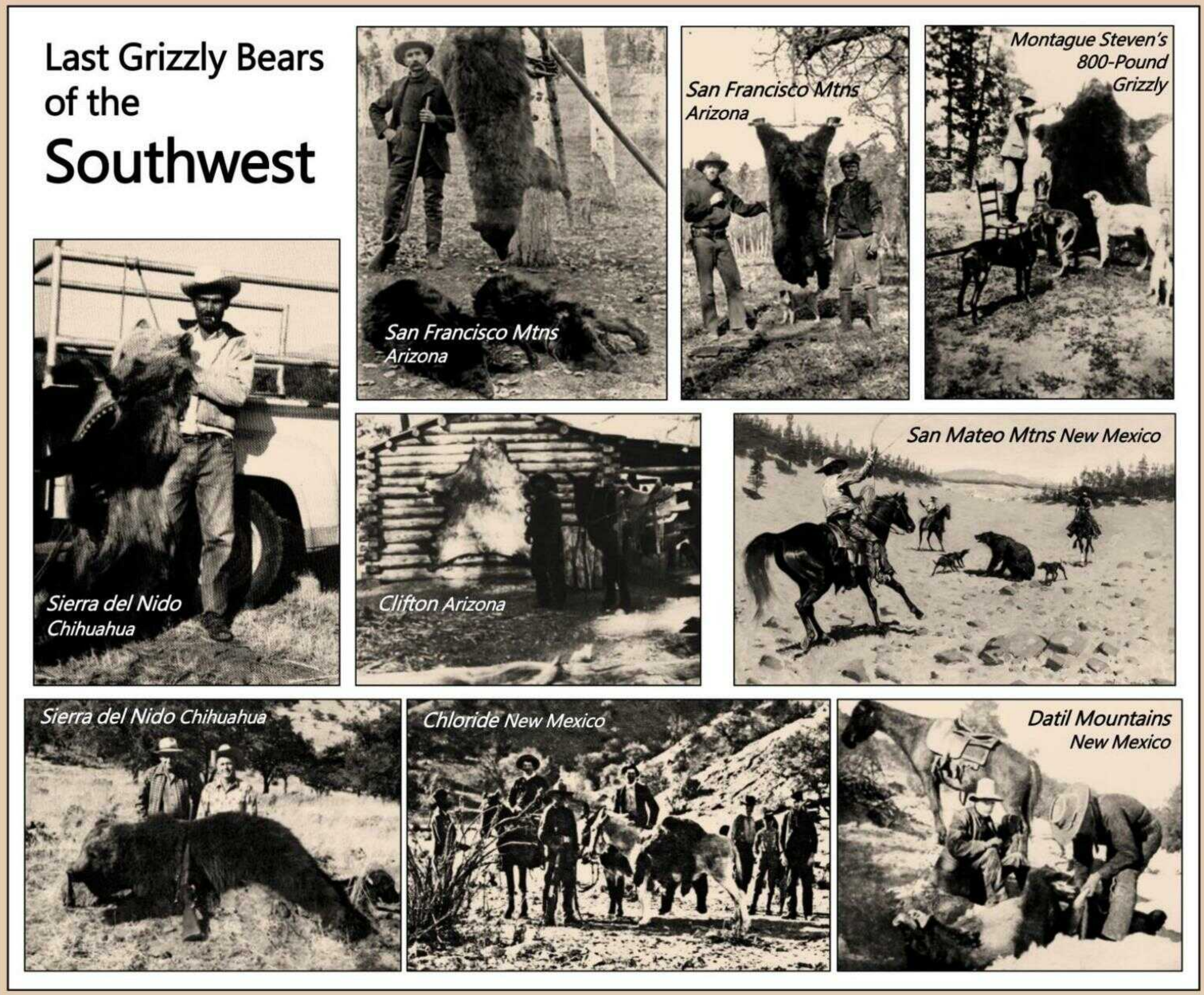
Montague Stevens was an expatriate British graduate of Cambridge University who in 1882 used remittances from home to establish himself as a rancher in New Mexico. He adapted his passion for hunting with horses and hounds to perfecting the pursuit of grizzly bears with dogs. Unlike Lilly and Straw, he was a sociable man who doted on horses and dogs and hunted primarily for pleasure. Regarding grizzlies, he became "...a zealous convert to their preservation, to prevent such a noble animal from going extinct."



Aldo Leopold
1887-1948

Aldo Leopold, founder of the discipline of wildlife management and formulator of the Land Ethic, lived in the Southwest during 1909-1924 as an employee of the newly-formed U.S. Forest Service. During his early years in the region he, like most of his contemporaries, viewed bears and other predators as varmints needing to be killed for the benefit of big game populations. His gradual transformation to an ecologist and champion of predators such as grizzly bears is memorialized in famous essays such as "Thinking Like a Mountain" and "Escudilla" (see Box 6).

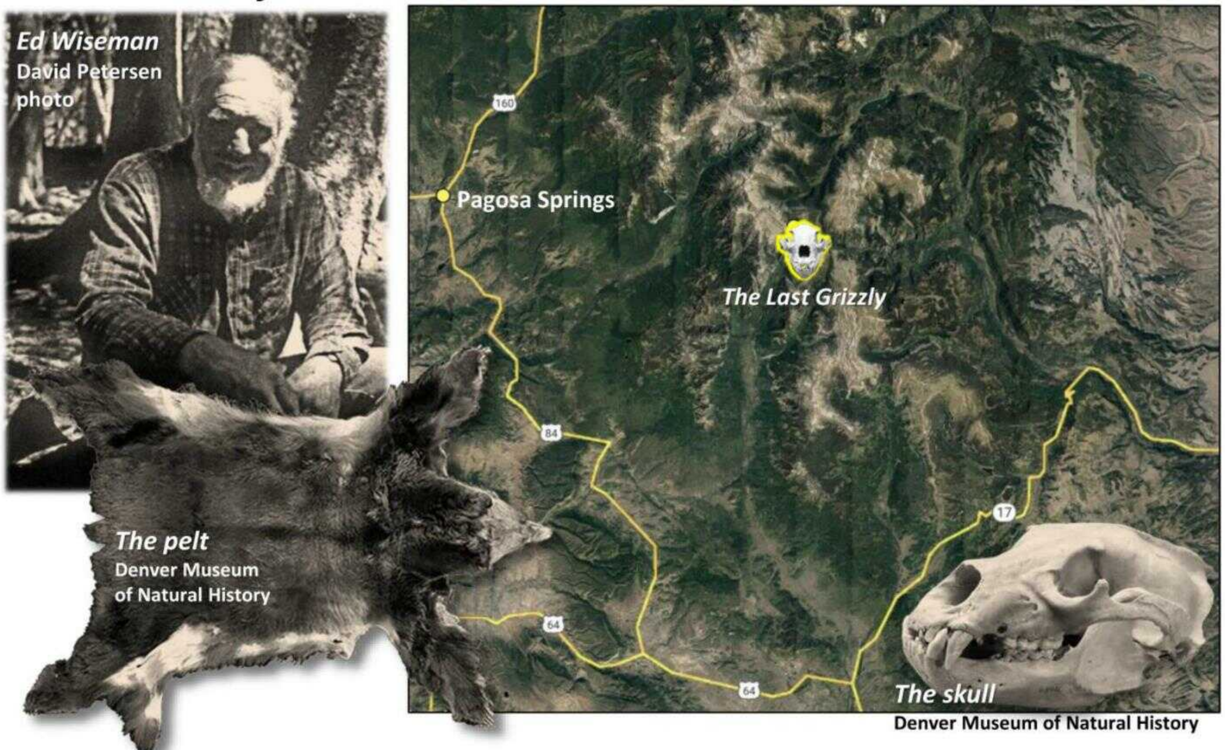
Box 4. The photos below are emblematic of some of the last known grizzly bears in the Southwest, noteworthy primarily because some enterprising local made the effort to document the bear's demise. The photos of grizzlies in the Sierra del Nido Mountains and from near Clifton are from Brown (1996). The photos from the Datil Mountains and of the "800-pound grizzly" are from Stevens (1943). The illustration of the San Mateo grizzly is from http://Frederic-Remington.org). The photos of bears in the San Francisco Mountains are from the Northern Arizona University, Colorado Plateau Digital Collections (https://cdm16748.contentdm.oclc.org/digital/) and of the bear on display in Chloride from Henry A. Schmidt (Museum of New Mexico, Neg. No. 12241).



Box 5. This compilation of images documents the last grizzly bear known to have lived in the Southwest, euphemistically known as "the Wiseman grizzly," in reference to the man who was presumed to have killed it during September, 1979, in the southern San Juan Mountains of Colorado.

The Last Grizzly Bear Killed in the Southwest

September, 23, 1979



Denver Museum of Natural History

The last grizzly bear known to live in the Southwest died on September 23rd, 1979, shortly after encountering Mike Niederee, an archery hunter from Kansas, and Ed Wiseman, his hunting guide. The bear's fatal encounter with these two men occurred in the headwaters of the Navajo River, east of Pagosa Springs, Colorado, just over a low divide from Blue Lake in the southern San Juan Mountains. The bear died from multiple wounds delivered by broad-head arrows. Despite an investigation by the Colorado Division of Wildlife that exonerated Ed Wiseman of any wrong-doing in the bear's death, the oft-told story of this last irrefutable encounter between man and grizzly bear in the Southwest still leaves me wondering about the exact circumstances. No one other than the two involved men will ever know, but a likely scenario emerged for me after wading through several accounts, including by Bass (1995), Petersen (1995), Brown (1996), Murray (2014), and a brief narrative on the Denver Museum of Natural History web site. Mike Niederee probably delivered a near-fatal wound from an arrow shot into the bear's rib-cage after initially encountering the animal in its daybed. Shortly after, Ed Wiseman encountered the same bear on a bench above a narrow defile. He speculates that the bear attacked because it felt cornered (Petersen 1995). It is equally likely that the bear attacked because it had already been wounded. Wiseman was mauled during the attack, but able to drive the bear off by stabbing it in the chest with one of his hunting arrows—aided perhaps by the fact that the bear had severe arthritis and abscessed upper canines. This bear has since been know as "the Wiseman grizzly," although I find this possessive reference to be misleading, if not worse, given that the bear was an autonomous individual eking out its own existence, indifferent to the prior existence of Ed Wiseman. This elderly female bear merely had the misfortune of dying shortly after encountering Wiseman. Grizzlies are still rumored to exist in the San Juan's, backed by several well-substantiated accounts of encounters (Bass 1995, Petersen 1995). Perhaps one of the hardest things to prove is the non-existence of a rare or mythical animal.

3.d. Synopsis of History

Box 6. This image from *Google Earth* shows the environs used by the last known grizzly bear in the Southwest just prior to her death in September 1979, in the headwaters of the Navajo River, southern San Juan Mountains, Colorado.

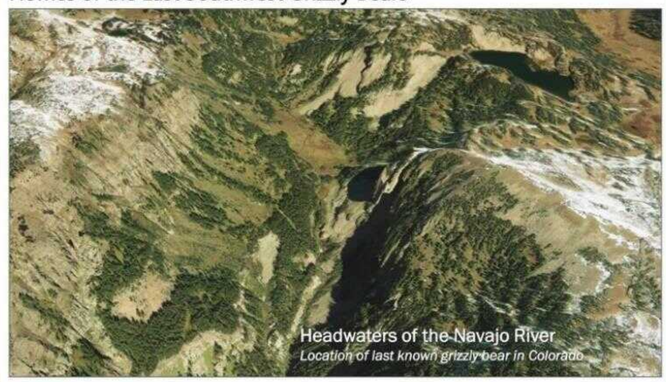


Figure 25, below, provides a visual synopsis of the past 2,200 years—a period of relatively clement climates but dramatic human-associated changes compared to the previous 30,000 years (see Section 3.a.ii). The figure is organized as a timeline from left to right, with different human and natural features of the environment arrayed top to bottom. The horizontal length of each bar correlates with the temporal duration of each feature and its associated effects, with different colors denoting different themes.

Salmon colors (A) identify sedentary indigenous cultures organized around agriculture, whereas blue (B) identifies indigenous cultures that tended to be more nomadic or otherwise mobile (Sections 3.a.iii). The burgundy-shaded bar (C) identifies periods when indigenous populations reached highest densities. Dark blue (D) identifies the period of equestrian life-ways among indigenous peoples (e.g., 3.b.ii). Yellow (E and F) identifies times when Europeans were politically and militarily dominant, staggered to represent an onset linked to an historical moment, with dark brown (G) identifying the period of widespread livestock production introduced by Anglo-Americans (Sections 3.b.i. and 3.c).

Of relevance to the biophysical environment, areas vertically shaded orange denote periods of drought, with dark orange identifying droughts that were particularly severe, whereas green shaded areas denote periods of comparative wetness (see Figure 18). The blue-shaded bar at bottom (H) depicts comparatively cold temperatures associated with the Little Ice Age.

In summary, indigenous agricultural societies arose and became dominant with advent of perfected agricultural systems, coincident with a prolonged period lasting from roughly 500 to 1250 C.E. during which there were lengthy intervals of favorable precipitation coupled with comparatively warm temperatures. The demise of these agricultural societies coincided with not only a lengthy drought during the late 1200s and onset of colder temperatures of the Little Ice Age, but also the comparative flourishing of Utes and Apaches. Spaniards arrived only a comparatively short time after the unravelling of most indigenous agricultural societies, along with associated major declines in indigenous populations—with the notable exception of peoples in the upper Rio Grande valley (Pueblo IV). Compared to indigenous cultures, the period of Spanish-Mexican political dominance beginning in the 1500s was comparatively brief, and that of Anglo-Americans three-hundred years later briefer yet.

The green and red-shaded bar (I) at the top of Figure 25 attempts to integrate the effects of all the changes represented in the graphics below into a hypothesized depiction of regional grizzly bear populations, with darker green denoting periods when these populations likely fared better and darker red-burgundy when they likely fared worse. This speculative reconstruction of grizzly bear populations not only integrates presumed and known effects of humans, but also likely effects of climate mediated through overall habitat productivity. This reconstruction reveals a potentially surprising episode during 875-1425 C.E. linked primarily to the effects of high human population densities (Section 3.a.iii), prospectively compounded by the effects of periodic drought—an episode that I provisionally call "The Crisis of 875-1425." Grizzly bears undoubtedly survived this hypothesized crisis, but likely at lower densities than came before or after. By contrast to this earlier hypothetical crisis, the "Terminal Crisis" beginning around 1850 is an historical fact linked to persecution by Anglo-Americans and the advent of large-scale cattle ranching (Section 3.c).

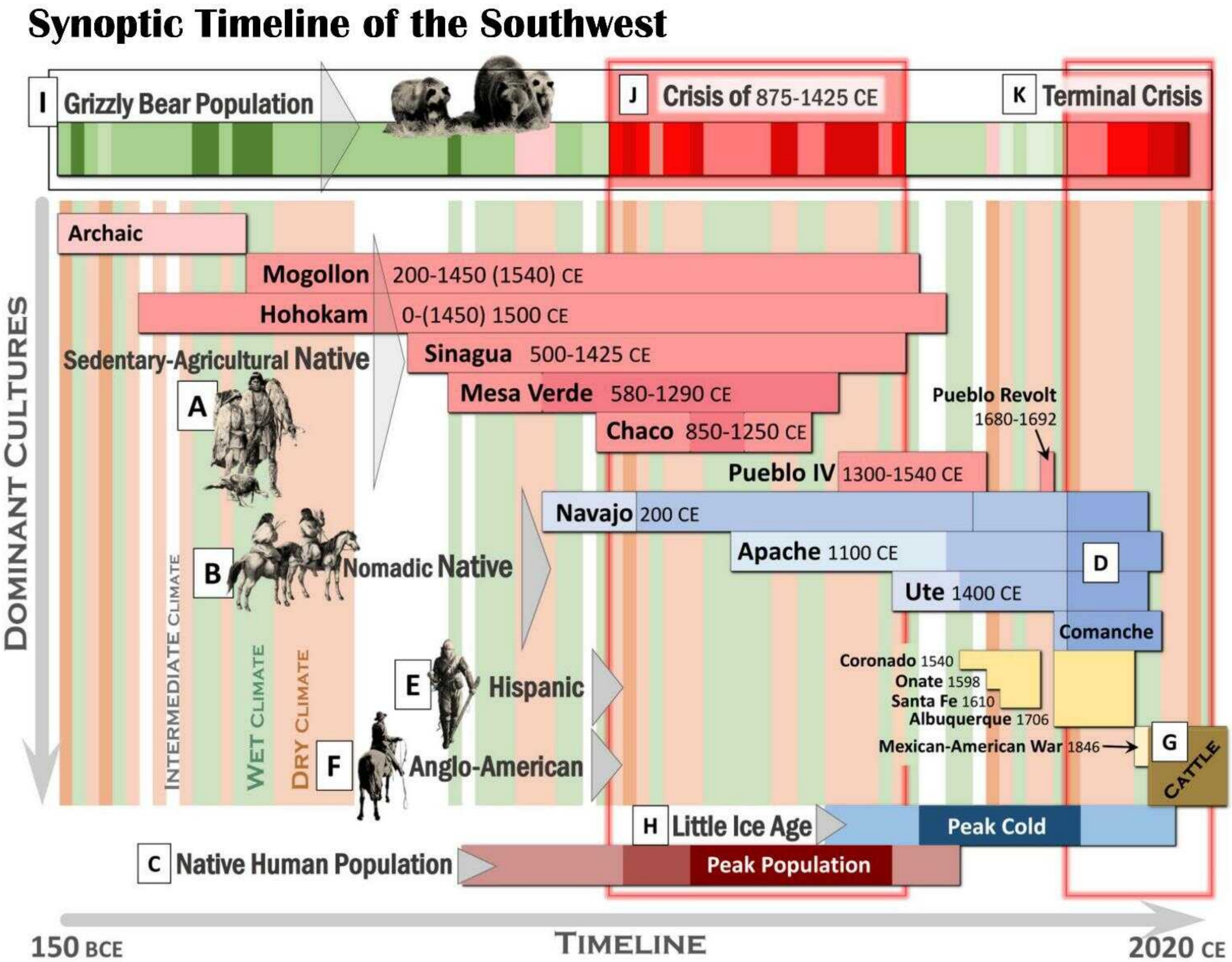
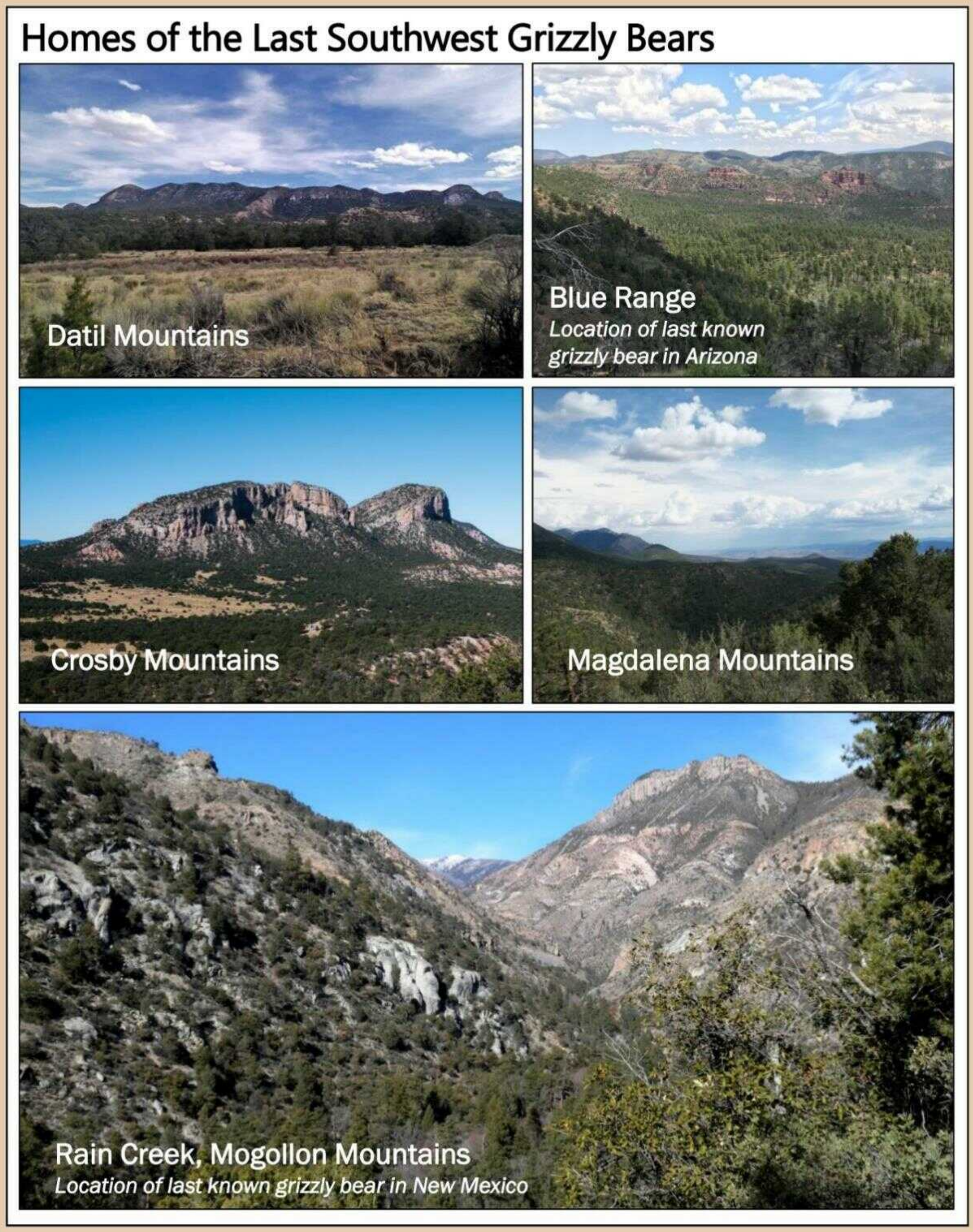


Figure 25. This graphic is my attempt to synthesize a number of climate- and human-related factors that plausibly affected grizzly bear populations during the late Holocene in the Southwest. Approximate periods during which various sedentary/agricultural societies flourished are shown as salmon-colored horizontal bars (A), each labeled with the name of the denoted culture (from Schroeder [1960], Lekson & Cameron [1995], Plog [1997], Bayman [2001], Kulisheck [2003], Hill et al. [2004], Stuart [2014], McClelland [2015]). Periods of fluorescence for various nomadic or pastoral cultures are denoted by blue horizontal bars (B), with the equestrian period (D) shaded darker blue (from Haines [1938], Worcester [1944], Brugge [1983], Opler [1983], Simmons [2001], Hämäläinen [2008], Seymour [2012], West [2016]). The period of peak Native population sizes prior to European colonization are shown in shades of burgundy by the bar third from the bottom (C; from Figure 8, Kohler et al. [2014]). Periods of Hispanic (E) and then Anglo-American (F) political dominance are shown in yellow, along with dates of notable intrusions by European colonists (from Eisenhower [1989], Simmons [1993], Roberts [2004], Flint [2008], Henderson [2010]). The advent of large-scale cattle husbandry (G) is shown in brown, arising coincident with the relegation of nomadic Tribes to reservations (see Figure 19). Vertical background bars denote periods of drought in shades of orange and unusually wet periods in shades of green (from Figure 17). Periods of peak cold during the Little Ice Age are shown in shades of blue (H; ca. 1300-1850 CE; Matthews & Briffa [2005], Miller et al. [2012]). The horizontal bar ranging from shades of dark green to dark burgundy (I) graphically represents my best estimate of how grizzly bear populations in the Southwest fared during the late Holocene as a function of climate- and human-related impacts. Darker green denotes periods when grizzly bear populations likely flourished, whereas darker red-burgundy denotes periods when grizzly bear populations were likely depressed. This synthesis suggests that grizzly bear populations went through a period of demographic "crisis" during 875-1425 CE (J) and then rebounded somewhat during the Little Ice Age and period of Spanish dominance prior to entering a terminal crisis ending in extirpation (K). This final crisis was associated with a period of drought, the advent of equestrian Native cultures, the arrival of Anglo-Americans, and, finally, the advent of widespread cattle husbandry.

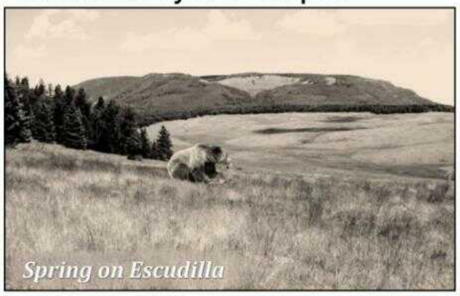
Box 6. The photos below are illustrative of locations where grizzly bears made a last stand in the Southwest, including the last know locations of grizzlies in Arizona (the Blue Range; from Tony Henrie at https://westerntrailrider.com/wordpress/blog/2018/08/ a-pack-trip-into-the-blue-range-primitive-area-arizona/#jp-carousel-2931) and New Mexico (the Rain Creek drainage in the Mogollon Mountains; from D. Mattson). The photo of the Datil Mountains is from "CibolaLover" at https://en.wikipedia.org/wiki/Datil_Mountains; of the Crosby Mountains from Jay Hemphill at https://www.newmexicomagazine.org/blog/post/hikes-in-new-medico-catron-county/; and of the Magdalena Mountains from https://www.fs.usda.gov/Internet/FSE_MEDIA/stelprdb5276848.jpg.



Box 8. One of the most beautiful and eloquent eulogies for grizzly bears in the Southwest was written by Aldo Leopold, published as "Escudilla" in his collection of essays entitled *Round River*. A excerpt of the essay is below.

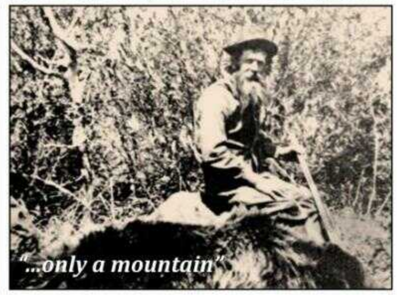
Escudilla by Aldo Leopold

Leopold, A. (1953). *Round River*. Oxford University Press, Oxford, United Kingdom



Spring on Escudilla

Fall on Escudilla



"...only a mountain"

Old Bigfoot was a robber-baron, and Escudilla was his castle. Each spring, when the warm winds had softened the shadows on the snow, the old grizzly crawled out of his hibernation den in the rock slides and, descending the mountain, bashed in the head of a cow. Eating his fill, he climbed back to his crags, and there summered peaceably on marmots, conies, berries, and roots...

No one ever saw the old bear, but in the muddy springs about the base of the cliffs you saw his incredible tracks. Seeing them made the most hard-bitten cowboys aware of bear. Wherever they rode they saw the mountain, and when they saw the mountain they thought of bear. Campfire conversation ran to beef, bailes, and bear. Bigfoot claimed for his own only a cow a year, and a few square miles of useless rocks, but his personality pervaded the country...

One spring, progress sent...[an] emissary, a government trapper, a sort of St. George in overalls, seeking dragons to slay at government expense. Were there, he asked, any destructive animals in need of slaying? Yes, there was the big bear.

The trapper packed his mule and headed for Escudilla.

In a month he was back, his mule staggering under a heavy hide. There was only one barn in town big enough to dry it on. He had tried traps, poison, and all his usual wiles to no avail. Then he had erected a set-gun in a defile through which only the bear could pass, and waited. The last grizzly walked into the string and shot himself...

It was only after we pondered on these things that we began to wonder who wrote the rules for progress...

The government trapper who took the grizzly knew he had made Escudilla safe for cows. He did not know he had toppled the spire off an edifice a-building since the morning stars sang together.

The bureau chief who sent the trapper was a biologist versed in the architecture of evolution, but he did not know that spires might be as important as cows. He did not foresee that within two decades the cow country would become tourist country, and as such have greater need of bears than of beefsteaks...

We forest officers, who acquiesced in the extinguishment of the bear, knew a local rancher who had plowed up a dagger engraved with the name of one of Coronado's captains. We spoke harshly of the Spaniards who, in their zeal for gold and converts, had needlessly extinguished the native Indians. **It did not occur to us that we, too, were the captains of an invasion too sure of its own righteousness.**

Escudilla still hangs on the horizon, but when you see it you no longer think of bear. It's only a mountain now."

4. Current Potential

Much has changed since the early 1900s when extirpations of grizzlies culminated in the Southwest. Some of these changes have been patently for the worse, whereas some have likely been for the better, at least when it comes to prospects for restoring grizzly bears to the region. There are many more people, buildings, and highways—in a number of areas enough to create impenetrable barriers and permanently alienate wildlife habitat. On the other hand, there are fewer cattle and many fewer sheep (Figure 24) as well as more deer and wapiti (Figure 9). Perhaps even more prominently for the better has been a positive change in laws and human attitudes. Grizzlies are protected in the Southwest under the U.S. Endangered Species Act, even in the absence of extant populations. Unchecked exploitation of wildlife has also been replaced by more judicious management. Even more importantly, worldviews that ascribe intrinsic values to wildlife have increasingly supplanted a devotion to domination, use, and intolerance that was imbedded in historical attitudes towards wildlife (Dunlap 1991, Kellert 1996, Manfredo et al. 2003). This last change alone offers hope for restoring grizzly bears to the Southwest.

The following sections offer an appraisal of the biophysical and environments of the Southwest with the goal of determining whether conditions are auspicious enough to warrant attempted restoration of grizzlies to the region. All of the content is either derived or directly extracted from the analysis reported in Mattson and Merrill (2021a), which provides a more comprehensive description of data, analytic methods, and results.

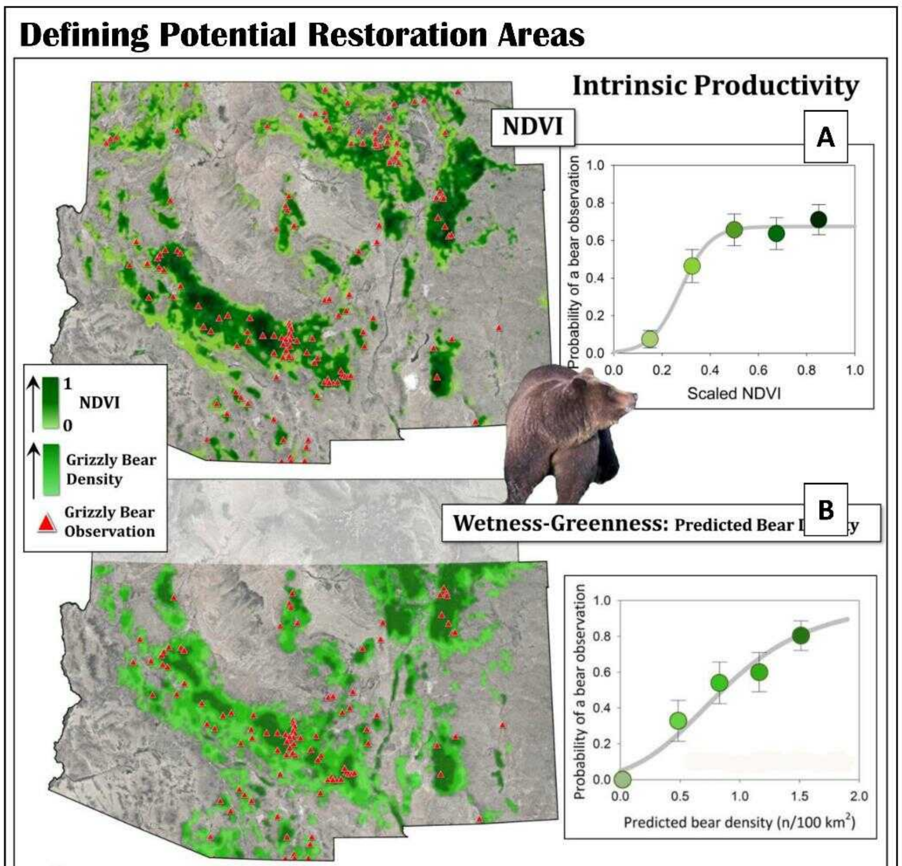


Figure 26. The maps in (A) and (B) show two different representations of intrinsic grizzly bear habitat productivity, in (A) based on imagery-derived NDVI (Normalized Difference Vegetation Index) for the entire study area and in (B) as predicted grizzly bear densities based on imagery-derived Wetness and Greenness, but only for Arizona and New Mexico (Mattson & Merrill 2021b). The graphs in (C) and (D) show logistic relations between the probability that a given 180-km^2 grid cell contained an historical grizzly bear observation versus a random point—in (C) as a function of NDVI and in (D) as a function of predicted grizzly bear density (Mattson & Merrill 2021a). Historical grizzly bear observations are shown as red triangles.

4.a. Defining Recovery Areas

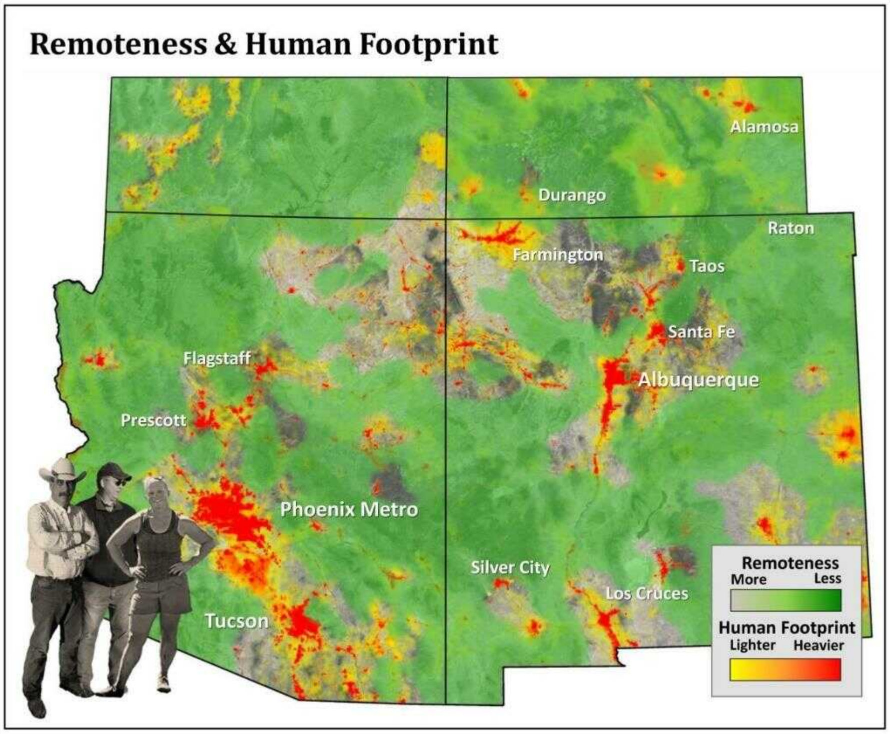


Figure 27. This map combines two different representations of human impacts in the Southwest study area. The "human footprint" is shown in shades of red to yellow, representing all physical impacts attributable to human infrastructure, including croplands, residences, and highways (from Conservation Biology Institute, The human footprint in the West). "Remoteness" (i.e., remoteness from humans) is shown in shades of green, integrating regional population sizes, local road densities, and likely levels of local human activity as a function of these two metrics (from Mattson & Merrill et al. [2021a, 2021b]).

Restoration of extirpated species is more often successful when undertaken in areas large enough to sustain large populations and in highly productive habitat where causes of historic extirpations have been rectified (Smith and Clark 1996, Wolf et al. 1998, Miller et al. 1999, Breitenmoser et al. 2001). Success rates also tend to be higher with omnivores and when undertaken in the core of historic range (Wolf et al. 1998). Grizzly bears benefit from being the consummate omnivores (see Section 2.a). On the other hand, the Southwest is not near the core of historic North American grizzly bear range, although it is not clear what being "near the core" means functionally (Lomolino & Channell 1998), especially given that grizzly bears were extirpated deterministically at scales considerably finer than the scale of their North American distribution (Mattson & Merrill 2002). More importantly, though, the most robust features of past successes have been the extent, productivity, and hazards of restoration areas.

The challenge here is to bridge from these generalities to a meaningful regional assessment. To achieve this, the analytic approach taken here employs standards and model metrics that explicitly address productivity, security, and extent of prospective restoration areas in the Southwest. Given that people are the primary cause of historical extirpations and the current cause of almost all grizzly bear deaths (Mattson et al. 1996a, McLellan et al. 1999, Mattson & Merrill 2002), security is logically defined in terms of site-specific remoteness from humans (i.e., potential frequency of contact) and potential for conflict (i.e., human lethality). Habitat productivity addresses the intrinsic ability of a given area to support bears. Standards for size and shape, as described by Mattson and Merrill (2021a), address the broader-scale sufficiency of potential restoration areas.

An additional challenge is posed by needing to convert dimensionless indices derived from the models of remoteness and productivity described by Mattson and Merrill (2021a, 2021b) into some meaningful measure of potential grizzly bear presence and likely persistence. This calibration was done for the productivity metrics used here by correlating them with documented historical locations of grizzly bears in the Southwest—shown in Figure 26a for the Normalized Vegetation Difference Index (NDVI) and in Figure 26b for Wetness and Greenness indices derived from Landsat imagery. In the case of remoteness, the consistency of meaning for this measure across disparate biophysical environments allows for calibration of this index using distributions of grizzly bears in currently occupied ecosystems of the northern Rockies (Mattson & Merrill 2021a). Raw values for remoteness are shown in Figure 27 along with a representation of the human footprint from the Conservation Biology Institute.

4.a.i. Suitable Grizzly Bear Habitat

Metrics based on both NDVI and Wetness-Greenness closely agree in showing a concentration of productive grizzly bear habitat in an arc extending southeast from Arizona's San Francisco Peaks along the Mogollon Rim through the White, Mogollon, and Black Range Mountains—as well as in New Mexico's Sacramento, Sangre de Cristo, Jemez, and San Juan Mountains (see Figure 1a). These areas furthermore coincide with maximum diversity of oaks, piñon pines, and fruit-producing shrubs in the region (Section 2.c.iv). With the exception of the Jemez Mountains, the San Francisco Peaks, and southern portions of the Sacramento Mountains, these highly productive areas are, moreover, remote from humans, including some of the most remote in the Southwest.

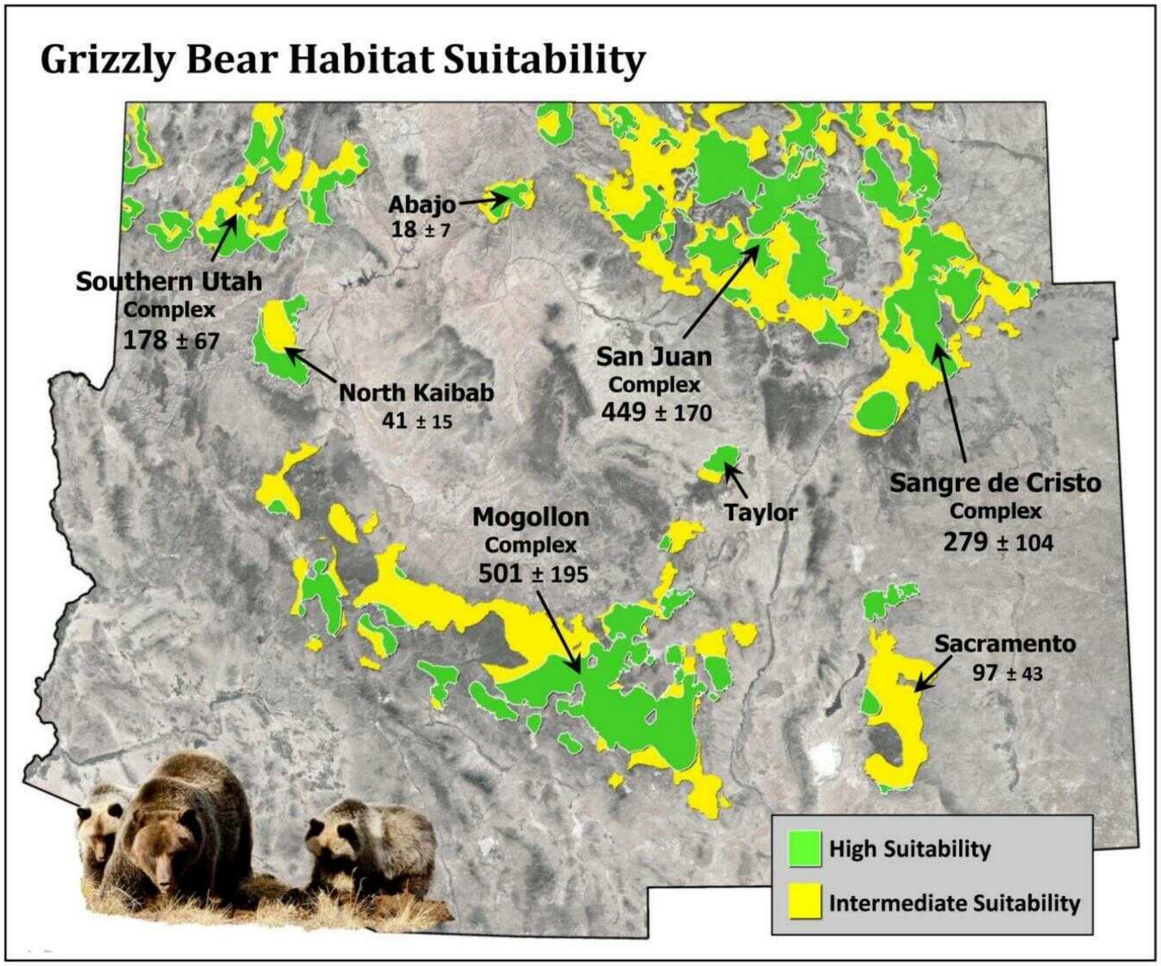


Figure 28. The map above shows the extent of areas deemed suitable for occupancy by grizzly bears based on intrinsic habitat productivity and remoteness from humans and human infrastructure (from Mattson & Merrill [2021a]). Highly suitable areas are shown in green and areas of intermediate suitability in yellow. Each complex of contiguous or nearby highly suitable or intermediate suitability habitat is labeled, along with the estimated number of grizzly bears likely to be sustained in each (mean plus or one minus standard deviation; from Mattson & Merrill [2021a]).

It is thus not surprising that areas best suited to supporting grizzly bears align with these patterns (Figure 28). The most extensive of these include the Mogollon, San Juan, and Sangre de Cristo Complexes, each respectively estimated to be capable of supporting around 500, 450, and 280 grizzly bears (Mattson & Merrill 2021a). These complexes are prime candidates for grizzly bear restoration, whereas other localized areas of suitable habitat in southern Utah, eastern New Mexico (Sacramento), and northern Arizona (North Kaibab) are either too small or too fragmented, or both, to be seriously considered. The San Juan and Sangre de Cristo Complexes are especially promising when viewed as a tenuously interconnected whole. When combined, these Complexes could support around 730 grizzlies.

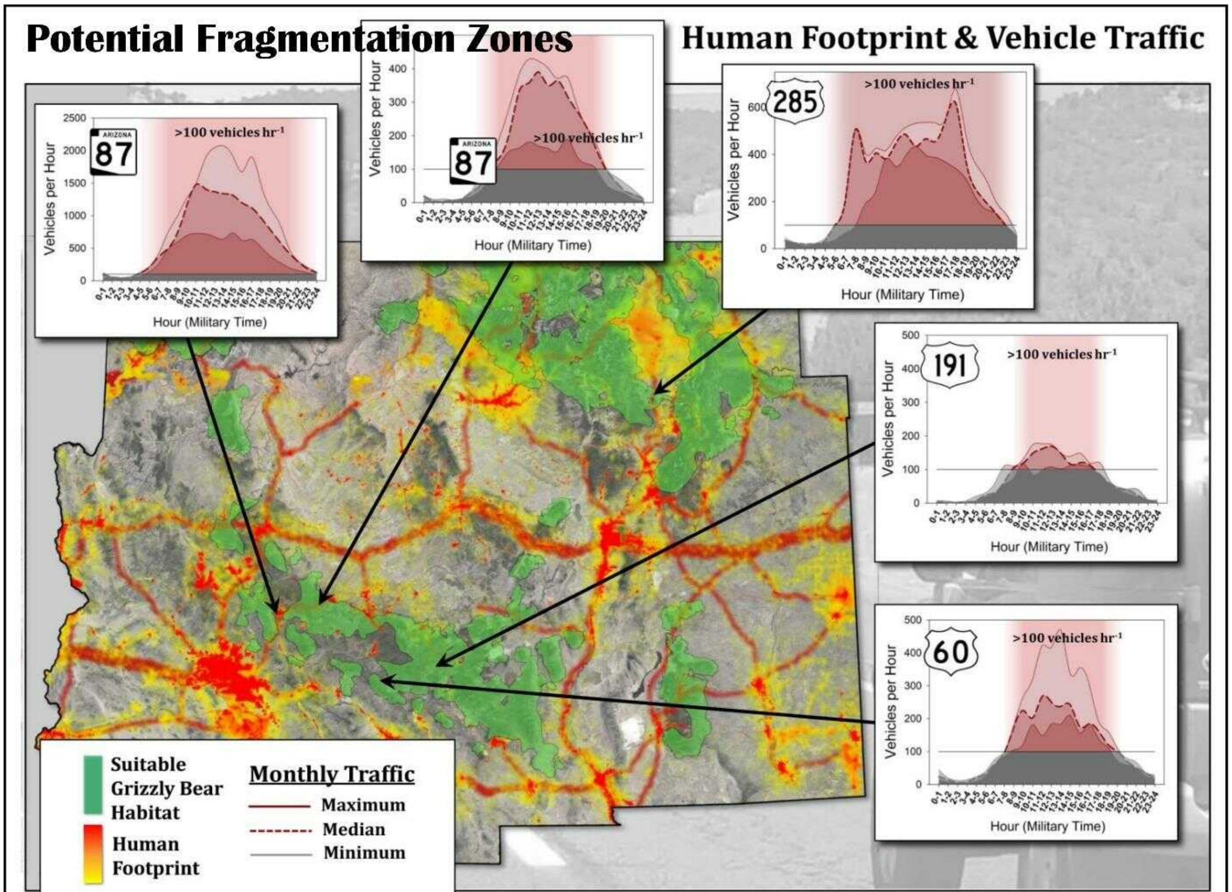


Figure 29. The map above shows the distribution of habitat remote enough and productive enough to support grizzly bears (i.e., 'suitable habitat', shaded green, from Figure 28) relative to the human footprint (from Figure 27), human population density, and major transportation routes. Areas of high human density are shown in bright red (from Center for International Earth Science Information Network [2017]). Major transportation corridors are shown as lineated areas shaded burgundy, with the width of shading proportional to average daily traffic volume (from U.S. Department of Transportation, Bureau of Transportation Statistics). The inset diagrams show median traffic volume for each hour of the day for five federal highways intersecting larger patches of suitable grizzly bear habitat, along with hourly values for months with maximum and minimum volumes (from Arizona Department of Transportation, Transportation Data Management System; Colorado Department of Transportation, Online Transportation Information System; and New Mexico Department of Transportation, Transportation Data Management System). Times of day during which traffic volume during most months of the year exceed 100 vehicles/hour are denoted by vertical burgundy shading.

One further level of analysis entails pruning the extent of otherwise suitable habitat to account for fragmentation introduced by heavily-trafficked highways and extensive urban areas, as shown in Figure 29. Research in the northern U.S. Rocky Mountains has suggested that highways become nearly impassable for grizzlies once traffic volumes exceed 100 vehicles per hour (Waller & Servheen 2005). Given that traffic volumes on Interstate Highways in the Southwest virtually never drop below this threshold, these highways almost certainly isolate the Mogollon Complex from the San Juan and Sangre de Cristo Complexes farther north as well as areas of otherwise suitable habitat to the northwest of I-15 and I-40 in the Flagstaff, Arizona, vicinity. One other highway that could further truncate suitable grizzly bear habitat is Highway 87 north of Phoenix (Figure 29). Between Phoenix and Payson average traffic has historically dropped below 100 vehicles per hour for only three hours in the middle of the night. Even though traffic drops substantially beyond Payson, the highway is still a hotspot for vehicle-wildlife collisions (Michael Baker International 2021). Even so, areas to the west of Highway 87 could be included in a prospective recovery area for grizzly bears if one assumes that current efforts to facilitate wildlife passage succeed (Michael Baker International 2021).

4.a.ii. Candidate Grizzly Bear Recovery Areas

The map in Figure 30 shows candidate Grizzly Bear Recovery Areas delineated on the basis of productivity, remoteness, and connectivity—as well as other considerations related to likely grizzly bear movements and the geospatial logic of management (Mattson & Merrill 2021a). Different shades of magenta define different areas on the basis of priority for grizzly bear restoration and protection. Restoration, Conservation, and Protection Areas are each respectively distinguished from the other by progressively lighter shades of magenta.

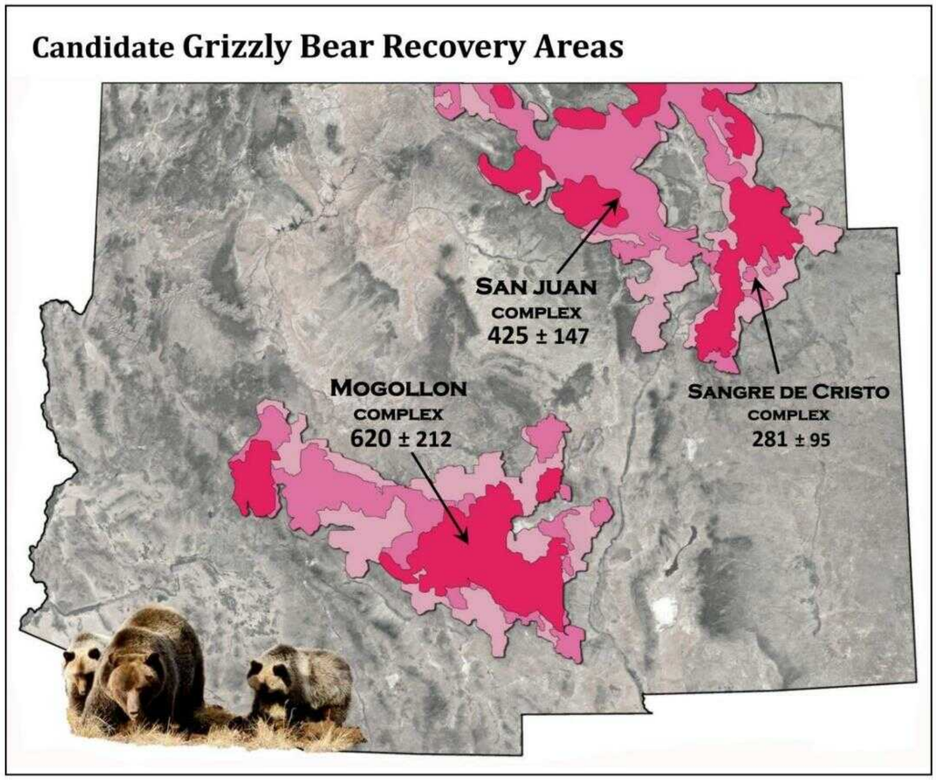


Figure 30. This map shows candidate grizzly bear Recovery Areas in shades of magenta, differentiating Restoration, Conservation, and Protection Areas within each Recovery Area. Restoration Areas (dark magenta) encompass highly suitable habitat, modified by delineations that encompass pronounced linear intrusions of less suitable habitat that do not comport with likely annual movements of newly reintroduced grizzly bears. Conservation Areas (intermediate magenta) are contiguous to or nearby Restoration Areas, and comprise comparatively secure and productive habitats which bears dispersing from Restoration Areas would likely colonize in the foreseeable future. Protection Areas (light magenta) have either, but not both, relatively unsecure or unproductive habitat adjacent to Conservation Areas and Restoration Areas into which grizzly bears will likely disperse either because they are attracted by productive habitats or because security is sufficient for occupancy despite low intrinsic productivity. Each Recovery Area is labeled and accompanied by an estimate of the number of grizzly bears likely to be sustained in each (mean plus or minus one standard deviation; from Mattson & Merrill [2021a]).

Restoration Areas encompass highly suitable habitat that has had its boundaries modified to encompass pronounced linear intrusions of less suitable habitat. These modified boundaries better comport with likely annual movements of newly reintroduced grizzly bears. Conservation Areas are contiguous to or nearby Restoration Areas and comprise comparatively secure

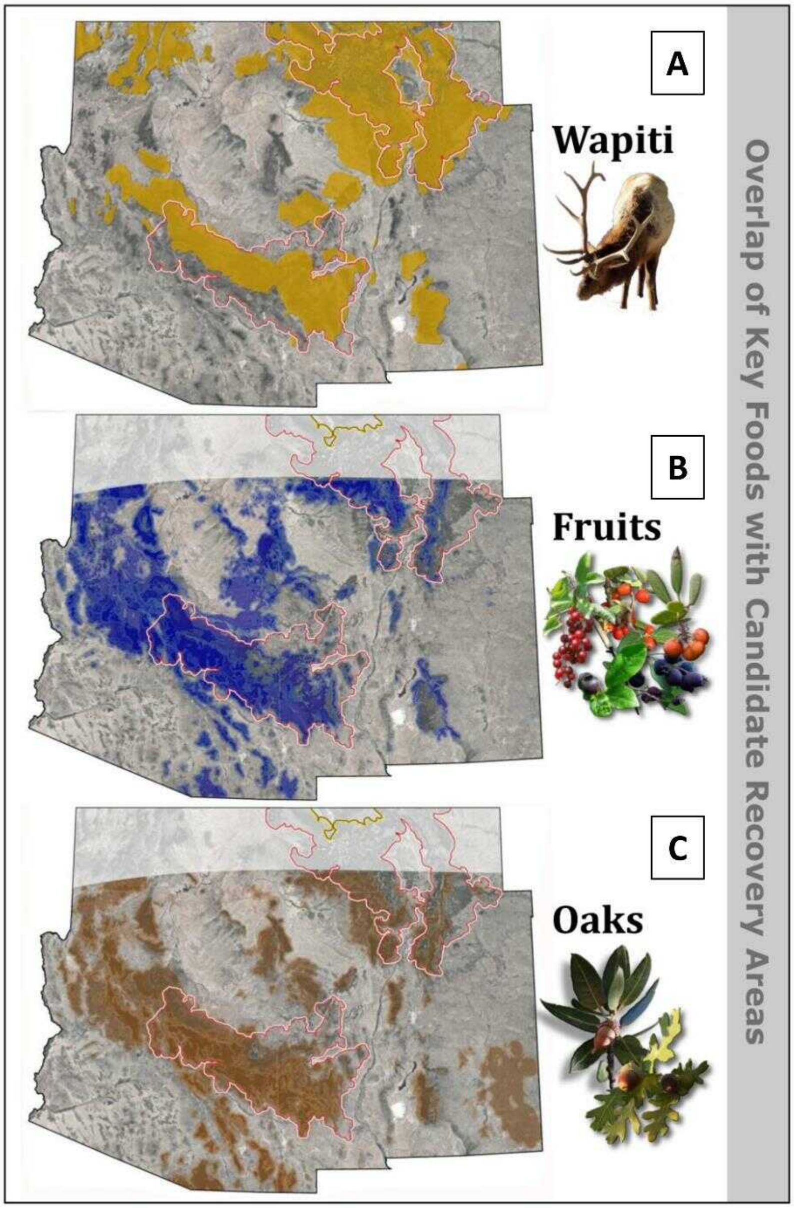


Figure 31. These maps show the superimposition of prospective Recovery Areas (from Figure 30) on distributions of prospectively important grizzly bear foods, including (A) wapiti (from Figure 9 and University of Colorado Boulder, GeoLibrary), (B) shrubs that produce edible fleshy fruits (from Figure 7), and (C) oaks that produce edible acorns (from Figure 6). All prospective Recovery Areas benefit from substantial overlap with these high-value bear foods.

and productive habitats which bears dispersing from Restoration Areas would likely colonize in the foreseeable future. Protection Areas have either, but not both, relatively unsecure or unproductive habitat adjacent to Conservation Areas and Restoration Areas. Grizzly bears would likely disperse into these areas either because they are attracted by productive habitats or because security is sufficient for occupancy despite low intrinsic productivity.

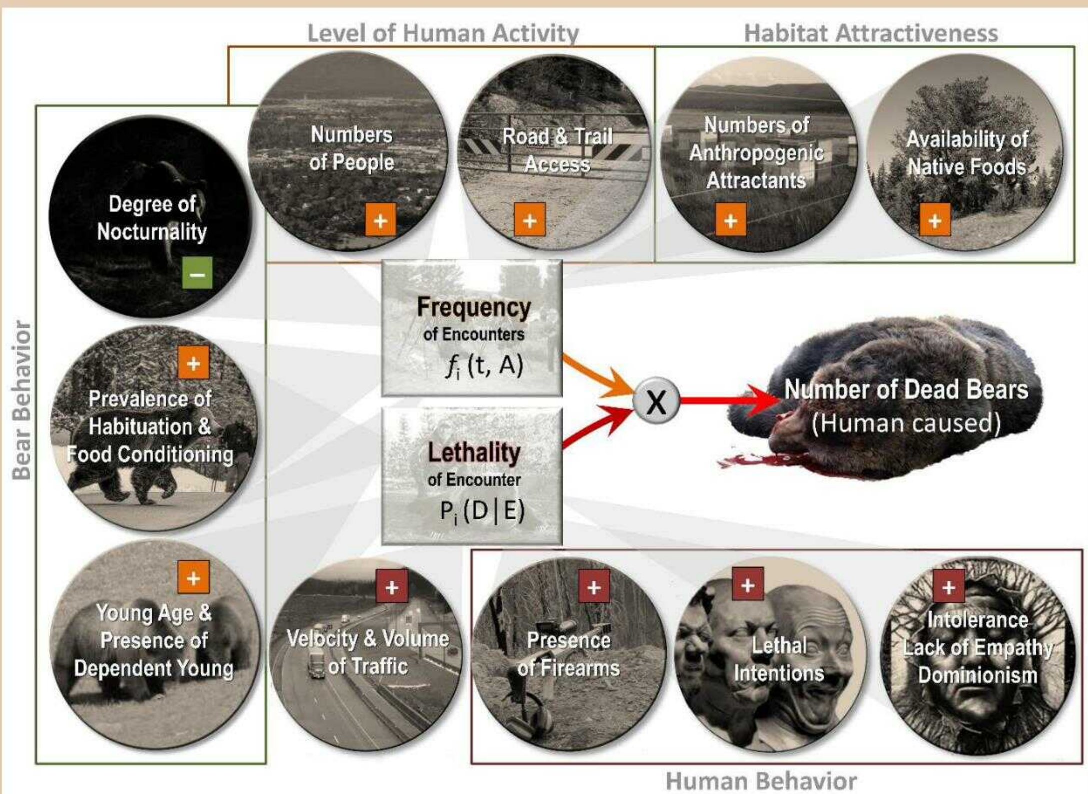
Two to three prospective Recovery Areas comprised of a complex of Conservation, Protection, and Restoration Areas emerge from this analysis, each defined by expansive areas of suitable habitat (Figure 30). The Mogollon Complex is the largest, most contiguous, and least lineated of the three. On its own, it could potentially support over 600 grizzlies, which is in excess of what the U.S. Fish & Wildlife Service (USFWS) has determined is needed to achieve population viability (Mattson & Merrill 2021a). The San Juan and Sangre de Cristo Complexes are sizeable, and if managed as a contiguous whole, could potentially support around 700 bears. Although in contrast to the Mogollon Complex this constitutes a larger potential bear population, these two complexes are intrinsically disadvantaged by a higher edge to area ratio and tenuous connections to each other. Even so, 700 bears are several-hundred in excess of the 500 used by the USFWS as a viability threshold.

Importantly, the abstract measures of habitat suitability used to define potential Recovery Areas in the Southwest correlate well with material features of direct relevance to grizzly bear reproduction and survival, notably abundance of high-quality bear foods. Figure 31 shows the overlap of prospective Recovery Areas with key foods or food groups introduced in Section 2.c., specifically wapiti, fruit-producing shrubs, and acorn-producing oaks. The overlap of candidate Recovery Areas with these three foods is nearly complete, suggesting that if grizzly bears were to be reintroduced, they would have access to a diverse array of high-quality foods offering the concentrations of nutrients needed for an optimal diet (Section 2.c.ii and 2.c.iii).

4.b. Hazards & Complications

Abstract measures of habitat security and productivity are useful for assessing geophysical dimensions relevant to restoring grizzly bears to the Southwest, but still leave considerations related to human attitudes, worldviews, and related practices unaddressed. These somewhat nebulous factors have very concrete implications for grizzly bear populations given that 70-90% of adult and adolescent grizzly bear deaths in the contiguous U.S. continue to be caused by humans—even with protections afforded by the Endangered Species Act (McLellan et al. 1999, Wakkinen & Kasworm 2004, Schwartz et al. 2006, Mace et al. 2012, Costello et al. 2016b). Arguably, worldviews determine more than anything else the likelihood that a person will kill a grizzly upon encountering one or engage in behaviors that encourage conflict (Kellert et al. 1996, Section 3.c).

Box 9. A conceptual model of factors driving the rate at which humans kill grizzly bears is potentially useful for assessing and managing threats to grizzlies, reducing conflicts, and developing a coexistence infrastructure. The model below builds on initial efforts by Mattson et al. (1996a, 1996b) while preserving the basic premise that bears are axiomatically killed by humans as a function of how often they encounter people and the likelihood that any given encounter will be lethal. Broadly speaking, frequency of encounter is dictated by levels of human activity, the attractiveness of habitats used by people, and bear behaviors, whereas encounter lethality is ultimately dictated by human worldviews, manifest in peoples' choices and behaviors.



One way of conceptualizing human-caused grizzly bear mortality is to deconstruct the rate at which people kill grizzlies into two components: (1) frequency of contact, and (2) the likelihood that any given encounter will be lethal for the involved bear (Mattson et al. 1996a, 1996b). In other words, the frequency and lethality of encounters with humans jointly dictate the rate at which adult and adolescent grizzly bears are killed by people, with grizzlies potentially able to thrive despite frequent encounters, but only as long as those encounters are benign—as in National Parks. By contrast, where people are highly lethal, grizzlies will only survive if they have access to extensive areas free of human activity—as was the case during the 1800s and early 1900s (Mattson & Merrill 2002). Box 9 visualizes this conceptualization, along with key factors that drive frequency and lethality of contact.

Trade-offs between frequency and lethality of contact are relevant to assessing what measures would be needed to sustain grizzly bears in the Southwest, and whether or not these measures make major impositions on people. If even a minority of people are intolerant and disinclined to practice prudent management of anthropogenic attractants, then restoration of grizzly bears will probably require large tracts of land free of human activity and access. If people are more uniformly willing to accommodate grizzly bears and engage in prudent behaviors, then there will be many fewer restrictions needed on access and activity (Mattson et al. 1996a).

The analysis described in Section 4.a addresses site-specific levels of human activity as well as velocities and volumes of traffic on highways. Of the human-related factors, this leaves human behaviors and attractiveness of human-associated environments unaddressed. As conceptualized in Box 9, lethal human behaviors are largely driven by whether people are armed, have malevolent intentions, or are intolerant. Less directly, the frequency and nature of interactions between grizzly bears and people is also driven by whether anthropogenic attractants are available, which is largely a function of the choices people make (Mattson 2021b). Historically, the most important of anthropogenic attractants have included garbage, vulnerable livestock, and other domesticated animals near domiciles (Gunther et al. 2004; Mattson 2019, 2021c).

4.b.i. Human Refuse and Foods at Domiciles

Human foods and refuse left available to bears near residences and campsites have a well-documented role in catalyzing human-bear conflict leading to the death of involved bears (Schullery 1986, Gunther et al. 2004). It is thus not surprising that some of the greatest reductions in human-bear conflict have occurred in areas where human refuse and foods were the root cause of most conflicts, notably in Glacier and Yellowstone National Parks (Gniadek & Kendall 1998, Gunther et al. 2004). Other successes have occurred in municipalities such as Durango, Colorado, and towns in the Lake Tahoe Basin, California, that experienced high levels of conflict organized around attractants at residences (see Get Bear Smart Society). Ordinances that required bear-resistant trash containers and limited when trash could be outside enclosures were key to success in these municipalities.

However, successes such as these are the exception to the rule, and have only occurred where the federal government has supreme authority and a compelling conservation mandate (e.g., National Parks), or in communities with resources and a wildlife-friendly culture. Even in the latter, implementation of sanitation ordinances to benefit wildlife are a highly contingent and difficult political process, sometimes because of scarce resources, but more often, as in the case of Teton County, Wyoming, because elected government officials are reluctant to contest the presumed primacy of private property rights (Willcox 2022), regardless of legal authorities and precedent (e.g., Rolston 1990, Sax 2002)

In the Southwest there is a dearth of laws prohibiting intentional feeding of wildlife, much less requiring that garbage be secured as a means of limiting conflicts. Existing mandates are highly-variable and geographically inconsistent, including rather peculiar provisions of Arizona Law that apply only to counties with a human population of >280,000 and, perhaps more understandably, expressly exclude agricultural operations (Arizona Criminal Code § 13-2927). New Mexico has no state regulations, and offers only encouragement and guidance for those interested in reducing conflicts with wildlife (New Mexico Game & Fish, Keep Wildlife Wild). By contrast, Colorado has perhaps the strongest and most comprehensive regulations (Colorado Code of Regulations § 406-0-XI-021), but still addressing only intentional feeding, excluding agricultural operations, and leaving sanitation issues to the vagaries of county and municipal governments.

This inconsistency and dearth of regulations is guaranteed to complicate if not impede restoration of grizzly bears in the Southwest. Measures requiring storage of food and refuse can perhaps be most readily implemented on U.S. Forest Service jurisdictions, as has been done in the northern Rocky Mountains (Northern Continental Divide Ecosystem Flathead, Lewis & Clark, and Helena National Forests 2000; Idaho Panhandle National Forests 2011; Kootenai National Forest 2011; Custer-Gallatin National Forest 2014). However, there are guaranteed to be conflicts arising from unsecured human foods near domiciles any time grizzly bears venture near human-occupied areas. Given the history of struggles to implement sanitation laws in areas that have long had grizzlies, implementation of effective laws and regulations in the Southwest, where there is no tradition of living with grizzlies, will almost certainly be fraught as well as charged with the symbolic politics of private property rights.

4.b.ii. Livestock and Husbandry Practices

Grizzly bear predation can inflict a heavy toll on livestock (Sommers et al. 2010), although contingent on environmental conditions and dependent on the species and age-class of stock accessible to grizzlies (Mattson 1990). When available, domesticated sheep are by far the most likely to be killed by bears (Johnson & Griffel 1982, Jorgensen 1983, Knight & Judd 1983). Cow calves are next most likely—more so than any other sex and age-class of cattle (Murie 1948, Knight & Judd 1983, Mattson 1990, Anderson et al. 2002, Wells et al. 2019).

But context and differences among bears seem to drive levels of depredation more than intrinsic vulnerabilities of livestock. Not surprisingly, cattle and sheep are more likely to fall prey to grizzly bears when they are dispersed unattended on summer pastures, especially in remote high-elevation areas near productive bear habitats (Mattson 1990, Wells et al. 2019). Grizzly bears similarly prey more heavily on sheep and cow calves that are confined in pastures near riparian habitats serving as natural travel corridors (Wilson et al. 2005, 2006). And, not all bears are likely to be predators. Virtually every relevant study has shown that adult males are more likely to prey on cattle, and, even among this class of bears, only a handful are typically responsible for most incidents (Anderson et al. 2002, Wells et al. 2019)—consistent with the dietary strategies of male versus female grizzlies (Section 2.c).

Despite the attention given to predation, grizzlies more often scavenge the remains of cattle that have died for other reasons, including accidents, complications of birthing, and poisoning from consumption of toxic plants (Mattson 1990). This propensity to scavenge is consistent with how grizzly bears approach exploitation of bison, another large-bodied bovine, as well as the hazards of trying to kill large-bodied prey such as adult cattle (Mattson 1997a). However, grizzlies are at considerable risk even when they scavenge cattle carrion, especially from carcasses dumped in euphemistic "bone yards." These traditional disposal sites are often near ranch residences or areas with penned livestock, which increases the odds that scavenging grizzlies are seen as a threat and consequently killed (Wilson et al. 2005, Northrup & Boyce 2012). Even under other circumstances, scavenging is often interpreted by involved people to be the result of predation, with lethal results for implicated bears—as apparently often happened in the Southwest during the demise of grizzlies in this region (Ligon 1927; Brown 1996, 2009).

Traditional husbandry practices in the Southwest will, if anything, heighten the odds of livestock-related conflicts between people and grizzlies compared to even the most challenging environments in the northern Rockies (Mattson & Savage 2022). Especially in warmer drier regions of the Southwest, depauperate forage dictates cattle stocking rates far lower than in more clement regions currently occupied by grizzlies (e.g., Ashecroft et al. 2012). The resulting low densities of cattle necessitate year-round breeding to achieve adequate pregnancy rates which, together with mild winter conditions, gives rise to year-round calving. As a consequence, widely-dispersed vulnerable calves are serially available for much of the year to predators (Mattson & Savage 2022). This intrinsically problematic dynamic is often compounded by deficient oversight by livestock producers. In the absence of real-time information, ranchers are prone to ascribe most calf mortality to predation, with often lethal consequences for any nearby predators (Mattson & Savage 2022).

On the other hand, a number of ranches in the Southwest do have access to enough irrigated fields and pastures to allow for management that synchronizes breeding, with most calving occurring during February in confined pastures typically in or near riparian areas. Notable examples are along the Gila and Mimbres Rivers in New Mexico. This temporal and spatial concentration of vulnerable calves allows for greater surveillance by caretakers, but nearness to riparian corridors also has the potential to create some of the same problems that typify depredation-related conflicts in the northern Rockies (Wilson et al. 2006, Mattson 2019).

Even though grizzlies can take a toll on livestock, there are a number of proven measures for reducing depredations and related bear-human conflicts, albeit with efficacy contingent on context. Perhaps the most effective means of reducing grizzly bear predation on livestock is to remove sheep and cattle from depredation hotspots, as has been done to great effect in the Greater Yellowstone region through retirement of targeted grazing allotments on Forest Service jurisdictions (Wells et al. 2019, https://www.grizzlytimes.org/landscapes-of-conflict). Guardian dogs and electrically-charged fences around calving areas or sheep pastures have also proven to be effective (Huygens & Hayashi 1999, Smith et al. 2000, DeBolt 2001, Andelt 2004, Miller et al. 2016, Scasta et al. 2017, Smith et al. 2018, Kinka et al. 2019), although with the important proviso that applications in practice are limited to productive rangelands where livestock can be concentrated and entailing the expense and logistical difficulties of supervising guardian animals, closely surveilling livestock, and deploying fencing. Intuitively, increased oversight by human caretakers also has a role to play in reducing depredations (e.g., Barnes 2015), although the extent of this benefit has not been conclusively demonstrated by research.

4.b.iii. Encounters with Big Game Hunters

Numerous grizzly bears die in the northern Rockies each year during encounters with big game hunters, most commonly in the Greater Yellowstone area and in eastern portions of the Northern Continental Divide ecosystem (Mattson 2019a; https://www.grizzlytimes.org/patterns-of-mortality). Almost all of this mortality is concentrated on public lands outside of National Parks that host hunters in pursuit of wapiti during fall hunting seasons (Schwartz et al. 2010).

By the very nature of their activity, hunters magnify rather than reduce odds of risky confrontations with grizzlies (Mattson 2019b). Hunters often move stealthily, which increases the likelihood that bears will be surprised during an encounter. They are also typically active in areas where bears associate people with carrion (Ruth et al. 2003, Haroldson et al. 2004). Moreover, hunters are often closely associated either in the field or in camp with the remains of animals they have killed. Under such circumstances bears are likely to be purposefully searching for hunter-associated kills in hunter-frequented areas with the intent of appropriating available edibles (Ruth et al. 2003, Haroldson et al. 2004, Van Manen et al. 2019). Involvement of attractants under such circumstances predictably increases the odds that grizzly bears will act aggressively (Herrero 2002), and that involved hunters will respond with lethal force.

This potential dynamic and associated genesis of conflict characterizes portions of the Southwest that support wapiti, which overlaps almost wholly with areas biophysically suitable for grizzlies (Sections 4.a.i and 4.a.ii). Despite this, hunters can behave in ways that substantially reduce odds of conflict with grizzly bears. Many risk-reducing behaviors have been outlined in reports such as those by Interagency Grizzly Bear Study Team (2000) and Servheen et al. (2009). These and other reports recommend that hunters carry non-lethal self-protection such as pepper spray (Herrero & Higgins 1998; Smith et al. 2008, 2020); secure carcasses and other attractants at hunting camps; not leave carcasses unattended overnight; not hunt late in the day; hunt in parties of least two; be better educated about grizzly bear behavior; and not archery-hunt in areas occupied by grizzly bears. Although the effectiveness of these measures in isolation has not been rigorously addressed, each of these factors has been demonstrably linked to hazardous encounters between hunters and grizzlies.

4.b.iv. Human Worldviews and Attitudes

Human choices and behaviors are largely configured by how people view and emotionally experience the world. This amalgam of cognition and affect creates subjective world-views that selectively filter experience to conform with prior belief and biases, as well as motivate people to intentionally behave in certain ways. Historically, worldviews holding that the natural world existed to be dominated and exploited, with priority given to extractive human interests, was codified in narratives such as Manifest Destiny, with resulting catastrophic consequences for indigenous people and the natural world—including grizzly bears in the Southwest (Section 3.c). Although this worldview organized around domination and use is much less prevalent than during the 1800s and early 1900s (Kellert 1996), it nonetheless continues to hold sway over a minority in the United States, notably hunters and those who are economically dependent on agriculture (Bjerke & Kaltenborn 1999, Mattson & Ruther 2012, Slagle et al. 2019, Carlson et al. 2020, Ernhart et al. 2021). Hunters, farmers, and ranchers are increasingly outliers relative to others in the country, especially the vast majority who live in metropolitan areas, evident in greater comparative hostility among rural residents towards predators and large carnivores such as bears. The evidence for this comparative hostility is compendious, both in the United States and Europe (Teel et al. 2002; Williams et al. 2002; Bruskotter et al. 2007, 2009; Treves & Martin 2011; Johansson et al. 2012; Browne-Nuñez et al. 2015; Hogberg et al. 2016; McGovern & Kester 2015; Byrd et al. 2017; Carlson et al. 2020).

But intolerant or at best exploitive attitudes towards carnivores do not exist in isolation. They are a natural derivative of carnism, belief in the superiority of humans, and a corresponding tendency to discount the sentience of animals (Anderson et al. 2007, Dhont et al. 2016, Caviola et al. 2018, Graça et al. 2018, Manfredo et al. 2018, Becker et al. 2019). Of more direct relevance to politics of carnivore management in the United States, hunters are far more likely than the rest of Americans to identify as politically conservative and as Republicans (Responsive Management 2006, Chesapeake Beach Consulting 2012, Cooper et al. 2015). Perhaps not surprisingly, these political orientations and attitudes towards animals are positively correlated with authoritarianism, xenophobia, lack of empathy, and willingness to perpetuate inequalities among people (Dhont et al. 2014, 2016; Milfont & Sibley 2016; Graça et al. 2018; Caviola et al. 2019; Becker et al 2019; Jarmakowski-Kostrzanowski & Radkiewicz 2021).

There are several concrete implications of all this for prospects of restoring and recovering grizzly bears in the Southwest. For one, despite the fact that there is substantial support for reintroduction of grizzly bears to the region (Decision Research 2001)—as well as, more broadly, for doing so under auspices of a robust Endangered Species Act (Bruskotter et al. 2018)—most opposition is concentrated among hunters, ranchers, and their conservative political allies (Decision Research 2001). This skew introduces several important and weighty complications. For one, any reintroduction effort is destined to become politically polarized. For another, the very people who are likely to be implicated most directly in the deaths of grizzly bears—hunters and ranchers (Sections 4.b.ii and 4.b.iii)—will probably be among the most resistant to changing their behaviors to accommodate grizzlies.

Both of these prospects create daunting challenges.

On a more positive note, the struggles to recover Mexican wolves (*Canis lupus baileyi*) in the Southwest do not necessarily foreshadow the fate of efforts to restore grizzly bears, in part because people have such different symbolic constructions of the two species. With some notable exceptions, collective narratives of Europeans and their North American descendants historically featured demonic constructions of wolves that willfully perpetrated harm and suffering (Fritts et al. 2003, Lopez 2004). Not surprisingly, these narratives fueled persecution that was not only relentless, but also often savage and intentionally cruel (Brown 1983, Robinson 2005).

Although extirpation was also the fate of grizzly bears in the Southwest (Section 3.c), the cultural and even more immediate personal context of people involved in killing them differed. Indigenous constructions of bears have long featured relatedness and respect—motifs that ended up configuring European perceptions of brown and grizzly bears (Shepard & Sanders 1985, Rockwell 1991, Clark & Casey 1992, Brunner 2007). Although some cold-blooded bear killers such as Ben Lily went about their business without compunction (Dobie 2012), other bear hunters more often left accounts colored by respect for the strength, intelligence, and resourcefulness of grizzlies (Stevens [1943], Brown [1996], Evans [2003]; see Box 3). Only rarely did they depict their victims as demonic villains.

These distinctions continue to feature in rural narratives about grizzly bears and wolves. Wolves continue to be routinely constructed as vicious and intentionally cruel killers (Nie 2003, Decker 2013) whereas, in areas still occupied by grizzlies, local residents often express respect, albeit sometimes grudgingly, for an animal that they see as having traits they would like to ascribe to themselves: rugged individualism, strength, and resourcefulness (e.g., Hughes et al. 2020). Regardless of the realities, these narrational and symbolic differentiations offer opportunities to foster a more positive perception of grizzlies compared to wolves among those who have had traditions of coexistence severed a long ago—if they ever existed at all.

4.b.v. Geospatial Aspects of Hazards

Prospective hazards for grizzly bears in the Southwest are not uniformly distributed, in part because of differences in densities of humans, human infrastructure, and human-associated attractants, but also because of differences in prevalence of intolerant people. Considerations related to human densities are covered—albeit somewhat crudely—by the index of remoteness used to define biophysically suitable grizzly bear habitat (Section 4.a). The prevalence of people likely to be intolerant of grizzlies, and prone to kill them intentionally or with minimal provocation, is harder to geospatially depict. However, there are some plausible proxies, including research that has modeled wildlife-related attitudes (as per Section 4.b.iv) on a county-by-county basis, as well as delineations of jurisdictions that are more or less likely to engender human-grizzly bear conflicts—notably private property, public lands, and areas on both that are managed for conservation priorities.

The map is Figure 32 shows the relative prevalence of wildlife-related worldviews (or “values”) among residents of different counties encompassed by candidate grizzly bear Recovery Areas (as per Figure 32). The map is adapted from one in Manfredo et al. (2021) based on results of a model they derived from a large dataset

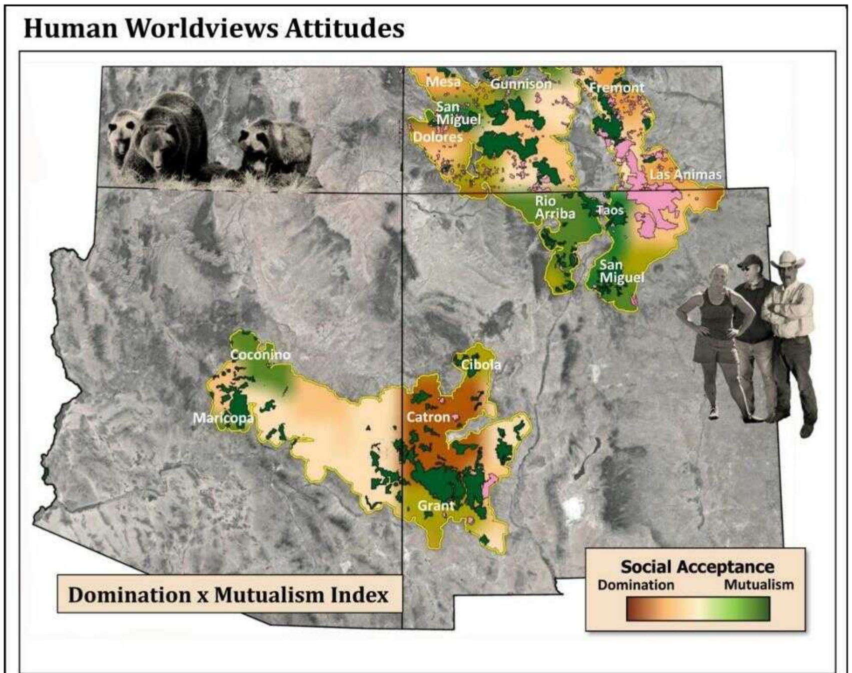
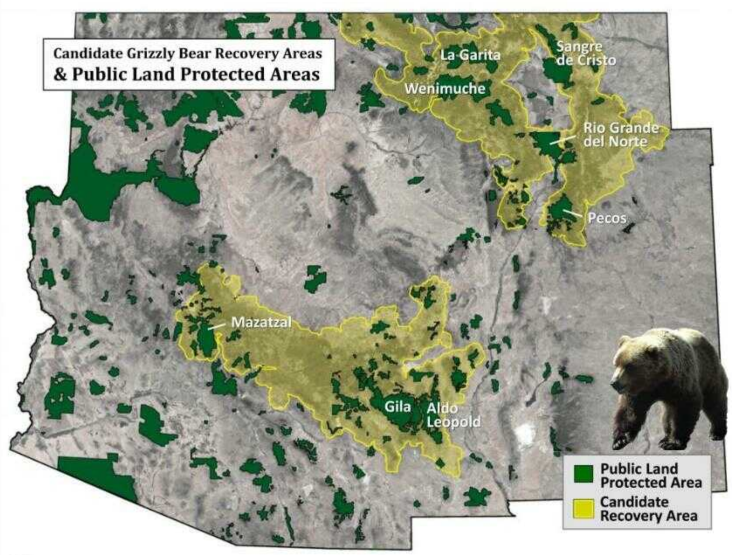


Figure 32. This map depicts the predominance of Domination-oriented versus Mutualist wildlife values among residents (Manfredo et al., 2021) of counties encompassed by candidate grizzly bear Recovery Areas, together with private conservation properties and public protected areas that mitigate against the potential lethality of predominantly Utilitarian Values. Counties with either pronounced Utilitarian or Mutualist Values are labeled in white.

consisting of surveys covering the entire United States (Manfredo et al. 2018)[1]. Darker green indicates prevalence of more benevolent or wildlife-tolerant values (i.e., "Mutualist") whereas darker brown indicates the opposite ("Domination"). Within the bounds of the San Juan and Sangre de Cristo Recovery Area Complexes, residents of Rio Arriba, Taos, and San Miguel counties in New Mexico, and Gunnison and San Miguel counties in Colorado, are plausibly the most likely to accept and accommodate grizzlies—whereas residents of Las Animas, Fremont, Mesa, and Dolores counties in Colorado are among the least likely. In the Mogollon Complex, greater likely acceptance of grizzlies is mostly concentrated towards the periphery in Cibola, Grant, Coconino, and Maricopa counites.

Perhaps not surprisingly, residents of Catron County stand out as candidates for being among the least accepting of grizzlies in the Southwest. The 3,500 or so residents of this county are well-known for their unrelenting hostility towards Mexican wolves (*Canis lupus baileyi*), with disproportionate impacts on wolf recovery efforts in the Southwest (Nie 2003, Decker 2013). This concentration of potential hostility in the core of what would otherwise be some of the most suitable grizzly bear habitat in the Southwest (Figure 28) clearly constitutes one of the greatest prospective challenges for any effort to restore grizzly bears—both politically and on-the-ground. The kinds of rural resentment, even rage, expressed by residents of Catron County in the wolf case, and the entanglements of this rage with identity, community, and feelings of entitlement and persecution are a classic recipe for vendetta



33. This map shows overlap of candidate grizzly bear Recovery Areas with legislatively protected areas on public lands (in green), including Wilderness Areas, Wilderness Study Areas, National Parks, National Monuments, National Conservation Areas, Wildlife Refuges, and State Parks (from Gap Analysis Project Protected Areas Viewer and U.S. Geological Survey Protected Areas Database of the US.).

[1]Parenthetically, I use the terms worldviews, attitudes, and values here more-or-less interchangeably to indicate the larger category of human perspectives, recognizing that the definition of each is hotly contested among academics (Mattson et al. 2011)

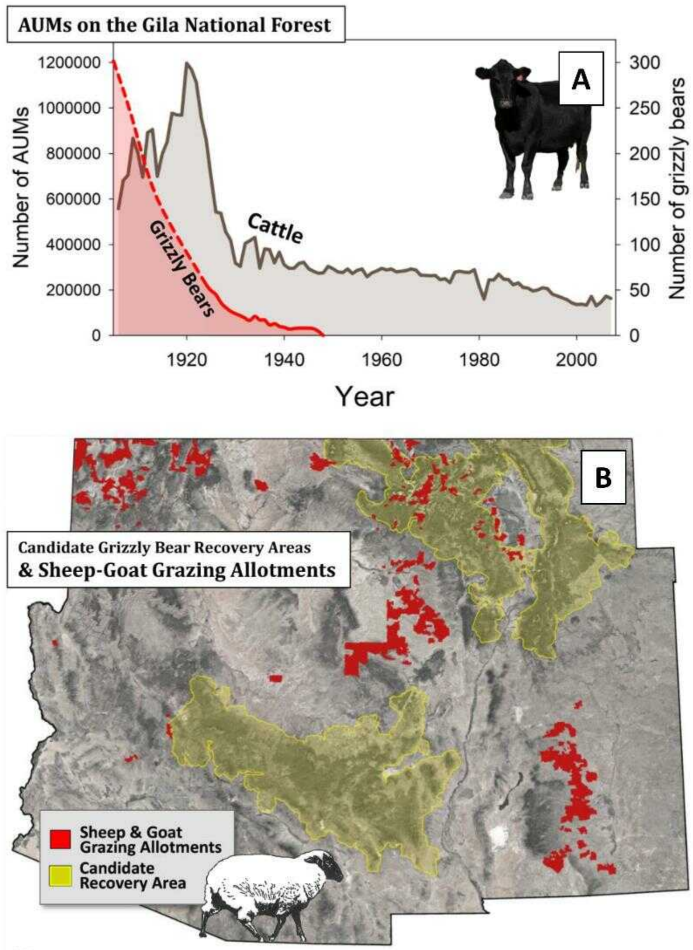


Figure 34. These figures highlight features of prospective grizzly bear Recovery Areas, both positive and negative, that relate to livestock. The graph in (A) shows trends in numbers cattle AUMs (animal unit months) from 1906 to 2007 on the Gila National Forest in brown (from Ashecroft et al. 2012), with the estimated terminal decline of grizzly bears in the Southwest superimposed on top in red (from Figures 26b and 26c). The map in (B) shows public-land allotments in red that are allocated to sheep and goats (from https://catalog.data.gov/dataset/range-allotment-feature-layer and https://gis.blm.gov/EGISDownload/LayerPackages_/BLM_National_Grazing_Allotments.zip). Data are incomplete for U.S. Forest Service lands in New Mexico and Arizona.

poaching with little prospect of policing by local peers (Muth & Bowe 1998; Eliason 1999, 2004; Gangass et al. 2013; Pohja-Mykrä 2016, 2017; Von Essen et al. 2015, 2018; Serenari & Peterson 2016; Carter et al. 2017; Von Essen & Allen 2017a, 2017b; Peterson et al. 2019; Skogan & Krange 2020; Louchouarn et al. 2021; Skogan et al. 2021).

Even so, substantial portions of Catron and adjoining Grant Counties are contained within some of the most extensive designated Wilderness Areas in the Southwest (Figures 32 and 33). Although Wilderness Areas are almost invariably open to big game hunting, and thus prey to the attendant hazards of contentious encounters between hunters and bears—roads, motorized trails, and motorized transport are prohibited. There are also no authorized grazing allotments specifically in the Gila Wilderness (e.g., Gila National Forest, March 2021), which uniquely removes the potential for most livestock-related human-bear conflicts in this area (Section 4.b.ii). The practical upshot of these management provisions is that people with a vested interest in livestock have no explicit motive to enter the Gila Wilderness, and here, as well as in all Wilderness Areas, people with malicious intent would find it inconvenient, if not impracticable, to find and kill grizzlies. This curbing effect matters because most grizzly bears in currently occupied areas are killed by humans near roads (Nielsen et al. 2004, Johnson et al. 2004, Schwartz et al. 2010, Boulanger & Stenhouse 2014, Proctor et al. 2020).

The potential for conflicts between humans and grizzly bears over livestock is otherwise pervasive in the Southwest given that virtually all public lands are designated as grazing allotments (Arizona Game & Fish Department, Allotment pastures; Bureau of Land Management, Arizona State Office & New Mexico State Office, Grazing allotments), and virtually all private holdings of any size are dedicated to raising cattle or sheep. More auspiciously, though, public land grazing allotments designated for cattle are stocked with orders-of-magnitude fewer AUMs (animal-unit-months) now compared to during the early 1900s when grizzly bears were being slaughtered to control depredation. The history of stocking rates on the Gila National Forest is emblematic (Figure 34a).

Areas stocked with sheep are far more hazardous to grizzly bears than areas stocked with cattle because highly-vulnerable sheep seem to be irresistibly attractive to grizzlies, with depredations almost invariably ending in the death of involved bears (Section 4.b.ii). Although sheep allotments are, overall, uncommon in suitable grizzly bear habitat (Figure 34b), they are common enough in northern portions of the San Juan Recovery Area Complex to be a demonstrable threat, notably around the Wenimuche and La Garita Wilderness Areas, and western margins of the San Luis Valley (U.S. Fish & Wildlife Service 2021; Figure 34b), in what would otherwise be highly suitable habitat for grizzly bears (Figure 28).

Private lands with livestock—which comprise virtually all large properties in or near suitable grizzly bear habitat (Figure 35)—also pose an overt threat, not just because of the potential for conflict with grizzlies over depredation and scavenging (Section 4.b.ii), but even more so because of perspectives commonly held by land- and stock-owners. Not only are ranchers likely to be intolerant of potential predators such as grizzlies (4.b.iv), they are also likely to hold views on property rights that make them loath to change behaviors at the behest of any government mandate or in support of a government-sponsored program such as restoration of grizzly bears (e.g., Cawley 1993, Inman & McLeod 2002, Jackson-Smith et al. 2005, Kreuter et al. 2006, Vaske et al. 2018). Although property rights are not, in fact, inviolate or all-encompassing (e.g., Dwyer et al. 1995, Sax 2002, Kleinsasser 2005), land- and stock-owner perspectives on "rights" constitute a social and political reality that complicates any prospective effort to restore grizzly bears to the Southwest.

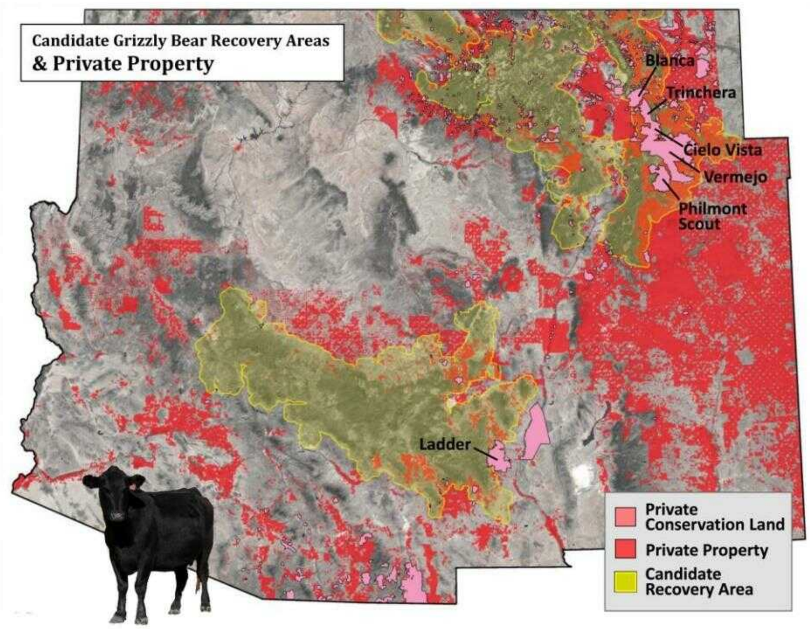


Figure 35. This map shows the overlap of deeded private lands (in red, from Gap Analysis Project Protected Areas Viewer) and candidate grizzly bear Recovery Areas (shaded yellow), with private lands managed as conservation properties shown in pink (from National Conservation Easement Database). This latter category includes lands in conservation easements as well as Turner Ranches (from Merrill et al. [2019]).

On a more positive note, there are several very large (>50,000 acre) ranches in or adjacent to prospective Grizzly Bear Recovery Areas that are in conservation easements, notably Ted Turner's current and former Vermejo Park and Ladder Ranches, and the Trinchera and Blanca Ranches in the Sangre de Cristo Conservation Area (Figure 35; U.S. Fish & Wildlife Service 2012). Although such easements do not axiomatically translate into support for restoration of grizzly bears, private conservation lands potentially could be the most secure of any jurisdiction for a recovering grizzly bear population. Unlike public land managers, owners of private property have the prerogative to limit if not altogether exclude access by the public. The complex of proximal private properties comprised of the Philmont Scout, Vermejo Park, Cielo Vista, Trinchera, and Blanca Ranches are, in fact, potentially critical to any prospective restoration of grizzly bears in the Sangre de Cristo Recovery Area given that this complex is comprised largely of deeded private lands—with conservation properties accounting for most of the core area (Figure 35).

4.b.vi. Jurisdictional Complications

The U.S. Fish and Wildlife Service has ample precedent for constituting groups comprised of representatives from multiple jurisdictions to coordinate or even govern recovery efforts for endangered and threatened species, including grizzly bears in the northern U.S. Rocky Mountains and Mexican wolves in the Southwest.

Given the large individual home ranges of grizzly bears (prospectively 200-400 km^2 for females and 900-1,300 km^2 for males in an area such as the Southwest; Blanchard & Knight [1991], Graham et al. [2014], Seryodkin et al. [2019]), and the large area required to support a viable population (Sections 4.a.ii and 4.a.iii), management of habitats and individual bears would necessarily entail multiple jurisdictions. As both a practical and political matter, the Fish and Wildlife Service would also need to address state claims of authority over management of wildlife through cooperative agreements and on-the-ground arrangements, much like the Mexican Wolf Interagency Field Team (https://www.azgfd.com/wildlife/speciesofgreatestconservneed/mexicanwolves/).

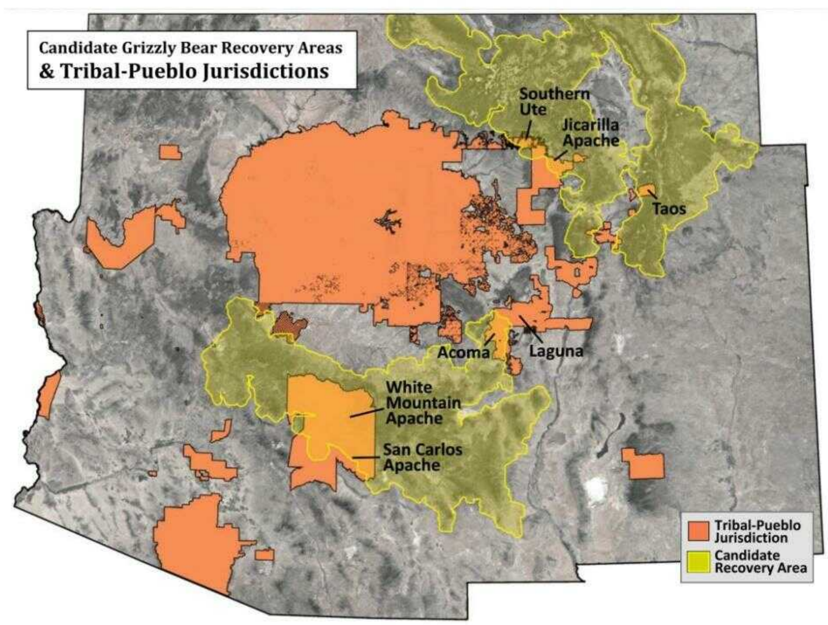


Figure 36. This map shows the overlap of candidate grizzly bear recovery areas with Indigenous lands contained within federally-recognized jurisdictions. Indigenous jurisdictions that substantially overlap with recovery areas are labeled in black. Delineations of tribal and pueblo jurisdictions are from the Protected Areas Database of the US (PAD-US 2.1; https://maps.usgs.gov/padus/).

Although cooperation among representatives of multiple jurisdictions is invariably complex, the candidate Mogollon Recovery Area Complex constitutes probably the most tractable jurisdictional landscape given that much of this Complex is on lands managed by the U.S. Forest Service. The states of Arizona and New Mexico are prospectively additional necessary partners, as in Mexican wolf recovery efforts. Perhaps the most complicated, unpredictable, but critically important arrangements would need to be with Tribes and Pueblos holding authority over significant areas encompassed by the Mogollon Complex—notably the White Mountain and San Carlos Apache Tribes, and the Acoma and Laguna Pueblos (Figure 36). Engagement of the Apache Tribes could be facilitated by the fact that they are signatories to the *Grizzly Bear Treaty* (or more formally, *The Grizzly: A Treaty of Cooperation, Cultural Revitalization and Restoration*) that calls for reintroduction of grizzlies to suitable tribal lands and mandatory consultation by the federal government with Tribal and Pueblo sovereigns about bear management on their lands (https://www.piikaninationtreaty.com/).

Compared to the Mogollon Complex, the jurisdictional landscapes of the San Juan and Sangre de Cristo Recovery Areas are notably more complex. Much of the San Juan Complex is on lands administered by the Forest Service, although there is considerable overlap with trust lands of the Southern Ute and Jicarilla Apache Tribes, neither of which are signatories to the *Grizzly Bear Treaty*. This Complex also completely overlaps with the U.S. Park Service-administered Valles Caldera National Preserve as well as portions of the Rio Grande del Norte National Monument administered by the Bureau of Land Management.

But the Sangre de Cristo Complex is even more complex yet. Even though portions of the Complex are administered by the Forest Service, most consists of deeded private property, lands administered by the Bureau of Land Management for multiple use or as the Rio Grande del Norte Monument, plus areas administered by the Fish and Wildlife Service as part of their Refuge System, including the Sangre de Cristo Conservation Area. Although small in land area, the Taos Pueblo is also a potentially important participant in grizzly bear restoration here given its signatory status on the *Grizzly Bear Treaty*. The mosaic characterizing this Complex entails not only diverse federal agencies and private owners, but also diverse legal mandates and authorities—even without considering the overlay of state claims to authority over wildlife.

4.c. Realizing the Potential

There is ample habitat in the Southwest biophysically suitable for grizzly bears—both productive enough and remote enough from human infrastructure and activity to allow grizzly bears to survive and reproduce. Abstract reckonings of productivity are, moreover, in accord with the presence of diverse high-quality bear foods—notably acorns, fleshy fruits, pine seeds, and elk—that, in toto, provide a buffer against annual vagaries in abundance of each, all augmented by lower quality fallback foods such as roots, insects, and foliage. Perhaps even more important, there is enough contiguous suitable habitat in the Mogollon, San Juan, and Sangre de Cristo Complexes to support robust populations of grizzlies (Merrill 2005)—large enough in theory to survive centuries of environmental vagaries.

However, this conclusion comes with two major provisos. Reckonings of security as a function of remoteness hold only if the prospective lethality of humans in areas otherwise suitable for grizzlies in the Southwest is no greater than human lethality in comparably remote areas occupied by grizzlies in the northern U.S. Rocky Mountains. If this premise does not hold, then interpretation of an index of remoteness calibrated to conditions in the northern Rockies would be in doubt (Section 4.a). Likewise, juxtapositions of attractive but lethal habitat (i.e., ecological traps) with population source areas also need to be comparable to obviate source-sink dynamics in the Southwest that could bleed source areas (i.e., suitable habitat) at a higher rate than in the northern Rockies. Ecological traps almost invariably occur when bears are lured into human-occupied areas by either anthropogenic foods such as livestock or concentrations of high-quality natural foods such as fruit. The resulting inevitable conflicts typically lead to the deaths of involved bears (Nielsen et al. 2006; Northrup et al. 2012; Lamb et al. 2017, 2020; Penteriani et al. 2018).

Regarding prospective ecological traps, there is no indication from the analysis presented here that lineated intrusions of human-occupied or agriculturalized landscapes are more common or pronounced in prospective Grizzly Bear Recovery Areas in the Southwest compared to areas occupied by grizzlies in the northern U.S. Rockies. Even so, the ratio of edge length to core area in the Sangre de Cristo Complex is high, tantamount to a high proportion of population sinks (near-edge habitats) to population sources (core habitats), with resulting diminished odds of long-term population persistence (Doak 1995, Pease & Mattson 1999, Wiegand et al. 1999, Mattson & Merrill 2002). The Selkirk and Cabinet portions of the Cabinet-Yaak Recovery Areas in the northern Rockies are comparably lineated, although smaller in size. The fact that grizzly bears populations in both these areas are small and acutely threatened by human-caused mortality is instructive, but with the proviso that much of this mortality is caused by malicious killing and black bear hunters mistakenly shooting grizzlies (McLellan et al. 1999, Wakkinen & Kasworm 2004, Proctor et al. 2005).

Regarding comparative human lethality, there is no way to reliably assess whether people who might directly interact with grizzly bears in the Southwest are any more intolerant or otherwise prospectively lethal than their counterparts in the northern Rockies. Even so, the majority of those who interact directly with grizzlies will almost certainly be big game hunters, livestock producers, and rural residents, as in northern ecosystems, with on-the-ground methods proven to reduce human-bear conflicts in grizzly bear-occupied areas undoubtedly serving the same purpose in the Southwest (as per Sections 4.b.i, 4.b.ii, and 4.b.iii). The key consideration, as in the north, will be whether people adopt ameliorative practices and behaviors, and in response to what inducements or mandates—but with little prospect of changing underlying worldviews and values to serve the purpose (Manfredo et al. 2017b).

Although a veritable library-full of material has been written about the contingencies, complexities, and comparative efficacies of approaches to promoting change in peoples' behaviors and perspectives, some general principles plausibly apply to any program for bringing grizzly bears back to the Southwest. Efforts to honestly inform people about risks, risk-reducing behaviors, as well as benefits of having grizzly bears in the region should begin well in advance of when grizzlies are actually on-the-ground. But any informational effort should be proceeded by targeted outreach designed to elucidate peoples' knowledge of grizzlies, as well as their related concerns, fears, and appreciations. Surveys have a role to play, but are notoriously prey to bias and limitations introduced by what researchers choose to ask and how they choose to ask it (e.g., Choi & Pak 2005). Focus groups and workshops based on Q methodology more reliably elicit peoples' subjectivities (Zabala et al. 2018). Where practicable, risk-reducing infrastructure and measures should be promoted and implemented well in advance of when grizzlies arrive in an area so as to prevent the emergence of a syndrome of resentment and retribution organized around conflicts.

The organizational auspices for all such efforts are necessarily contingent on aspects of context, but with one proviso. Given that any restoration effort would have to be under authority of the ESA, implemented by the U.S. Fish and Wildlife Service, and entail measures that required the cooperation and consent of numerous federal and state authorities (as per Section 4.b.vi), an interagency trans-jurisdictional body would almost certainly need to be convened in advance to provide a framework for planning, deliberations, and codified agreements. Even so, the details of how such a group functioned would determine whether it served a greater good or simply promoted bureaucratic inertia and dysfunction (for a sampler of what can go wrong see Clark [2008] and the case studies in Clark et al. [1994]).

Other than this, there is almost certainly a place for collaborative efforts involving non-governmental organizations focused on finding common ground among diverse stakeholders and promoting coexistence measures. One of the best examples in occupied grizzly bear habitat is the Blackfoot Challenge in Montana (Wilson et al. 2014), but with the critical proviso that emergence and success of any such effort is contingent on a number of often fortuitous factors and convergences, as in the case of the Challenge. Many arenas ripe with the potential for conflict will almost certainly not fall under the umbrella of a functional collaborative venue for promoting human-bear coexistence.

This unfortunate reality, combined with the equally unfortunate fact that a mere handful of people intent on willfully promoting conflict and maliciously killing bears can have a disproportionate effect on any recovery efforts (Liberg et al. 2012, Agan et al. 2021, Sunde et al. 2021), will necessitate coercive enforcement of laws where needed as well as deployment of creative economic measures. The latter could be especially important if resources were focused on buying out targeted public-land grazing allotments (especially sheep; Sections 4.b.ii and 4.b.v) or private holdings likely to be chronic hotspots of conflict. Purchase of agricultural properties is prospectively feasible given the precarious economic status of many smaller ranches typified by poor husbandry practices and the desirability of providing current owners a graceful economic exit (Mattson & Savage 2022).

One of the greatest foreseeable challenges for those wishing to restore grizzly bears to the Southwest will predictably arise from the human environment of Catron County, New Mexico. There is little doubt that residents of this county are likely to be among the most hostile of any in the Southwest to grizzly bears and grizzly bear restoration efforts largely because of prevailing worldviews, attitudes, grievances, and community narratives—the latter shaped by on-going conflict over recovery of Mexican wolves (Section 4.b.v). Unfortunately, there is little prospect of defusing this prospective hostility through outreach and collaboration.

The amalgam of ingredients fueling potential enmity are likely to be too potent for amelioration by outsiders attempting to find common ground on grizzly bear restoration.

Yet Catron County matters. This county encompasses much of the area with greatest biophysical promise for restoring grizzly bears to the Southwest (Figure 28). The area is productive, remote, and comparatively unroaded (Figures 26 & 27). Much of the most suitable habitat is contained within large wilderness areas (Figure 33). But, as with wolves and grizzly bears in the Selkirk and Cabinet-Yaak Ecosystems, history has shown that comparatively few malicious people sustained by a supportive local community—even if no more than a few thousand—can kill enough wolves and grizzlies to stymie recovery efforts (Section 4.b.v).

Neutralizing this threat would plausibly require neutralizing prospective poachers while at the same time avoiding backlash from the local community. However, there is little reason to think that this dual outcome can be easily achieved. Poachers are potentially subject to criminal penalties, but only if they can be apprehended and successfully prosecuted—which is predictably difficult to accomplish if poachers are surrounded by a supportive community (Gangass et al. 2013; Serenari & Peterson 2016; Pohja-Mykrä 2016, 2017; Petersen et al. 2019). As it turns out, community support for those who illegally kill wildlife is commonplace among rural populations dependent on extracting natural resources, partly because carnivore management is usually entangled with other symbolically weighty issues, including perceived impositions by an increasingly urbanized national population and resentments of state and federal governments (Krannich & Smith 1998, Yung et al. 2010, Wuthnow 2018, Ulrich-Schad & Duncan 2018, Berlet et al. 2019). All of this likely applies to Catron County.

To the extent that there is a solution to the Catron County problem, it will require skill, creativity, and perhaps a disproportionate allocation of resources on the part of those promoting return of grizzly bears. Otherwise, Catron County will likely turn out to be the setting for an endless series of crises threatening the success of grizzly bear restoration and recovery.

5. The Future

The Southwest has undergone major changes in the human and natural environments during the Holocene—even more so since the late Pleistocene (Section 3). With the exception of newly-arrived Anglo-Americans, grizzly bears survived all of the challenges posed by these environmental changes. Restoration of grizzlies to the Southwest is now a very real possibility given recent positive trends in human attitudes and the persistence of extensive wildlands that encompass productive bear habitat (Section 4.a).

But any useful assessment of prospects must also address foreseeable environmental change. Reintroducing bears into a rapidly worsening situation with prospects of indefinite deterioration would not only be a tragedy for the affected bears, but also a recipe for frustration and wasted resources. That having been said, any useful exercise requires that projections be realistic, evidence-based, and adequately comprehensive (Lasswell 1971). Too often projections end up being selective as well as plagued by evidence-free assertions and uncritical projections of past trends. The assessment of foreseeable changes by the U.S. Fish and Wildlife Service in its analysis of prospects for restoring grizzly bears to the San Juan Mountains of Colorado (U.S. Fish & Wildlife Service, 2021: Appendix A) is a classic example of all these failings—in addition to presenting a deficient analysis of current potential (Mattson & Merrill 2021a).

In this penultimate section I provide my assessment of foreseeable environmental changes likely to substantively affect prospects for recovering a reintroduced population of grizzly bears in the Southwest. As is the case everywhere on Earth, climate change promises to trigger a cataclysmic upheaval of ecosystems, with changes in human populations, societies, and cultures prospectively either amplifying or mitigating this ecological tumult.

5.a. Human-Related Projections

Human-related changes of relevance to survival of grizzly bears can take two forms—either as numbers of humans and/or changes in access to previously secure areas, or as changes in worldviews and attitudes that affect tolerance. These types of changes would underly, in the first case, changes in frequency of contact between grizzlies and humans and, in the second, likelihood that grizzlies would end up dead as a result of that contact (Section 4.b).

Despite past trends in most urban areas as well as blithe assertions by the U.S. Fish and Wildlife Service regarding projections for the San Juan Mountains area (U.S. Fish & Wildlife Service, 2021: Appendix A), increases in human populations have not been uniform in the Southwest, nor will they likely be uniform in the future. In fact, human populations have been static, with little prospect of changing, in many rural parts of the Southwest. Figure 35 shows past and projected future population trends for counties encompassing prospective Grizzly Bear Recovery Areas, differentiating those that have experienced rapid, moderate, and slow—if any—growth. Only Yavapai (Arizona) and Archuleta (Colorado) Counties have experienced truly rapid population growth, whereas seven have experienced little if any increase in human numbers, including several such as Catron and Grant Counties in New Mexico that encompass some of the most promising areas for restoring grizzly bears.

Although projections of human population growth are always beset with uncertainty, they are not entirely unpredictable given the extent to which past growth has been highly correlated with infrastructure, community, and landscapes (Rasker & Hansen 2000, Hansen et al. 2002, Gude et al. 2006, Rasker et al. 2009). The projections in Figure 35 assume that future population growth will be driven by many of the same amenities and typified by the same degree of decade-upon-decade variation. The results suggest that slow-growing rural counties will largely remain so, with the greatest uncertainty applying to counties typified by high rates of past growth—prospectively including rapidly escalating populations as well as plateauing human numbers. Of particular relevance, counties with the greatest biophysical potential to sustain grizzlies will likely not have that potential compromised by major increases in numbers of humans.

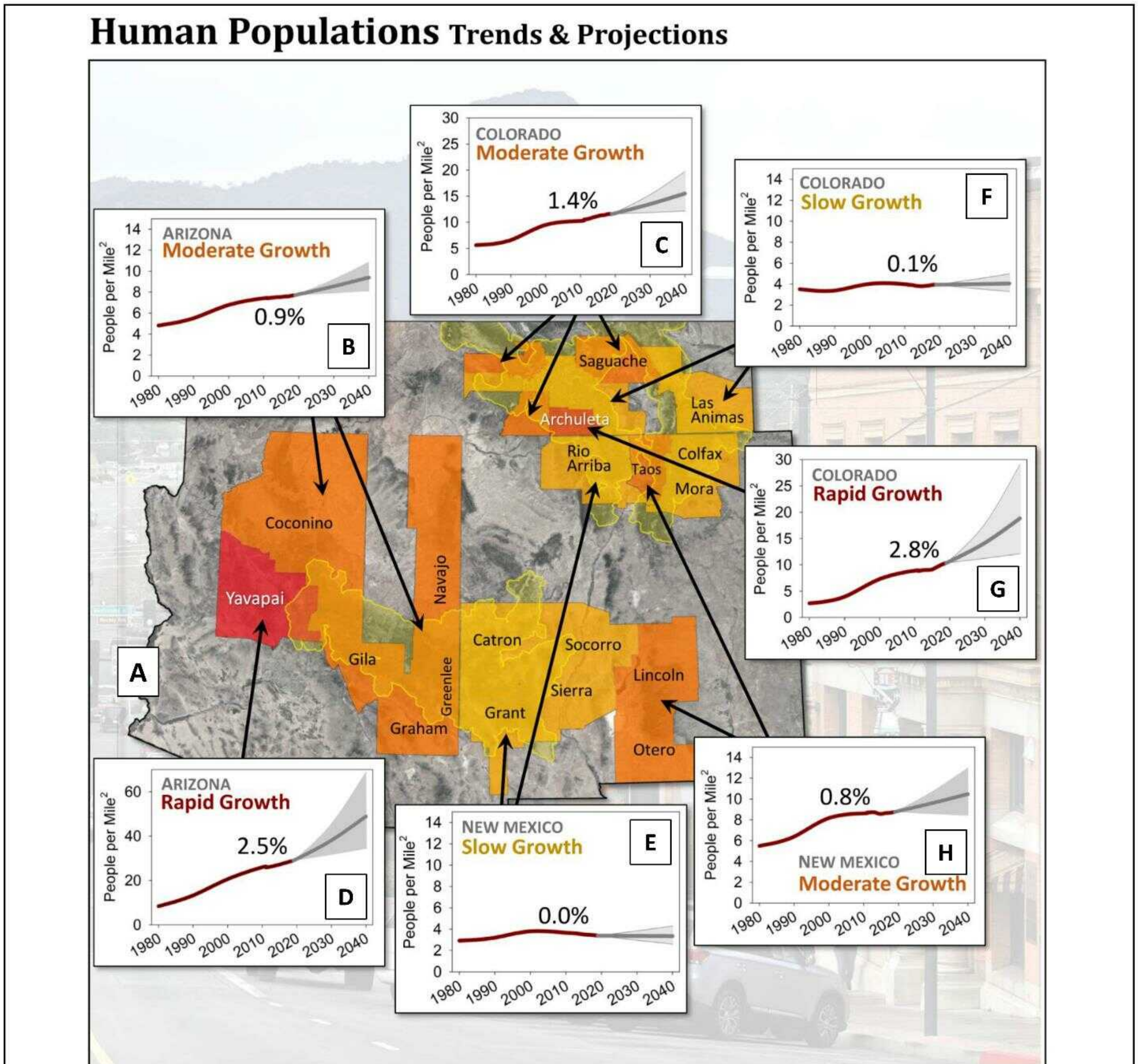


Figure 35. These graphics summarize past and projected growth of human populations in counties containing substantial areas of habitat suitable for grizzly bears (as per Figure 28). The inset graphics (B)-(H) show past trends in human populations for Arizona, Colorado, and New Mexico as dark burgundy lines, differentiated by whether counties had experienced slow (F & E; 0 to 0.5% per annum increase), moderate (B, C, & H; 0.6 to 1.75% per annum increase), or rapid growth (D & G; >1.75% per annum increase). Projected increases for each category of counties are shown as dark gray lines, with projection uncertainties shown as lighter gray cones calculated using growth rates one standard deviation greater or less than historical averages. Historical averages and standard deviations were calculated giving greater weight to rates of change since 2010; i.e., by giving annual changes since 2010 equal weight to average annual rates of change for each previous decade going back to 1980. Counties that experienced greater variability in rates of population increase, especially during recent years, are thus typified by greater uncertainty in future projections. The map in (A) shows county boundaries superimposed on prospective Recovery Areas, with counties differentiated by low (yellow), moderate (orange), and high (red) rates of past and prospective future population increase. Data for all graphics are from World Population Review.

Insofar as attitudes and tolerances are concerned, there is always a chance that past trajectories in these intangibles could be reversed by unforeseeable global changes. Even so, trends have been remarkably durable during the last century—and for explicable reasons (Kellert 1996; Kellert et al. 1996; Manfredo et al. 2003, 2009, 2021). Notably, trends have been unambiguously towards greater tolerance of large carnivores, albeit concentrated in urban populations without any direct dependence upon agriculture. These demographics are far more numerous—increasingly so—than the demographic of rural hunters and ranchers that is likely to be least tolerant. This disproportionality is evident in majority support for conservation and recovery of large carnivore populations in almost all population-wide surveys (e.g, Decision Research 2001; Teel et al. 2002; Williams et al. 2002; Bruskotter et al. 2007, 2009; Treves & Martin 2011; Remington Research Group 2016; Byrd et al. 2017; Manfredo et al. 2018; Responsive Management 2019).

Of relevance to future attitudes towards grizzly bears in the Southwest, odds are that acceptance and tolerance will increase. Most of this increase will likely continue to be concentrated in an increasingly urbanized populace, but with consequent perpetuation of problems arising from intolerance among hunters and ranchers interacting with grizzly bears. More positively, growing numeric differences in people holding divergent views of carnivores will likely affect political transactions, with trickle down positive effects on policies governing management of animals such as reintroduced grizzly bears.

5.b. Climate Projections

There is overwhelming (>99%) scientific consensus that the Earth's atmosphere is rapidly warming, largely driven by anthropogenic inputs (Lynas et al. 2021). Current trends furthermore comport with the more extreme RCP8.5 scenario (Wang et al. 2021), with resulting entrainment of potentially catastrophic environmental consequences, including rapid sea level rise (Schwalm et al. 2020), related worsening of storm surges and other extreme wave events (Ting et al. 2019), made all the more likely by a projected increase in landfall by intense oceanic storms (Vousdoukes et al. 2018). Further devastation will likely be wrought by accelerated ocean acidification (Jiang et al. 2019) and amplification of stratification and velocities of ocean currents (Peng et al. 2022). All of these changes in the ocean system will have spill-over effects that amplify the severity of impacts caused by changes intrinsic to the terrestrial system.

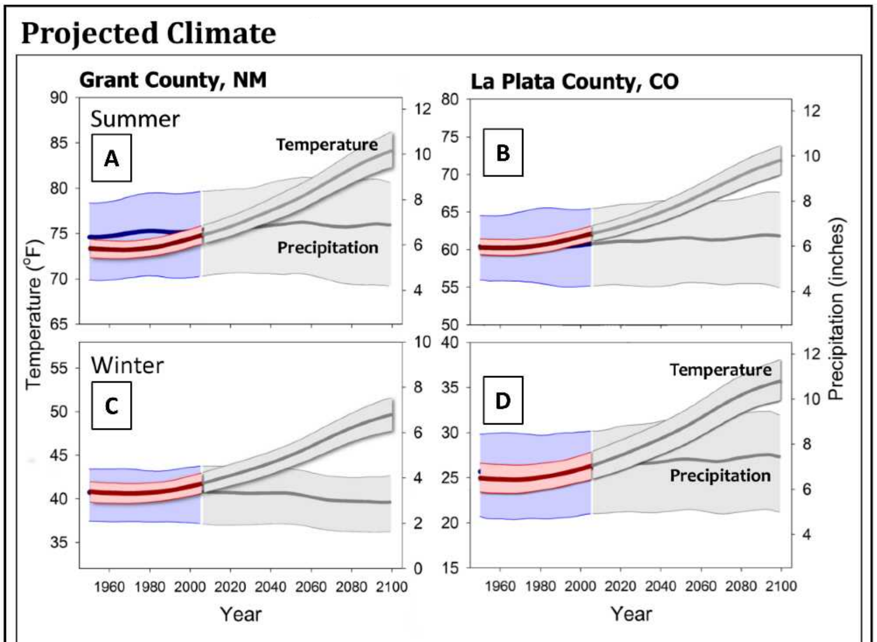


Figure 36. These graphs show past and projected future trends in average summer and winter temperatures and precipitation for two counties emblematic of southern (A & C; Grant County, NM) and northern (B & D; La Plata County) portions of the Southwest. Historical temperature records are shown in shades of red. Historical precipitation records are shown in shades of blue. Projections are based on a high emissions scenario (RCP8.5) and shown in shades of gray. Uncertainty is defined by bounds containing 95% of past records and future projections. Historical records and future projections are both from U.S. Climate Resilience Toolkit, Climate Explorer.

The Southwest obviously does not exist in isolation from the global climate, which means that the climates of this region will likely change dramatically during the next century as well (Garfin et al. 2013)—without regard for the protests of climate-change deniers. The questions are to what extent and in what ways. Although projections are always beset by uncertainty, there is an emerging consensus regarding the answers. There is virtually no doubt that average seasonal and annual temperatures will increase substantially (Garfin et al. 2013, U.S. Environmental Protection Agency 2016, U.S. Climate Resilience Toolkit), with greatest increases in the Great Basin and Mojave Deserts (Figure 38a, Stavros et al. 2014). There is greater uncertainty regarding changes in precipitation, but with an emerging consensus that any changes will be minor, especially in contrast to the magnitude of temperature increases. Figure 36 provides a snapshot of these projections for summer and winter for two locations, one in the north (La Plata County, Colorado) and the other in the south (Grant County, New Mexico; from U.S. Climate Resilience Toolkit).

This divergence of thermal and moisture inputs leads to a predictable result. Drought frequency will likely increase, with an increasing number of these droughts more severe than any documented during the past 2,000 years (Seager et al. 2007, Woodhouse et al. 2010, Garfin et al. 2013, Cooke et al. 2015, Williams et al. 2020). Perhaps paradoxically, changes in vegetation triggered by increases in temperature and atmospheric CO_2 concentrations will likely further reduce available soil moisture during drought periods, even in areas benefiting from greater precipitation (Seager et al. 2013, Tietjen et al. 2017, Manikin et al. 2019).

The effects of increased drought will probably not be geospatially uniform. Relative to the current-day benchmark, the greatest near-future *increases* in drought are expected to occur in the Mojave and Sonoran Deserts and lowlands of New Mexico (Figure 38b, Stavos et al. 2014), whereas *absolute frequency* of severe droughts is expected to be greatest on the Colorado Plateau and in southern and eastern portions of the Great Basin (Figure 38c, Thorne et al. 2018). Although droughts, overall, will almost certainly worsen, prospective Grizzly Bear Recovery Areas are not likely to be as severely impacted as many parts of the Southwest (Figures 38b and 38c).

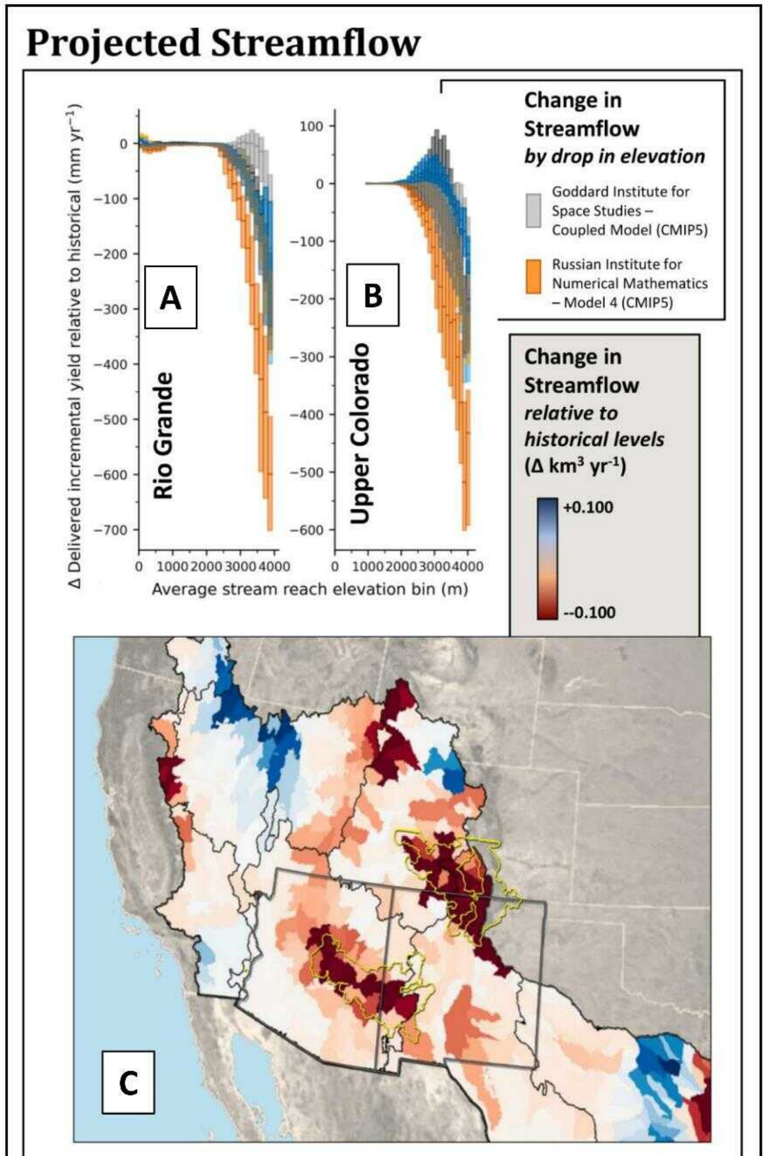


Figure 37. These graphics show projected changes in flows of major river systems in the Southwest by *circa* 2080 C.E. assuming a high-emissions climate scenario of RCP8.5 (from Miller et al. [2021]). The graphics in (A) and (B) show change (Δ) in the amount of streamflow added in a given catchment that makes it to the river network outlet relative to average elevation of the catchment (from low elevation, left, to high elevation, right). The climate model showing least projected diminishment is depicted in gray (Goddard); the climate model showing greatest projected diminishment is depicted in orange (Russian Institute). The map in (C) shows these same results in geospatial form, emphasizing that the greatest diminishment in contribution to flows at river outlets will occur in the highest-elevation catchments, denoted by dark burgundy shading. The perimeters of prospective grizzly bear Recovery Areas are shown as yellow lines (from Figure 30).

Perhaps not surprisingly, run-off and related inputs into river systems of the Southwest are projected to decline, potentially substantially (Seager et al. 2013, Stewart et al. 2015). Figure 37 shows results that introduce some paradoxical nuance into this broad-brush projection, notably that stream-flows will decline most substantially in headwaters of the Colorado and Rio Grande Rivers—with inevitable effects downstream (Miller et al. 2021). Of relevance to grizzly bears, most biophysically suitable habitat is located in headwater areas likely to most affected by diminished stream flows.

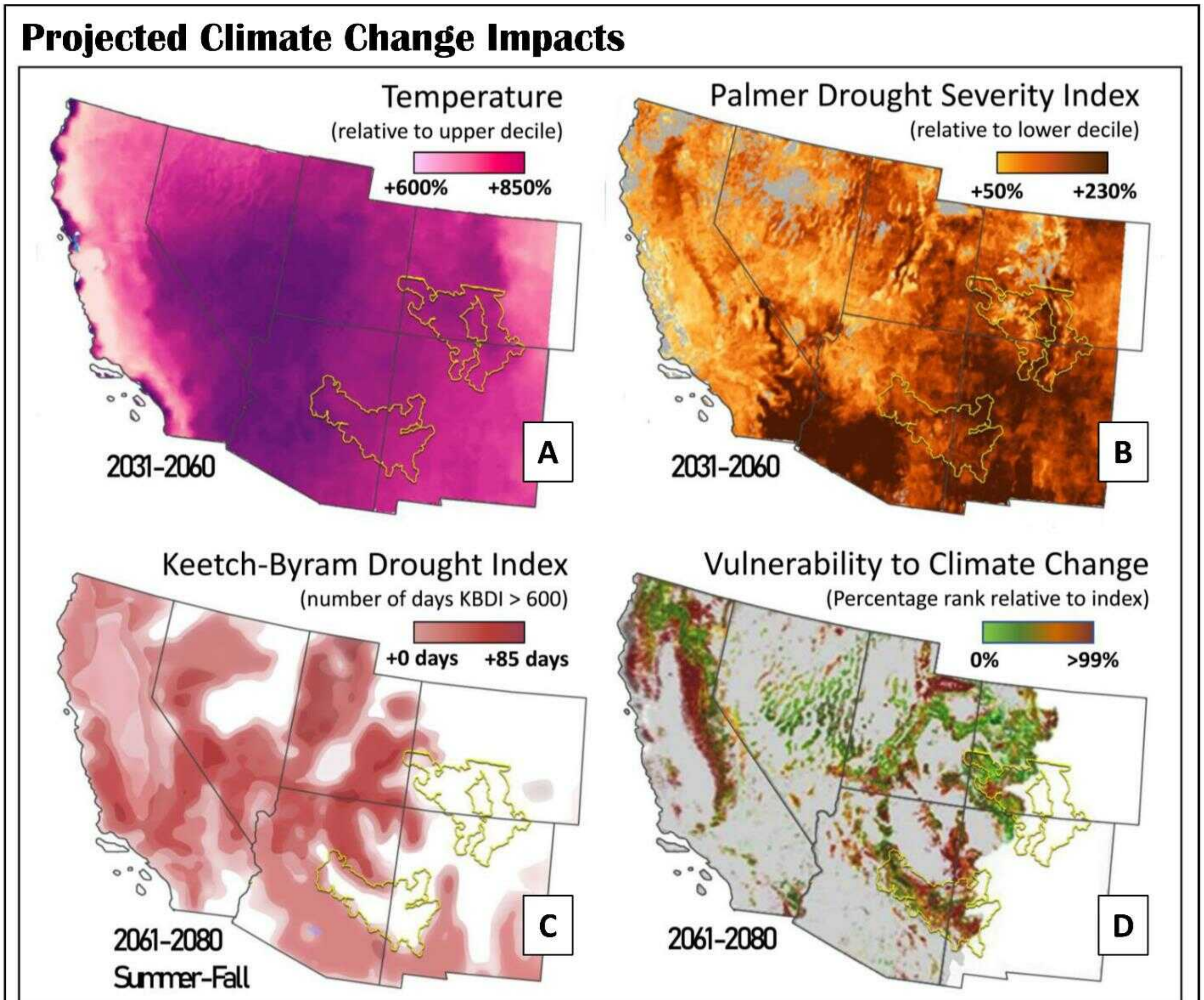


Figure 38. These maps show various projections related to the impacts of climate warming on climates and vegetation in the Southwest, with implications for the productivity of bear habitats. Maps (A) and (B) from Stavos et al. (2014) show projected increases in annual temperature (A) and drought severity (B) for 10-30 years in the future, both reckoned relative to the relevant deciles (extreme 10%) of past temperatures (upper decile) and drought (lower decile), the latter reckoned in terms of the Palmer Drought Severity Index. The map in (C) shows *absolute frequency* of drought reckoned according to a different drought index (Keetch-Byram) for a period 40-60 years in the future (from Thorne et al. [2018]). Finally, the map in (D) shows the relative vulnerability of vegetation to climate change for the same period of time (from Brown et al. [2021]). All of these projections assume a high-emissions climate scenario of RCP8.5. Major increases in drought severity are projected for much of New Mexico and the Sonoran Desert, but with protracted drought most severe in a latitudinal belt from southern California through the Four Corners region. Vegetation in the Southwest is projected to be most vulnerable to climate changes along the border of Arizona and New Mexico, plus the Sierra Nevada. The perimeters of prospective grizzly bear Recovery Areas are shown as yellow lines (from Figure 30).

The implications of these robust projections for the Southwest and global climate are clear. Everything affected by moisture availability, extreme weather, and thermal limits will be impacted either directly or indirectly—including grizzly bears (Sections 2.a and 2.b).

5.c. Habitat Projections

More than any other factor, climate configures the environments of terrestrial animals. Although warming of the Southwest will likely erode the area within which grizzly bears can adequately thermoregulate, the greatest impacts will be through effects on foods and vegetation. Given the extent to which grizzly bear population densities correlate with vegetal productivity (Section 2.b), projected aridification of the environment will likely challenge any grizzly bears prospectively reintroduced to the Southwest.

Changes in vegetal and animal bear foods will predictably be driven by a combination of migrating climates, unleashed pathogens and predators, and amplified wildfire regimes. Piñon pine has already experienced massive die-offs in the Southwest caused directly by bark beetles and indirectly by drought stress, foreshadowing similar die-offs of dominant plants species as the regional climate warms and dries (Breshears et al. 2005). Most species-specific projections of climate impacts show substantial northward shifts in distributions of major food-producing trees such as piñon pine, southwestern white pine, and oaks, accompanied by contraction of total distributions among the pines (Cole et al. 2008, Crookston et al. 2010, Thomas et al. 2012b, Shirk et al. 2018). Even so, the net effect of these changes on aggregate abundance of mast-producing oaks within prospective Grizzly Bear Recovery Areas is projected to be minor (Figure 39, Thomas et al. 2012b).

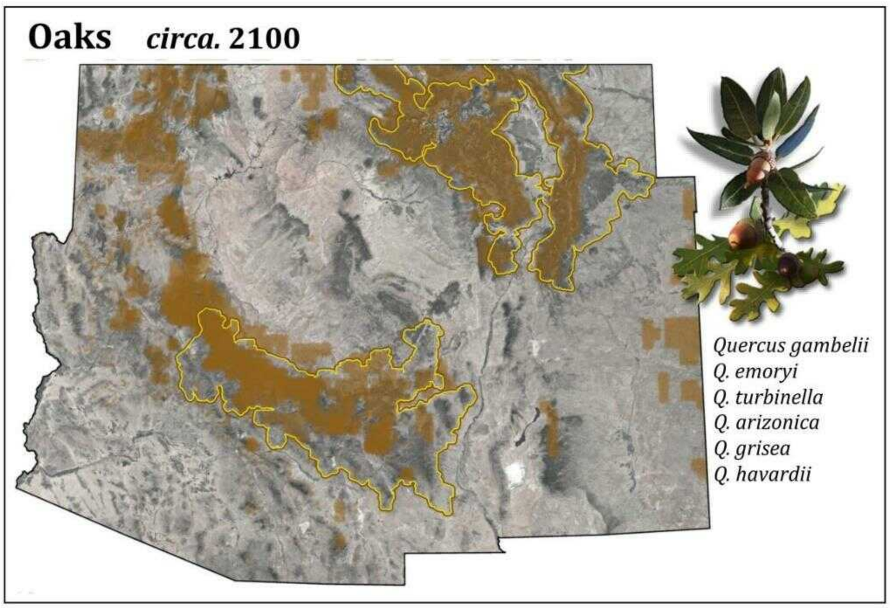


Figure 39. This map shows the projected cumulative distribution of oaks (*Quercus* sp.) that produce potentially edible acorns *circa* 2100 C.E. (from Thomas et al. [2012b]). Compare this distribution to the one shown in Figure 6. Projections assume a high-emissions scenario (Intergovernmental Panel on Climate Change scenario A2). The perimeters of prospective grizzly bear Recovery Areas are shown as yellow lines (from Figure 30).

These changes in distributions of individual plant species will predictably manifest in changes in vegetation communities. Up-elevation migration of vegetation types has already occurred in many parts of the Southwest (Brusca et al. 2013), but with even greater changes at the aggregate community level projected during the next 100 years. Of all the major vegetation types, riparian, piñon-juniper, and Douglas-fir communities are expected to be the most vulnerable to climate change (Thorne et al. 2018), but with major losses of subalpine communities and near-total elimination of alpine environments also expected (Rehfeldt et al. 2006). Infilling by perennial species better adapted to emerging climates is likely to lag well behind local losses largely because most late-successional species have limited dispersal rates (Cole et al. 2008, Cole 2010). Novel or “extramural” vegetation communities will be the predictable result (Rehfeldt et al. 2006, Cole 2010).

But, as with the recent losses of drought-stressed piñon pine to an outbreak of native bark beetles, the proximal catalyst for churn in vegetation and changes in species distributions will likely not be mortality caused directly by drought stress, but rather mortality from drought-amplified disturbance regimes—notably increases in wildfires. Although there are important nuances to various projections, all are in agreement that the average area burned each year by wildfires will increase (Liu et al. 2013, Brey et al. 2021), with greater average intensity (Brown et al. 2021), often as part of very large fires (Stavros et al. 2014). The implications of this increase in frequency, intensity, and extent of wildfires for grizzly bears in the Southwest are uncertain, although, as a general proposition, grizzlies could benefit from increased abundance and productivity of fire-adapted plants, especially species such as manzanita and Gambel oak that sprout from roots after being burned. Even so, wildfires of unprecedented frequency could nullify the adaptive strategies of even the most fire-adapted plant species.

5.d. Implications

Few future projections are auspicious for a recovering population of grizzly bears in the Southwest—even assuming that restoration efforts have succeeded. The productivity of currently-suitable habitat will likely erode as the effects of climate warming and drying play out, although declines will probably not be geospatially uniform. Potential carrying capacity for grizzlies will also likely decline, albeit to an uncertain extent, and with most declines likely concentrated at lower elevations and latitudes.

More auspiciously, despite the likelihood that human populations will continue to grow, most of this growth will probably be concentrated in areas where impacts on grizzlies are minimal. Prevailing attitudes vis-à-vis carnivores will concurrently likely improve, with benefits for grizzlies especially at the policy level. The net result could be a decrease in overall human lethality, albeit contingent on the extent to which attitudes change one way or another among hunters, livestock producers, and rural residents. In an optimistic scenario, improvements in survival of bears could be enough to offset declines in reproduction, although this sort of prospective outcome is bound to be highly uncertain and geospatially variable.

But the evolutionary history of grizzly bears provides perhaps the best reason for optimism. Grizzly bears have survived enormous environmental variation spanning hundreds of thousands of years, including many millennia at mid-latitudes of North America. Grizzlies survived not only the inhospitable deeps of the Ice Ages in Asia and Beringia, but also the heat and drought of the Altithermal on this continent. They furthermore managed to survive the numerous large carnivores that could have readily killed them. It was only highly-lethal Anglo-Americans that drove them to extinction in the Southwest, which is why human attitudes—more than anything else—will likely determine the future fates of restored grizzly bears.

6. An Imperative to Act

Aldo Leopold famously wrote "One of the penalties of an ecological education is that one lives alone in a world of wounds…An ecologist must either harden his shell and make believe that the consequences of science are none of his business, or he must be the doctor who sees the marks of death in a community that believes itself well and does not want to be told otherwise" (Leopold 1989). As for so many naturalists and ecologists, Leopold's insightful observation resonates deeply with me.

I grew up on a small ranch in the Black Hills of South Dakota at a time when the largest wild animals in the area were white-tailed deer and coyotes, just east of the location where a cousin of mine determined that Custer had killed "his grizzly," and south of Harding County where my grandfather had raised sheep and participated in a posse that killed the last wolf in the state. Even as a young teenager I experienced an inchoate sense of loss, largely for reasons I could not articulate, which nonetheless drove me to seek out wild places to work, including Yellowstone, where, even there, wolves had long before been eradicated.

I remain confounded by numerous relatives and acquaintances who are content living in landscapes autoclaved by white Europeans for the purpose of producing human goods and services—all the while refusing to see "the marks of death." This perverse persistence among those I have lived with has fueled pessimism, even despair, about prospects for healing the ecological wounds. And yet, miraculous healing has occurred. Mountain lions and wapiti had returned to our ranch by the time I was in college. Black bears are now reappearing. Wolves have been restored to Yellowstone and the northern U.S. Rockies. People with vision, optimism, persistence, and skill can imagine a better world—and make those imaginings come true.

This proposition is obviously relevant to restoring the Southwest's grizzly bears. This report hopefully not only clarifies the ample prospects for restoration, but also the rich historical tapestry of grizzly bears and their lives in the Southwest. As much to the point, I have tried to bring to life a shared journey of grizzly bears and people in this region that lasted for many millennia. The contentious terminal decades of relentless slaughter by Anglo-American featured in so many books and treatises were a tragic anomaly. They do not comport with the norm of human-bear relations for nearly all of the Holocene, and perhaps even the late Pleistocene. All of this hopefully serves to foster a new vision, at least for those who have an interest in nurturing it—a realizable vision of grizzly bears restored to and enriching the wild ecosystems of the Southwest.

The objective existence of ample habitat biophysically capable of supporting grizzly bears offers affirmative encouragement for restoration efforts in the Southwest. However, there is also a moral argument that conceivably creates an imperative. White Europeans bear an obligation of atonement for the devastation wrought by their ancestors on indigenous peoples and native ecosystems. Put bluntly, we have a legacy of blood on our hands. Barring an unfortunate residual minority, Americans are no longer driven by or offered the justification of a narrative that permits the willful perpetration of genocides and extinctions. Restoring grizzly bears to the Southwest would be one small atonement for the slaughter of every living thing that interfered with a presumed manifest destiny, including all of the grizzlies that once lived in the Southwest.

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Appendix A. This table presents estimated digestible energy, crude protein, ether extract, and total dietary fiber content on a dry matter basis for documented or potential bear foods in the Southwest and adjacent Mexico. Esimated sizes of targeted diet items are also given in grams dry matter for each food. Foods shaded dusky greeen are characteristic of the U.S.-Mexico borderlands, whereas foods shaded light purple are characteristic of higher latitudes.

	Digestible energy (kcal/g dry matter)		Crude protein (% of dry matter)		Ether extract (% of dry matter)		Total dietary fiber (% of dry matter)		Unit mass (g dry matter)		
Species or Genus of Food	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
Yucca spp.	0.64	0.11	8.0	2.1	2.2	0.3	74.5	1.3			Grazed Foods
Dasylirion leiophyllum	0.77	0.24	4.3	2.2	1.1	0.7	64.5	20.5			
Graminoids	0.93	0.10	20.3	5.0	2.1		52.0	1.3	0.14	0.04	
Trifolium spp.	1.13	0.20	22.5	2.3	2.6		44.3	6.0	0.21	0.07	
Taraxacum officinale	1.16	0.15	18.2	3.5			43.9	0.8	0.33	0.34	
Opuntia spp.	1.48	0.46	6.6	5.1	1.3	0.7	47.1	18.3			
Lycium pallidum	0.93		16.5		3.2		55.9				Fleshy Fruits/Sporocarps
Prosopis spp.	1.06	0.57	14.8	2.0	3.1	0.4	56.5	14.2	1.15	0.18	
Prunus virginiana	1.16	0.11	8.0	0.8	4.3	1.4	43.2	11.4	0.28		
Arctostaphylos pungens	1.19		2.7		4.0				0.39	0.34	
Prunus serotina	1.28	0.29	4.3	3.1	1.9	2.6	27.9		0.46		
Rhus trilobata	1.37		10.1	1.1	15.5		47.8	4.0			
Ribes cereum	1.34		5.6		1.9		41.0		0.16		
Amelanchier alnifolia	1.40	0.86	5.8	2.8	3.8	1.1	39.3	8.1	0.83	0.09	
Arctostaphylos uva-ursi	1.68		3.3	0.6	5.4		48.3		0.19		
Berberis trifoliata	1.68										
Yucca spp.	1.77	0.43	4.2	2.2	5.0	5.5	33.8		2.40	0.50	
Opuntia spp.	1.78	0.23	2.9	1.3	1.6	2.0	11.8		6.60	0.70	
Mushrooms	1.89	0.31	11.5	2.8	4.0	1.5	28.3	6.5	7.60	5.00	
Arbutus xalapensis	2.10	0.46	4.2		3.0		32.7		1.05		
Diospyros spp.	2.13	0.65	3.6	0.1	1.8	0.3	21.1	6.7			
Shepherdia canadensis	2.28	0.17	12.0	5.9	5.7	2.6	23.8	3.6	0.20	0.02	
Vaccinium membranaceum	2.48	0.54	4.3	0.6	3.1	0.8	21.5	5.7	0.32	0.06	
Juniperus spp.	0.80	0.16	4.0	0.5	14.7	8.4	75.1	5.4			Hard Mast
Quercus spp. - white oaks	1.89	0.62	5.7	0.9	7.8	6.3	40.2	8.1	3.89	1.53	
Quercus spp. - red oaks	2.56	0.70	5.7	0.8	20.5	3.9	31.3	8.1	4.20	0.81	
Pinus monophylla	3.19		9.0	1.4	35.5	16.2	20.0	0.0	0.24	0.06	
Pinus edulis	4.21	1.76	12.8	3.5	55.9	16.1	24.0	15.0	0.24	0.06	
Formicidae adults	2.02	0.88	44.9	8.8	30.3	11.9	53.7	16.9	0.005	0.005	Animals
Vespidae	2.34	0.29	49.1	7.9	8.6	2.5	25.0	1.8	0.010		
Formicidae pupae	2.87	0.14	49.6	6.9	26.8	4.3	28.0	3.2	0.004	0.005	
Odocoileus spp.	4.06		79.5		12.6		6.3		15700	3100	
Cervus elaphus	5.33	1.03	57.1	15.3	35.7	17.5	4.6	1.0	56000		

Per gram digested energy (DE) was estimated as the product of percent dry matter digestibility (DMD) and per gram energy content (E). Per gram energy content was estimated according to a standard equation that summed energy concentration of specific nutrients multiplied by the fraction of each in a given food: E = (3.99 x % Crude Protein) + (8.96 x Ether Extract) + (3.99 x Nitrogen Free Extract) + (1.86 x Total Dietary Fiber).

DMD was averaged from two different formulas that related DMD to Total Dietary Fiber (TDF) using bear-specific data presented in Prtichard & Robbins (1990): (1) $DMD = 113.6 - (7.002 \times TDF^{0.618})$, and (2) $DMD = 105.16 - (2.171 \times TDF) + (0.0169 \times TDF^2)$. Statistics for the two respective formulas are $r^2 = 0.93$, $F = 84.0$, $p < 0.0001$; and $R^2 = 0.94$, $F = 87.2$, $p < 0.001$; with $n = 15$ for both.

Given that fractional composition of fiber for different foods is rarely given in terms of TDF and more often presented in terms of Acid Detergent Fiber (ADF), Neutral Detergent Fiber (NDF) or Crude Fiber (CF), I used a data set in which TDF, ADF, NDF, and/or CF were estimated for the same foods to estimate relations that I could then use to convert ADF, NDF, and CF into TDF, which I could then use in the formula to estimate DMD for bears. The formuals for converting each of the respective representations of fiber to TDF are: (1) $TDF = 2.540 + (2.608 \times ADF)$; (2) $TDF = 1.116 + (0.928 \times NDF)$; and (3) $TDF = 7.836 + (2.618 \times CF) - (0.0239 \times CF^2)$. The statistics for each of these respective formulas are: (1) $r^2 = 0.69$, $F = 42.0$, $n = 21$; (2) $r^2 = 0.97$, $F = 656.7$, $n = 21$; and (3) $R^2 = 0.77$, $F = 115.5$, $n = 71$. Type I error p-values for all equations are < 0.0001.

Appendix B.

Refences for Nutritional Composition Bear Foods

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The Grizzly Bear Recovery Project

P.O. Box 2406,
Livingston,
Montana