LIVESTOCK DEPREDATION BY GRIZZLY BEARS ON FOREST SERVICE GRAZING ALLOTMENTS IN THE GREATER YELLOWSTONE ECOSYSTEM

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Animal and Range Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

July 2017

DEDICATION

To my parents, Faye and Jerry, for shaping me into a natural resource professional and for sharing their love of adventure into parts unknown. To Adam, my supportive, encouraging partner through life’s journeys.

ACKNOWLEDGEMENTS

I am very grateful to Dr. Daniel B. Tyers, U.S. Forest Service, for his role in initiating and supporting this project and for providing me with countless resources and opportunities to be successful. My sincere thanks to my advisor Dr. Lance McNew and the rest of the Montana State University Wildlife Habitat Ecology Lab for their guidance and support on this project and my future career. Also my sincere thanks to the rest of my committee members Dr. Frank T. van Manen and Dr. Daniel J. Thompson for their insights and guidance. I am appreciative of the USGS Interagency Grizzly Bear Study Team, especially Lisa Landenburger and Mark Haroldson, who provided not only data but their time and effort towards this project. I thank the U.S. Forest Service and the Montana Agricultural Experimental Station for their financial support. I would like to thank the U.S. Forest Service and National Park Service personnel who helped me collate historic grazing allotment information across the ecosystem, with particular thanks to Kim Reid, Chauntelle Rock, Reggie Clark, Cara Noseworthy, Susan Lamont, Kevin Suzuki, Heidi Heyrend, Andrew Pils, Paul Archual, David Booth, Dave Cottle, Todd Stiles, Ann Roberts, Kelly McCloskey, and Dan Reinhart. I would also like to thank U.S. Forest Service and Wyoming Game and Fish Department personnel who guided field tours of grazing allotments throughout the ecosystem, especially Andrew Pils and Kevin Suzuki. I am thankful for the statistical advice from Joao Rossi and Mark Greenwood. Lastly, I would like to recognize my family, friends, and fellow graduate students who supported and encouraged me throughout this process.

TABLE OF CONTENTS

TABLE OF CONTENTS – CONTINUED

LIST OF TABLES

Table Page

LIST OF FIGURES

ABSTRACT

Grizzly bear population growth and range expansion over the last several decades in the Greater Yellowstone Ecosystem (GYE) has led to increased human-bear conflicts, including livestock depredation on public land grazing allotments. A better understanding of patterns and relationships between grazing allotment management and grizzly bear depredation of livestock is needed for adaptive, sustainable management in the ecosystem. Historic U.S. Forest Service and National Park Service livestock grazing records, grizzly bear habitat attributes, and documented livestock depredations by grizzly bears were collated for 316 public land grazing allotments within the grizzly bear Demographic Monitoring Area (DMA) during 1992–2014. Spatio-temporal relationships between annual livestock depredation counts and grazing allotment characteristics were modeled for each allotment during the study period at two spatial extents, representing daily and annual grizzly bear activity areas. As the Yellowstone grizzly population expanded during the last several decades, more public land grazing allotments were exposed to potential livestock-grizzly bear interactions and results indicated that both livestock stocking and grizzly bear habitat characteristics in and around allotments were related to documented depredations during 1992–2014. Annual numbers of livestock and grizzly bear density on allotments had a large, positive effect on average livestock depredation event counts. Allotment size and summer grazing both were related to higher depredation event counts while the presence of bulls and/or horses was related to lower counts. Allotments with less rugged terrain, lower road density, relatively higher vegetative primary productivity, greater amounts of whitebark pine, and further from forest edge on average were associated with higher average livestock depredation event counts. Managers and livestock producers could use these results to support adaptive management approaches and long-term planning such as increasing herd supervision, especially in areas with quality grizzly bear habitat and high grizzly bear density, or altering grazing management strategies and grazing locations to limit potential livestock depredation events. Results provide insight into historic livestock-grizzly bear conflicts on public lands in a large, complex ecosystem and although challenging, results could support cooperative management strategies to sustain the grizzly bear population and livestock operations in the GYE.

LITERATURE REVIEW

Yellowstone Grizzly Bear Population Status

The grizzly bear (*Ursus arctos horribilis*) is an iconic omnivore of much of the western United States and Canada and has been the focus of numerous conservation efforts during the last several decades. Westward human expansion that brought farming, ranching, mining, and trapping significantly reduced grizzly bear populations and narrowed their range south of Canada to less than two percent of its original size (Servheen and U.S. Fish and Wildlife Service 1993). One of the remaining grizzly bear populations exists within the Greater Yellowstone Ecosystem (GYE). The Yellowstone population has been listed almost continually as a threatened species under the Endangered Species Act since 1975 and, with stringent conservation strategies, has recovered to a conservatively estimated 717 individuals in 2015 and all demographic recovery targets are being met (U.S. Fish and Wildlife Service 2007, Haroldson et al. 2015).

Human activities are the greatest cause of grizzly bear mortality (Schwartz et al. 2006). High human-use areas may create demographic sinks, or ecological traps, for bears (Schwartz et al. 2006, Northrup et al. 2012). In demographic sinks, deaths exceed births and immigration exceeds emigration, possibly leading to local population decline ($\lambda < 1$). Finite rates of population change estimated for grizzly bears inside ($\lambda > 1$) and outside ($\lambda < 1$) the Yellowstone Grizzly Bear Recovery Zone (YGBRZ; Figure 1) suggest a classic source-sink relationship (U.S. Fish and Wildlife Service 1993, Schwartz et al.

2006, Interagency Grizzly Bear Study Team 2012). High mortality due to human conflict is expected when large carnivores expand beyond the boundaries of protected areas, and this may influence grizzly bear conservation. For example, 85% of known subadult and adult grizzly bear mortalities in the GYE during 1983–2001 were human-caused, and bears that spent more time outside of Yellowstone National Park and the YGBRZ had poorer survival than bears that spent more time within these administrative boundaries (Schwartz et al. 2006). Most of the human-caused mortalities were attributable to management removals of food- or livestock-conditioned grizzly bears, killing in defense of life or property, and poaching. Female grizzly bears are critical to population viability and increased female mortality can affect the long-term trajectory of the population (Mattson and Reid 1991). However, if males predominately depredate on livestock, negative effects of management removals on population-level female fecundity and persistence would be unexpected (Reinhart et al. 2001). While individual grizzly bears may obtain significant energy from livestock, there is no clear evidence that use of livestock as a food source translates into a measurable population-level increase in female fecundity (Mattson 2000). Similarly, any positive population-level effects on grizzly bear reproduction from using livestock as a food source would likely be negated by higher death rates of depredating bears if management removal actions are implemented (Reinhart et al. 2001). Continued efforts to reduce human conflicts outside national parks and the YGBRZ could reduce overall mortality within the Yellowstone grizzly bear population.

A changing climate, including changes in precipitation timing and amount, snowpack, and temperatures, may reduce some important high-elevation grizzly bear foods. Army cutworm moth (*Euxoa auxiliaris*) abundance is influenced by climate conditions (French et al. 1994, Robison 2009). Whitebark pine (*Pinus albicaulis*; WBP) seed availability is influenced by climate conditions and the abundance of seed-dispersing animals including red squirrels (*Tamiasciurus hudsonicus*) and Clark's nutcrackers (*Nuctifraga columbiana*; Mattson and Reid 1991). Currently, mountain pine beetle (*Dendroctonus ponderosae*), white pine blister rust pathogen (*Cronartium ribicola*), and fire are the primary causes of WBP mortality (Bockino and Tinker 2012). Whereas WBP can be an important food source for grizzly bears in the GYE, use depends on its productivity and availability, and recent research has shown that even as WBP declined, grizzly bears were able to adjust their diets, obtain other foods within their home range, and maintain body condition (Interagency Grizzly Bear Study Team 2013, Costello et al. 2014, Schwartz et al. 2014). Moreover, declines in other grizzly bear foods caused by climate change and introduced species such as the lake trout (*Salvelinus namaycush*) may not threaten the sustainability of the Yellowstone population due to the grizzly bear's flexible and adaptive diet (Interagency Grizzly Bear Study Team 2013).

Historic inbreeding during Yellowstone grizzly bear population lows reduced genetic variability (Miller and Waits 2003). However, the current effective population is large enough to prevent inbreeding depression and to maintain long-term genetic viability (Kamath et al. 2015). Even so, historic low genetic variation and the isolation of the population suggest that gene flow with neighboring populations, such as the Northern

Continental Divide Ecosystem (NCDE) population to the northwest, could help maintain or increase genetic diversity of the Yellowstone grizzly bear population (Tallmon et al. 2004, Kamath et al. 2015). Protecting habitat and reducing human-bear conflicts in the region between these two ecosystems may allow grizzly bears to continue to expand their range and restore gene flow with neighboring populations.

Grizzly Bear Ecology

The grizzly bear is a mostly solitary mammal that presently inhabits relatively remote areas of the western United States and Canada. Contiguous, fairly undisturbed mountainous terrain characterizes historically occupied grizzly bear habitat. Inland grizzly bears predominately use relatively high elevations with steeper slopes and rugged terrain, and avoid areas of high human use, including roads and trails with human traffic (Apps et al. 2004, Steyaert et al. 2011, Northrup et al. 2012). Secure habitats for grizzly bears are defined as areas at least 4 hectares in size that are more than 500 meters from an open or gated motorized access route (U.S. Fish and Wildlife Service 2007). In the Cabinet-Yaak region of Montana, road densities exceeding 1.1km/km^2 negatively impacted grizzly bear space use (Mattson and Merrill 2004). Other habitat features important to grizzly bears include: vegetative diversity for seasonal food availability and numerous cover types, space, and solitude from human activities including logging, mining, grazing, and recreation (Servheen and U.S. Fish and Wildlife Service 1993).

Grizzly bear habitat use is hierarchical, where within the geographic range of the population (first order selection), bears select a home range (second order selection) and within the home range, bears select use areas (third order selection; Johnson 1980, Ciarniello et al. 2007). Therefore, grizzly bear habitat ecology and management strategies should be considered at multiple spatial extents (Ciarniello et al. 2007, DeCesare et al. 2012). Grizzly bears select for areas with dense vegetation that provide cover during the day when bedded and select for more open areas at night when foraging (Apps et al. 2004). At broad spatial scales, grizzly bears select areas of higher forest productivity that provide thermal and security cover, but within forests, daily movements are influenced by open forest canopy areas that provide herbaceous forage value and opportunity for predation on vulnerable ungulates like elk calves in the spring (Gunther and Renkin 1990, Mace et al. 1999, Apps et al. 2004, Stewart 2011, Steyaert et al. 2011). Grizzly bears select habitats close to streams for cover and herbaceous forage during at least part of the year, and several studies on bear-livestock conflict have found that many grizzly bear depredation take place in riparian areas (Murie 1948, Wilson et al. 2005, Steyaert et al. 2011). Grizzly bear home ranges overlap, indicating use of similar habitats and landscapes by different individuals (Craighead 1976). However, at high bear densities, social behaviors such as interference competition may lead to segregated habitat use where dominant, adult males use the most productive feeding sites while subordinate juvenile males and females with cubs use sub-optimal foraging areas (van Manen et al. 2016). Differences between female and male grizzly bear use of WBP habitats, vegetation cover types, topography, and human disturbance areas has been documented (Ciarniello et al. 2007, Costello et al. 2014). As grizzly bears expand into areas of less suitable habitats, less is known about habitat preferences. Current monitoring demonstrates that grizzly bears in suboptimal habitats are in good condition, but much more prone to negative interactions with humans (DeBolt 2016).

Grizzly bears are opportunistic omnivores that have large dietary breadth and flexibility. Grizzly bears consume almost any food available including insects, small mammals, ungulates, carrion, vegetation, nuts, berries, and garbage. Although grizzly bears are generalists, they prefer foods with higher gross energy content if easily obtained. Four high-calorie foods that have been identified as most important to the GYE grizzly bear population are: ungulates, cutthroat trout (*Oncorhynchus clarkii*), WBP seeds, and army cutworm moths (U.S. Fish and Wildlife Service 2007). Although these foods are important, the relative use of each depends on their availability in relation to other foods (Gunther et al. 2014). For example, the approximately 30 insect aggregation sites in the southeast portion of the Ecosystem provide a high-calorie food source for many grizzly bears in the area but this food source is not available to all Yellowstone grizzly bears and therefore not used by all bears (Bjornlie 2015). Other important food items for grizzly bears in the GYE include graminoids, ants (*Formicidae*), clover (*Trifolium* spp.), and dandelion (*Taraxacum* spp; Gunther et al. 2014). Livestock occuring on private and public grazing lands in the GYE present a high-calorie food source that may be an appealing diet choice for grizzly bears if they are abundant relative to other high-calorie food sources and easily found within a bear’s home range (Reinhart et al. 2001).

Yellowstone grizzly bear food habits change throughout the year. In spring (den emergence to May 15), grizzly bears, especially males, primarily use winter-killed ungulate carcasses because they provide a high benefit:cost ratio (Gunther et al. 2004). During the reproductive period, from May 16 to July 15, grizzly bears generally consume elk calves, cutthroat trout, and over-wintered WBP seeds if available. Early hyperphagia is during July 16 to August 31, when grizzly bears consume greater amounts of food to prepare for hibernation. Consumption of army cutworm moths and vegetation is common at this time. During late hyperphagia, from September 1 to denning, grizzly bears commonly feed on army cutworm moths, the current year's WBP seeds, and other obtainable high-energy foods (Gunther et al. 2004). Food habits differ substantially based on location, annual variation in weather, and other available foods (Interagency Grizzly Bear Study Team 2013).

Livestock Grazing on Public Lands in the GYE

Most areas adjacent to current grizzly bear range and part of bear range expansion are federal or private lands often used for livestock grazing (Schwartz et al. 2002). Livestock grazing on forest reserves in the west began even before the creation of the U.S. Forest Service (USFS) in 1905, and is an economically important industry in the region (Rowley 1985). The breeds of beef cattle as well as meat and wool sheep breeds grazing consist of those that are adapted to cool, semi-arid climates of the west. Most impacts to grizzly bears from livestock grazing are related to the human side of livestock operations. Homesteading in the late 19th and early 20th centuries lead to habitat loss from cultivation, lower ungulate numbers from hunting, and higher grizzly bear mortalities from human protection of livestock and crops (Mattson 1990). Livestock grazing may also negatively impact grizzly bear habitat by reducing the vigor or abundance of bear foods including grasses, forbs, and berry-producing shrubs, or by reducing the amount of security cover including riparian shrubs and trees (Stivers 1988, Mattson 1990, Reinhart et al. 2001). However, impacts to vegetation are dependent on the season, duration, and intensity of livestock grazing, and with modern grazing management, livestock likely have minimal effect on the biomass and structure of vegetation consistently used by grizzly bears (Stivers 1988, Mattson 1990). Additionally, grazing may increase introduced species palatable to grizzly bears such as clover and dandelion (Stivers 1988, Mattson et al. 1991, Gunther et al. 2014).

Since the onset of livestock grazing on public lands, many regulations have been developed to control livestock numbers and to manage their impacts on vegetation and other wildlife habitat (Rowley 1985). National forests within the GYE use a variety of strategies to minimize habitat deterioration and livestock depredation. Livestock stocking, timing of grazing, and duration of grazing are manipulated to minimize the loss of forage for resident wildlife species. Inside the YGBRZ, no new grazing allotments can be created and sheep are being phased out of allotments because they are commonly preyed upon by grizzly bears (U.S. Fish and Wildlife Service 2007). Forests in the GYE generally require livestock producers with grazing permits in occupied grizzly bear habitat to properly dispose of carcasses and store livestock food in order to minimize attractants that can result in grizzly bear conflicts on federal allotments (USDA Forest Service 1997;2015).

Grizzly Bear-Livestock Conflicts

Conflicts between humans and grizzly bears have existed since the human settlement of grizzly bear range in the early 1800s. Predation control, unregulated hunting, protection of human life, and habitat loss were major causes of grizzly bear mortality and reduced population numbers and distribution within mountainous areas as well as within previously occupied prairie habitats in the 19th and 20th centuries (Servheen and U.S. Fish and Wildlife Service 1993). Murie (1948) provides a historic account of grizzly bear depredation on cattle and the subsequent killing of bears by stockmen on the Spread Creek and Black Rock Creek Forest Service grazing allotments near Jackson, Wyoming. Although the killing of bears and livestock grazing impacts on habitat are much more regulated today, human-bear conflicts still occur on public and private lands. Reports of grizzly bear depredations on livestock have increased during the last decade, with many of the conflicts occurring on USFS grazing allotments in the GYE (DeBolt 2016, Frey and Smith 2016). Increased depredations result in more intensive grizzly bear management practices on the landscape, such as relocations or removals from the population, and these practices are the primary component of conflict management and grizzly bear conservation in the GYE. Management removals of grizzly bears due to livestock depredation in the Montana portion of the GYE have more than tripled from 5% of average annual mortalities during 1994–2004 to 17% during 2005–2015 (Frey and Smith 2016). Whereas management removals due to livestock depredations have increased over time, they still remain a relatively small portion of overall grizzly bear mortality compared to the combination of other human-related deaths such as vehicle collisions and other conflict removals as well as natural deaths.

The likelihood of livestock-bear interactions has increased over the last several decades with grizzly bear population growth, grizzly bear range expansion, and continuing livestock grazing on USFS lands surrounding Yellowstone National Park (Figure 1). Grizzly bears have expanded outside of the YGBRZ, especially to the south, east, and southeast into Wyoming, and human-bear conflicts are tied to these areas of expansion (Schwartz et al. 2002). From 1992 to 2000, 69% of livestock depredations by grizzly bears in the GYE occurred outside of the YGBRZ, and 80% of depredations occurred on public lands (Gunther et al. 2004). The distribution of the Yellowstone grizzly bear population has expanded by 11% in only the last two years (2014–2016; D. Bjornlie, Wyoming Game and Fish Department, unpublished data). Forest Service lands on the periphery of the ecosystem provide large expanses of relatively undisturbed, high-quality habitat that will become more important for grizzly bears as occupied range continues to expand well beyond the recovery zone boundaries.

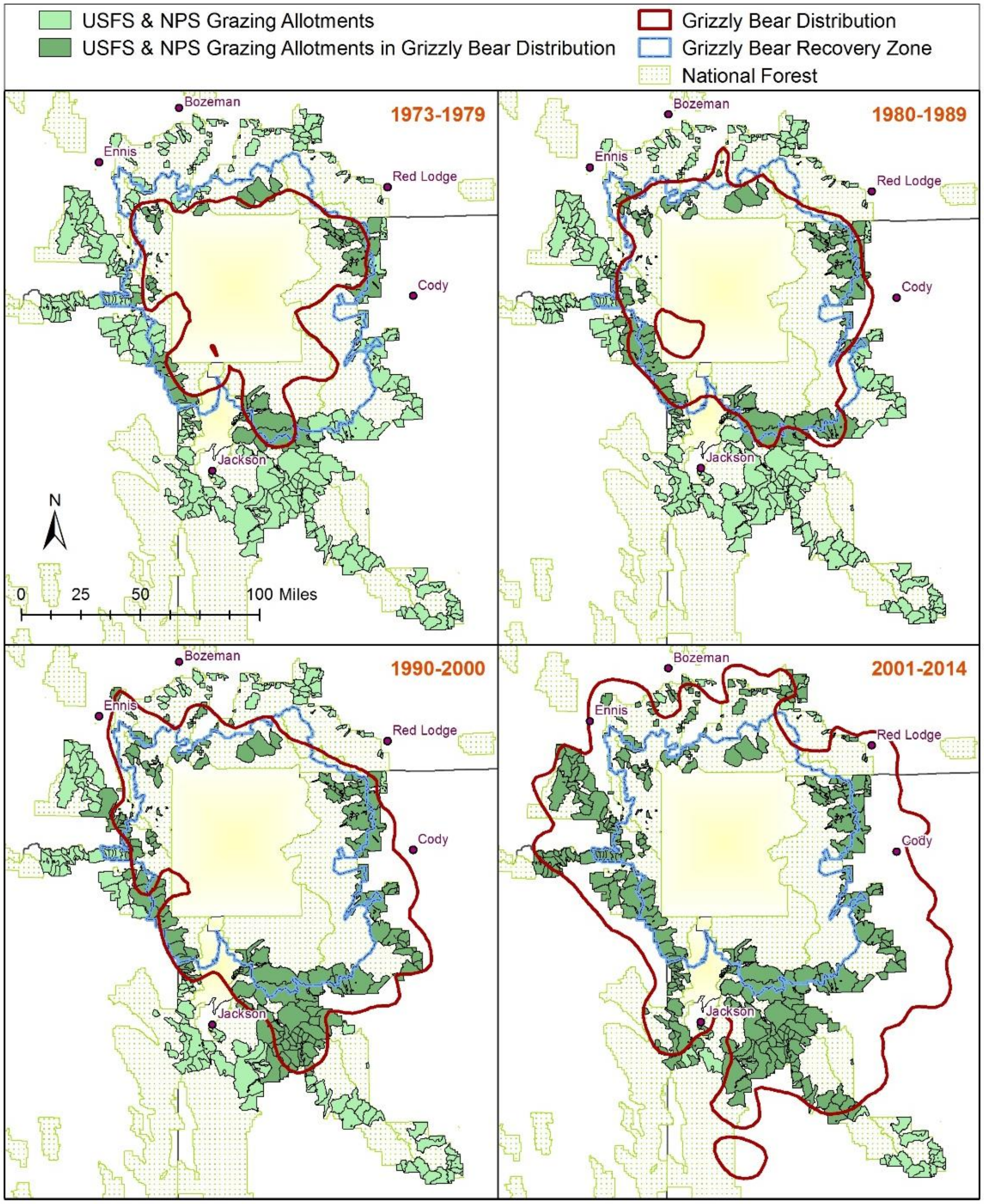

Figure 1. Grizzly bear distribution in relation to U.S. Forest Service (USFS) and National Park Service (NPS) grazing allotments during 1973–2014. Allotments shown are those stocked during 1992–2014 and are within the grizzly bear Demographic Monitoring Area (DMA). Outlier grizzly bear observations in the 1990s and 2000s are not shown. Data sources: Bjornlie et al. 2014a, USGS Interagency Grizzly Bear Study Team, Montana State Library, WyGISC, NPS, USFS.

Grizzly bears often prey on ewes, lambs, and young cattle (calves and yearlings), and typically the livestock harmed are not sick or injured (Murie 1948, Mattson 1990, Anderson et al. 2002, Wilson et al. 2005). For example, depredation on the Blackrock-Spread Creek and Elk Ranch East Forest Service grazing allotments near Jackson, Wyoming during 1994–1996 removed 1.3–2.2% of the calf herd (Anderson et al. 2002). Grizzly bears rarely prey on bull cattle and horses, likely due to their large body size and increased human presence associated with the management of these livestock classes (Mattson 1990). Tall larkspur (*Delphinium occidentale*) is a poisonous forb responsible for the majority of cattle deaths on mountain rangelands in the west, where approximately 5–15% of cattle herds are lost when larkspur is abundant (Pfister et al. 1997). Cattle carcasses from larkspur deaths can attract grizzly bears to livestock use areas. However, previous studies have found no evidence that bears scavenging cattle carcasses became depredatory (Claar et al. 1986, Madel 1996).

In 2015, 117 livestock were killed by grizzly bears on Forest Service lands in the GYE, including 100 calf and yearling cattle (Interagency Grizzly Bear Study Team 2015). While a relatively small proportion of the thousands of livestock grazing public lands, economic losses from animals that do not produce a profit can be significant for livestock operations. For example, during 1995–2004, the Upper Green River Forest Service cattle allotment in Wyoming lost an average of 1.9% of the calf herd annually to grizzly bear depredation, producing economic losses estimated at $260,000 during this period (Sommers et al. 2010). In 2016, the state of Wyoming paid over $440,000 in damage claims attributed to grizzly bears (D. Thompson, Wyoming Game and Fish

Department, unpublished data). Similarly, from the 31 cattle depredations due to grizzly bears claimed in the Montana portion of the GYE in 2016, the Montana Livestock Loss Board compensated operators approximately $40,000 (Livestock Loss Board 2016). Along with providing monetary compensation for livestock killed, agencies also provide substantial time and resources towards conflict management and depredation investigations.

Wilson et al. (2005) found that almost half of all grizzly bear-livestock conflicts in the Rocky Mountain East Front of Montana occurred within 200 meters of dense riparian and wetland vegetation. Historical records similarly point to stream bottoms, willow cover, and forest edges as areas of likely conflict (Murie 1948). Wilson et al. (2005) also found that the majority of grizzly bear-livestock conflicts in the Rocky Mountain East Front of Montana occur within a small geographical area of the landscape, termed conflict hotspots. Most depredations occur at night, likely due to greater grizzly bear activity during this time (Anderson et al. 2002). Grizzly bears can exhibit significant spatial associations with cattle and not prey on them. However, during depredation periods (e.g., late summer/early fall), more grizzly bears are spatially associated with cattle than during non-depredation periods (e.g., early spring), suggesting that bears opportunistically take advantage of livestock already present in the area (Anderson et al. 2002).

Depredation on livestock increases through the summer season and peaks during hyperphagia in late July–August (Gunther et al. 2004). Most depredations are caused by adult males but adult female and subadult male grizzly bears will also kill livestock

(Murie 1948, Anderson et al. 2002). Adult female and subadult male grizzly bears are often displaced by territorial adult males and move into marginal habitats that have greater human influence, such as grazing allotments, which may lead to depredations (Mattson 1990, Wilson et al. 2005). Some studies have found that livestock depredation in an area is limited to a few problem bears, whereas others have found that many bears in an area will prey on cattle opportunistically (Murie 1948, Anderson et al. 2002).

The probability of livestock depredation has been found to be 55 times higher on livestock operations that experienced depredation in the last 12 months compared with other operations in the same region, suggesting spatial associations between grizzly bears and livestock at carrion feeding sites lead to more depredations, grizzly bear memory of livestock in the area as a food source, or social learning of depredatory behaviors (Karlsson and Johansson 2010). Other studies have found that offspring of female grizzly bears involved in conflicts were more likely to be involved in human-bear conflict behaviors on agricultural lands, including livestock depredations, compared with offspring from non-conflict females (Morehouse et al. 2016).

Grizzly Bear Management

Management of grizzly bears involved in conflicts within the YGBRZ is standardized within the Final Conservation Strategy for the grizzly bear in the Greater Yellowstone Ecosystem (U.S. Fish and Wildlife Service 2007). However, management of grizzly bear conflict events throughout the entire GYE is inconsistent across administrative boundaries. Incidental Take Statements for grizzly bears are developed by the Fish and Wildlife Service for individual allotments or small groups of allotments. Excess grizzly bear removals on some allotments have led to multiple amendments of the Incidental Take Statements on those allotments and thus livestock conflict management has become case-specific. Understanding ecosystem-wide patterns of depredations and the consequences on the overall Yellowstone grizzly bear population is critical for the sustainability of the Yellowstone grizzly bear population and land uses of the region.

Selective removals of offending individual bears has been demonstrated as an effective management tool for grizzly bear conservation and maintaining landowner/producer tolerance if there are a few grizzly bears responsible for the majority of depredations in an area (Anderson et al. 2002). However, if many bears prey on livestock opportunistically, other management methods must be used to minimize depredations (Murie 1948). Removal of carcasses that attract grizzly bears may reduce the concentration of bears in areas used by livestock. However, carcass removal does not prevent grizzly bears from developing depredatory behaviors and does not repel them from livestock-use areas (Anderson et al. 2002). Hazing or translocation of depredatory bears to distant locations may provide temporary, local relief from depredation but grizzly bears often return to their original use areas and home ranges. However, translocation could be useful in sensitive situations where individual bears, such as adult females, are important for population viability. Hazing and translocation could also separate habitual from opportunistic depredators (Anderson et al. 2002). Electric or traditional fencing can protect livestock from interactions with grizzly bears but can be expensive and unrealistic on public lands (Wilson et al. 2005). It has been suggested that predation could be reduced by limiting livestock grazing in riparian areas to late fall and winter, when the seasonal overlap of livestock and grizzly bears would be minimized (Wilson et al. 2005).

Conclusion

Grizzly bears and domestic livestock, both long-time inhabitants of the Greater Yellowstone Ecosystem, have shared increasing amounts of habitat as the grizzly bear population has expanded. Such spatial associations have led to an increase in human-bear conflicts, including livestock depredations, over the last several decades. Public land grazing allotments provide relatively intact, mountainous landscapes of quality grizzly bear habitat but conflicts on these allotments remain a source of grizzly bear mortality through management removals and pose management challenges to agencies. Livestock losses from depredations present economic challenges to local communities, organizations, and agencies. A better understanding of how public land grazing allotments are related to livestock depredation by grizzly bears could improve the sustainability of the Yellowstone grizzly bear population as well as livestock operations in the GYE.

LIVESTOCK DEPREDATION BY GRIZZLY BEARS ON FOREST SERVICE GRAZING ALLOTMENTS IN THE GREATER YELLOWSTONE ECOSYSTEM

Justification

The Greater Yellowstone Ecosystem is home to the entire Yellowstone grizzly bear population. The region, including the federal, state, and private lands that surround Yellowstone National Park, provides large expanses of mountainous terrain and suitable habitat that sustain grizzly bears and other wildlife species (Servheen and U.S. Fish and Wildlife Service 1993). The human population in the GYE is one of the fastest-growing in the U.S. and human impacts on the perimeter of this ecosystem are becoming more prominent (Hansen et al. 2002). Inconsistent regulations across administrative boundaries in the GYE prevent standardized practices that limit grazing allotment impacts on grizzly bears as well as human-caused death of grizzly bears (Servheen and U.S. Fish and Wildlife Service 1993).

The Yellowstone grizzly bear is an excellent species to investigate how human activity, specifically livestock grazing, relates to human-wildlife conflicts within the GYE for several reasons:

1. The Yellowstone grizzly bear is currently listed as a threatened population because of human impacts on the population over the last several centuries. Although numerous factors affect the population, humans are the largest cause of mortality, and human activity can significantly affect bear habitat use and conflicts (Apps et al. 2004, Northrup et al. 2012).

2. Livestock depredations by grizzly bears have increased in the last three decades (Gunther et al. 2004, DeBolt 2016, Frey and Smith 2016). Depredations may result in the removal of grizzly bears from the population but primarily result in the loss of livestock. For example, the Upper Green River Forest Service cattle allotment in Wyoming has experienced high depredation rates in the last several decades (USDA Forest Service 2014). During 1995–2004, an average of 1.9% of the calf herd was lost annually to grizzly bear depredation (Sommers et al. 2010). As of 2016, an estimated 13% of the calf herd in this same area was lost annually to depredation (D. Thompson, Wyoming Game and Fish Department, personal communication). Grizzly bear presence or aggression may force cattle into undesirable grazing areas or increase stress, leading to poorer nutrition and possibly illness (Anderson et al. 2002). Knowledge about what factors of livestock grazing on public lands are leading to depredation could help reduce depredations, economic impacts to livestock operations in the GYE, and depredation-related grizzly bear mortalities.
3. Livestock depredation by grizzly bears in the GYE during 1992–2000 has been found to be unrelated to the availability of bear foods (Gunther et al. 2004). Thus, grazing allotment stocking attributes, other grizzly bear habitat attributes, or combinations of stocking and habitat attributes could be more related to livestock depredation events and should be investigated. Also, the relationship between depredations and bear food availability should be further investigated following

the increase in grizzly bear abundance and density during the most recent years (post-2000) in the GYE.

Previous studies on livestock-bear conflicts have been limited to areas of high conflict and did not identify the mechanisms of grizzly bear space use of the greater landscape in relation to allotments (Anderson et al. 2002, Wilson et al. 2005). Schwartz et al. (2010) estimated grizzly bear survival as a function of landscape features and included allotment locations but no allotment attributes (Schwartz et al. 2010). It is necessary to examine grizzly bear habitat characteristics and allotment attributes that influence grizzly bear depredation events throughout the ecosystem, not only in allotments with high levels of conflict. Management is different inside and outside of the YGBRZ, and bear removals outside of the zone can create a demographic sink (Schwartz et al. 2006). An understanding of ecosystem-wide grizzly bear depredation of livestock on public lands is needed to effectively and consistently manage the conflicts occurring across the ecosystem.

Objectives

All subsequent references to USFS and National Park Service (NPS) grazing allotments in the GYE will be simply referred to as ‘grazing allotments’, unless otherwise stated. To address several key management questions, my study objectives were to: 1) quantify and summarize characteristics of grazing allotments in the GYE during 1992–2014 including livestock management, grizzly bear habitat attributes, and grizzly bear depredation of livestock; and 2) evaluate the relationships between grazing allotment characteristics and grizzly bear depredation of livestock during 1992–2014 at multiple spatial extents.

Hypotheses

Analyses aimed to address the study objectives as well as *a priori* hypotheses based on previous research regarding the associations of livestock stocking attributes and grizzly bear habitat characteristics with livestock depredations. Although little is known about relationships between public land livestock grazing and grizzly bear depredation, I hypothesized that larger allotments with more livestock that were grazed for longer periods of time would be positively associated with more depredations because there would be greater opportunity of spatial and temporal overlap between livestock and grizzly bears. Large-bodied bulls and horses are less vulnerable to predation and are generally associated with more intensive management by humans, therefore I hypothesized that the presence of these livestock classes would be negatively related to depredations.

Because grizzly bears are solitary animals that generally avoid areas of high human use, I hypothesized that measures of remoteness, including relatively high elevations, steep, rugged terrain, and low road densities would be positively related to depredations (Apps et al. 2004, Mattson and Merrill 2004, Northrup et al. 2012). Both grizzly bears and livestock aim to maximize feed efficiency and minimize energy expenditure by selecting areas of high-quality food sources, available water, and sufficient thermal cover, which could lead to spatial and temporal overlaps and more interactions (Wilson et al. 2005, Steyaert et al. 2011). Therefore, I hypothesized that allotments with relatively high primary productivity (NDVI), high stream density, and near forest edge would be positively related to depredations. Most documented livestock depredations in the GYE have occurred during the summer season (July 16–August 30), when grizzly bears are in early hyperphagia (Gunther et al. 2004). Therefore, I hypothesized that fewer depredations would be associated with allotments that were not stocked in the summer (spring or fall grazing only). Because greater numbers of grizzly bears may increase the opportunity for spatial overlap with livestock and may push subordinate bears into areas of higher human use, including grazing allotments, I hypothesized that the grizzly bear density index was positively associated with depredations (Stringham 1983, Mattson 1990, Wielgus and Bunnell 1994, van Manen et al. 2016). Many depredations during the study period have occurred in areas where grizzly bears have expanded their range in the last two decades, therefore I hypothesized that average depredation counts would be higher closer to grizzly bear range edge where grizzly bears are newly encountering humans and livestock on public lands.

Study Area

My study encompassed much of the Greater Yellowstone Ecosystem (58,314 km^2 of occupied grizzly bear range in 2014; Bjornlie et al. 2014a), including Yellowstone National Park, Grand Teton National Park (GTNP), John D. Rockefeller, Jr. Memorial Parkway, portions of five adjacent national forests (Bridger-Teton, Beaverhead-Deerlodge, Caribou-Targhee, Custer Gallatin, and Shoshone National Forests), and state and private lands in Montana, Wyoming, and Idaho (Figure 2). The study area was defined by the grizzly bear Demographic Monitoring Area (DMA; U.S. Fish and Wildlife Service 2013), from which all demographic criteria for the Yellowstone grizzly bear population are monitored and evaluated and which is deemed biologically suitable habitat for grizzly bears. Currently, 94% of the DMA is occupied by grizzly bears (D. Bjornlie, Wyoming Game and Fish Department, unpublished data). Within the DMA, 311 USFS grazing allotments on the five national forests in the GYE and five NPS grazing allotments in GTNP were stocked with livestock during 1992–2014. Of those allotments within the DMA, 295 allotments were within grizzly bear distribution during the study period (Figure 2). Of those allotments in the DMA and within grizzly bear distribution, a total of 254 allotments were stocked with cattle or sheep (no bull- or horse-only allotments) and were included in my analysis.

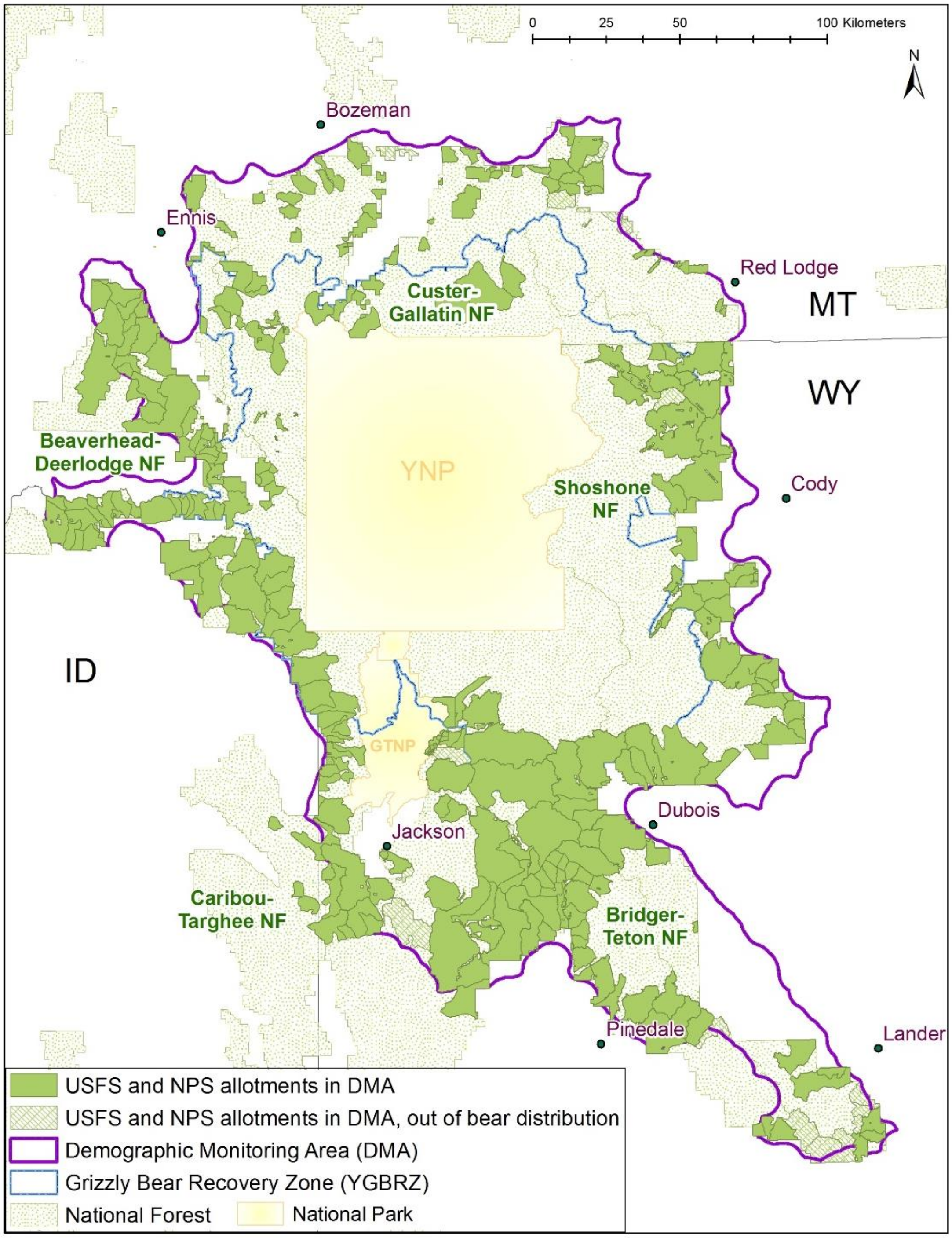

Figure 2. U.S. Forest Service (USFS) and National Park Service (NPS) grazing allotments within the grizzly bear Demographic Monitoring Area (DMA), 1992–2014. Allotments within grizzly bear distribution include those within established decadal distributions as well as those within outlier grizzly bear observations in the 1990s and 2000s. Data sources: Bjornlie et al. 2014a, USGS Interagency Grizzly Bear Study Team, Montana State Library, WyGISC, NPS, USFS.

Methods

Objective 1: Grazing Allotment Characteristics

Analyses of historic records of USFS and NPS grazing allotments in the GYE and documented grizzly bear depredations throughout this region presented an opportunity to gain an ecosystem-wide understanding of grizzly bear-livestock conflict in relation to public land grazing allotments. Collating livestock stocking information in addition to other allotment attributes was necessary to examine the relationships between grazing allotment characteristics and grizzly bear livestock depredations on livestock. Detailed public land livestock stocking information has not been quantified in other human-bear conflict studies in the region largely because such stocking information has not been readily available. Much of the grazing records in the GYE, especially historic records, were in hard-copy form and needed to be converted into digital form. By collating grazing allotment stocking information, habitat attributes, and depredations from 1992–2014 into a database, livestock-bear conflicts across the GYE over the last several decades could be explored. The combined USFS and NPS grazing allotment database may be useful for land and wildlife managers as well as for future studies related to livestock grazing and wildlife management in the GYE.

Livestock Grazing. Stocking information for 316 federal grazing allotments within the DMA during 1992–2014 was provided by various USFS and NPS natural resource managers or was recorded from hard-copy files in district offices. Recorded allotment livestock stocking information included forest name, ranger district, allotment name and ID, year, status (open, vacant, closed), whether it was stocked or not, date livestock were stocked on an allotment, date livestock were moved off an allotment, livestock kind (cattle, sheep, horse, mixed) and class (cow/calf, yearling, mature cow, bull, mixed cattle, ewe/lamb, horse), and the number of livestock. Allotment stocking information related to term grazing permits was included in data collection while temporary grazing permits and livestock use permits, typically issued for well-supervised pack animals, were excluded because stocking under such permits was usually minimal, variable, and difficult to quantify. Allotment stocking information was quantified for each year from 1992–2014 because livestock stocking was mostly constant within a year but could change dramatically from year to year, especially when allotments were rested (non-use) or grazing permits were altered. Allotment permittees could take non-use due to poor resource availability, management changes, or when sorting out grazing conflicts, but non-use could not be taken for more than three consecutive years without the permittee's grazing permit being invalidated. Vacant allotments were those with no current grazing permit but could potentially be grazed periodically by other permittees at the discretion of the agency. The U.S. Forest Service Actual Use reports supplied by the permittee after each grazing season provided the most accurate stocking information. However, if Actual Use reports were not available, Annual Operating Instructions (AOIs), which outline allotment livestock stocking prior to the grazing season, or term grazing permits were used to record stocking information.

Heifer and steer livestock classes were combined into a single yearling class and ewe livestock classes were lumped in with the ewe/lamb class. Because no depredation of horses or bulls was recorded over the study period, these large-bodied livestock classes were not included in the livestock numbers or classes present per allotment. For example, if an allotment was stocked with 200 cow/calf pairs along with 10 bulls, the allotment would be classified as being stocked with 200 cow/calf pairs. Instead, an attribute was included to account for the presence or absence of horses and/or bulls on an allotment. Stocking classes categorized as ‘mixed cattle’ were mainly stocked with cow/calf pairs and yearling cattle.

If allotments were run together (i.e., livestock moved between allotments during the grazing season), those allotments were combined into one larger allotment and stocking information was recorded for the single larger allotment. The most recent allotment boundaries provided by the USFS and NPS were used for analysis and to calculate allotment size. While some allotment boundaries had been altered during 1992–2014, most alterations were minimal and the current boundaries were representative of allotment boundaries over the 23-year period.

Seasons of livestock grazing were defined based on seasonal changes in grizzly bear movements, behavior, and food habits. Seasons were defined as: spring (March 1–July 15), summer (July 16–August 31), fall (September 1–November 30), and winter (December 1–February 28; Mace et al. 1999, Haroldson et al. 2002, Gunther et al. 2004). Whether or not an allotment was stocked the previous year was hypothesized to be related to grizzly bear memory and subsequent depredation, and was created as another stocking attribute.

Stocking density, or the number of livestock in a given area at a point in time, could not be accurately calculated because livestock were generally constrained to smaller pastures within allotments and pasture data were lacking from historical allotment records. Also, some allotments lacked fencing or strict pasture rotations so livestock could often be spread throughout the allotment even if pastures existed. Thus, livestock numbers by class, grazing season length, and allotment size were used to represent stocking rate instead of traditional range management measures such as animal units (AUs) and animal unit months (AUMs). Animal units and AUMs are commonly used to describe potential range utilization and condition (Holechek 1988), and because livestock grazing under modern grazing management generally does not reduce bear foods considerably over the larger landscape, utilization is likely a poor metric for grizzly bear response to livestock grazing (Mattson 1990). Instead, it is more likely that grizzly bears perceive the number and distribution of livestock on the landscape and how long they are there. The three metrics of stocking rate were kept separate during modeling to parse out which metrics were most related to grizzly bear depredation and to make results and interpretations most useful to managers. For example, if the three metrics were combined to create a measure of livestock head month^{-1} acre^{-1}, and this measure had a positive relationship with grizzly bear depredations, it would be impossible to conclude if higher livestock numbers, longer grazing seasons, or smaller allotments were most related to depredations.

Grizzly Bear Habitat. Numerous geospatial habitat attribute layers important to grizzly bear space use were provided by the U.S. Geological Survey's Interagency

Grizzly Bear Study Team (IGBST) or retrieved from online data clearinghouses (Appendix A). Physical grizzly bear habitat attributes previously found to be related to grizzly bear space use and livestock depredations included: streams, roads, elevation, slope, vector ruggedness measure (VRM), grizzly bear population distribution by decade, and estimated annual grizzly bear density (Apps et al. 2004, Steyaert et al. 2011, Northrup et al. 2012, Bjornlie et al. 2014a, Bjornlie et al. 2014b, van Manen et al. 2016). I used the line density spatial analyst tool in ArcMap 10.3.1 (ESRI 2015) to calculate stream density within an approximately 8-km^2 area (1.6-km radius) representing the area used by a grizzly bear during a 24–48 hour period (Wilson et al. 2005). I used the same line density spatial analyst tool to calculate road density within an approximately 0.25-km^2 area (280-m radius), representing the approximately 500 meter distance from a road defined as secure grizzly bear habitat (U.S. Fish and Wildlife Service 2007, Schwartz et al. 2010). I used the slope spatial analyst tool in ArcMap 10.3.1 to calculate the percent slope for a digital elevation model (DEM) with a 30-m resolution. I used the benthic terrain modeler (BTM) toolbox in ArcMap 10.3.1 to calculate a vector ruggedness measure (VRM) from the DEM, which is a useful metric of terrain in mountain environments (Sappington et al. 2007, Wright et al. 2012).

Biotic grizzly bear habitat attributes previously found to be related to grizzly bear space use and livestock depredations included: distance to forest edge, vegetation cover classes, elk security cover, whitebark pine presence and annual production, army cutworm moth feeding site proportion of area, and the normalized difference vegetation index (NDVI; Gunther and Renkin 1990, Apps et al. 2004, Gunther et al. 2004, Stewart

2011, Steyaert et al. 2011, Costello et al. 2014). Vegetation cover classes for 2001, 2008, 2010, and 2012 were retrieved from the LANDFIRE program (LANDFIRE 2013) and were simplified based on grizzly bear ecology and space use to forest, grass/shrub, and riparian cover classes. Elk security cover was defined as areas with ≥40% forest canopy cover in patch sizes ≥ 26 ha (Crane et al. 2016). I used a map of WBP distribution in the GYE produced by the Greater Yellowstone Coordinating Committee (GYCC) Whitebark Pine Subcommittee in 2010 to quantify the proportion of WBP in and around allotments during the study period (GYCC 2011, Macfarlane et al. 2013). Along with WBP presence, I included the annual median number of cones produced per tree in the GYE adjusted for WBP tree mortality provided by the Interagency Grizzly Bear Study Team to quantify annual variation in WBP cone production and to account for the increase in tree mortality due to mountain pine beetle outbreaks after the early 2000s (Macfarlane et al. 2013, Interagency Grizzly Bear Study Team 2016). Although grizzly bear use of over-wintered WBP seeds in the spring has been documented, most use of WBP seeds occurs in the late summer and fall on the current year’s WBP cone crop (Costello et al. 2014). Therefore, I used the current year median WBP cone production adjusted for mortality from 1992–2014 to account for annual WBP seed availability and grizzly bear use.

Because army cutworm moth sites are limited to the southeastern portion of the ecosystem, I calculated the portion of the greater landscape around allotments that had moth sites instead of simply measuring the distance from each allotment to the nearest moth site. I used the most current documented army cutworm moth sites to calculate moth site proportions (M. Haroldson, Interagency Grizzly Bear Study Team, unpublished data). Over half of the moth sites had been present in the study area since the early 1990s but several were newly documented during the study period (Bjornlie 2015). However, it is possible that these new sites were used by grizzly bears for many years before they were identified by managers. Approximately 95% of the locations of male bears using moth sites annually are within 42 kilometers of moth site feeding locations in the GYE (M. Haroldson, Interagency Grizzly Bear Study Team, unpublished data). Therefore, moth site proportion for each 30- × 30-meter pixel within the GYE was calculated as the area of moth sites within an approximately 5,542-km^2 area (42-km radius) of the pixel using the focal statistics spatial analyst tool in ArcMap 10.3.1 (ESRI 2015).

The normalized difference vegetation index (NDVI) was used as a proxy for bear food availability throughout the year. Vegetative changes, as reflected in NDVI values, has been found to influence grizzly bear habitat selection and the NDVI can serve as a measure of primary productivity and the availability of vegetation used by bears including grasses, forbs, roots, and berry-producing shrubs in summer and fall (Gunther et al. 2004, Coughenour 2005, Maraj 2007, Steyaert et al. 2011). Therefore, vegetation NDVI in grazing allotments relative to the larger landscape may relate to bear space use and interactions between livestock and grizzly bears. While other indirect measures of grizzly bear food availability such as spring precipitation and winter severity could have been used, these metrics are related to seasonal food availability (spring/summer vegetation and spring ungulate carcasses) and therefore NDVI may be a better representation of season-long bear food availability and may correspond better to annual measures of depredation. NDVI information was available as a 14-day AVHRR satellite image composite at 1- × 1-km resolution for each year during the study period and from this, I extracted an annual, spatially-explicit NDVI value from mid-late July when primary production was generally the highest throughout the ecosystem.

Human impacts on grizzly bear space use due to large ungulate hunting on Forest Service lands were not considered because 90% of grizzly bear depredations on livestock occurred before October 15th, the average opening day of general rifle seasons in the GYE. Also, many allotments were no longer stocked with livestock by this date. It was assumed that archery and rifle hunting earlier in the fall were less intense and had minimal impacts on grizzly bear habitat use and livestock depredations on grazing allotments during the study period in the GYE.

Because of the large expanse and diverse topography of the GYE, it may be impossible for some regions to take on certain values of habitat features. For example, the southeastern region of the GYE is at an overall higher elevation than the western region, and grizzly bears in the western region could not select for elevations similar to those in the southeastern region because they do not exist. Therefore, region-specific habitat variables were z-transformed ($z = \frac{x-\bar{x}}{SD_x}$) to create a relative measure within a defined area. A 596-km^2 area (13.7-km radius moving window), the average size of a grizzly bear management subunit in the GYE, was used as the area from which to standardize each pixel for elevation and NDVI attributes (Interagency Grizzly Bear Study Team 1988). The focal statistics spatial analyst tool in ArcMap 10.3.1 was used to calculate the mean and standard deviation of elevation and NDVI within a 13.7 km radius of a pixel and these measures were then used in the z-transformations of both habitat attributes (ESRI 2015).

Because grizzly bear space use occurs at multiple spatial scales (Ciarniello et al. 2007), spatially-explicit habitat attributes were evaluated at two spatial extents. The first spatial extent was 8 km^2, representing the estimated area used by foraging grizzly bears during a 24–48 hour period and previously used to predict human conflicts (Wilson et al. 2005). The second spatial extent was 196 km^2, representing the average size of a female grizzly bear's home range in the GYE (Bjornlie et al. 2014b). I used a moving window approach with the focal statistics spatial analyst tool in ArcMap 10.3.1 to calculate an average value for each 30- × 30-meter resolution pixel within an 8-km^2 area (1,600-m radius) and within an 196-km^2 area (7,900-m radius) for: stream density, road density, relative elevation, percent slope, VRM, distance to grizzly bear range edge, distance to forest edge, moth site proportion, and relative NDVI (1- x 1-km resolution pixels; ESRI 2015). Pixels of vegetation cover layers including forest, grass/shrub, riparian, and WBP were classified as 1 (present) or 0 (absent) and I used the same moving window approach to get the proportion of cover for each 30- × 30-meter resolution pixel at both spatial extents. I then used the zonal statistics spatial analyst tool in ArcMap 10.3.1 to calculate the average value of each habitat attribute (at both spatial extents) within each allotment polygon (ESRI 2015). The result was an average grizzly bear habitat attribute value for every allotment and year at both spatial extents. Because the spatial resolution of the grizzly bear density index was 14- × 14-km (196-km^2 area), I used a weighted average of the proportion of cells in an allotment and the cell values to calculate average annual grizzly bear density index per allotment only at the home range scale.

By using a moving window approach, the adjacent landscape within 1.6 km and 7.9 km of an allotment was incorporated into the average habitat attributes of those allotments. That is, if a depredation occurred near the boundary of an allotment, the greater landscape adjacent to the allotment would be considered when describing that allotment's habitat attributes. Moth site proportions for each 30- × 30-meter pixel represented moth sites within 42 km of that pixel. Therefore, pixels included in the moving windows around an allotment represented moth sites present at much further distances from the allotment than 1.6 and 7.9 km. This was done to account for the potential use of moth sites away (up to 42 km) from a grizzly bear's usual daily activity area or home range in which grazing allotments were located (Bjornlie 2015).

<u>Livestock Depredation</u>. Grizzly bear-livestock conflict information was provided by the IGBST from their conflict database that spans 1992–present. Livestock depredations included livestock that were killed or injured by grizzly bears. Because the magnitude of depredation events has implications for grizzly bear conservation (where bears are often removed from the population after several depredation events) and for the degree of livestock losses, I recorded the count of depredation events on an allotment each year rather than simply whether or not an allotment experienced conflict in a given year. One depredation event was defined as livestock killed or injured in the same day in the same location. Because several livestock can be killed or injured in a depredation event, total depredated animals was also calculated and represented the number of

individuals killed or injured. Depredations were pooled based on year and allotment, resulting in a count of depredation events and total depredated animals each year for each allotment. Grizzly bear management removals due to livestock depredation was also provided by the IGBST from their conflict database from 1992–2014. Management removals were attributed to allotments and the number of days that livestock were grazing an allotment between a removal and the next livestock depredation was calculated.

The depredation information provided by the IGBST conflict database is likely a conservative estimate of grizzly bear-livestock conflicts on grazing allotments because only documented, confirmed cases of livestock depredation by grizzly bears are included. It is likely that more depredations by grizzly bears on grazing allotments are undiscovered, unreported, or unconfirmed. Depredations were rarely attributed to individual grizzly bears due to a low likelihood of observing depredations and therefore unique bear identification was not recorded.

Approximately 50 livestock depredation events (~5% of all livestock depredation events in the GYE during 1992–2014) were attributed to allotments that were recorded as not being stocked with livestock. Such a discrepancy could be due to a poor estimation in the location in the depredation, livestock trailing through an otherwise vacant allotment, or stray animals. The 50 inconsistent depredation events were excluded from analysis.

Because depredation has been shown to be a learned behavior and depredation of livestock by large carnivores in previous years may influence the likelihood and intensity of subsequent depredations, I created an attribute representing whether or not allotments had experienced recurring conflicts (Karlsson and Johansson 2010, DeCesare et al. 2016, Morehouse et al. 2016). An allotment with a recurring conflict was one in which livestock depredation by grizzly bears occurred during three or more years of the last five-year period (GYA Grizzly Bear Habitat Modeling Team 2016).

Objective 2: Livestock Depredation by Grizzly Bears

Data Analysis. An examination of livestock stocking, grizzly bear habitat, and depredations on grazing allotments during 1992–2014 in the GYE shows some patterns and dynamics of the ecosystem's ecology. Although variations in livestock stocking and grizzly bear habitat attributes were likely influenced by various factors such as climate, topography, ecological processes, agency administration, and management, such variations may be important in explaining the depredation patterns observed. Differences in livestock stocking, grizzly bear habitat, or a combination of these factors were hypothesized to be related to depredation of livestock on USFS lands during the study period and Objective 2 aimed to identify such factors and their effects.

My analysis included those USFS and NPS grazing allotments within the DMA from 1992–2014 that were stocked, did not stock only bulls and/or horses, and were inside of grizzly bear distribution, including outlier grizzly bear observation locations. In all, 254 allotments had at least one year that met these criteria during the study period and were included in analysis. Year was used as the time interval for all measures because livestock stocking characteristics on an allotment could change dramatically from year to year (e.g. drought years where stocking is much reduced to protect resources, changes in term grazing permits). Because the magnitude of depredations on allotments was of interest, the response variable during analysis was the count of livestock depredation events per allotment per year.

Generalized linear models (GLMs), which are extensions of traditional regression models, are commonly used to evaluate the relationships of non-normal responses and explanatory variables (Coxe et al. 2009). Based on the nature of the response variable (count of depredations), a Poisson or negative binomial distribution function was most appropriate for modeling (Coxe et al. 2009, Zuur et al. 2009).

Poisson family distribution functions assume that the variance (σ^2) of the response is equal to the mean (μ) of the response. However, this assumption is often violated when using ecological count data where the variance is larger than the mean ($\sigma^2 > \mu$), termed overdispersion (Coxe et al. 2009, Zuur et al. 2009). The negative binomial distribution function includes a dispersion parameter in the variance of the response, which can account for overdispersion while modeling and therefore is more suited for analyzing count data over Poisson when overdispersion is present. Because many allotments had zero depredations and there were presumed correlations among observations within allotments, overdispersion in depredation event counts was likely present (Zuur et al. 2009). To test for overdispersion, I compared a GLMM including all potential explanatory variables and allotment ID as a random intercept with a Poisson family distribution (natural log link function) to the same model with a negative binomial distribution (natural log link function) using $\mathrm{AIC_c}$ model selection in R (Kéry and Royle 2015, R Core Team 2016). The negative binomial distribution model was >2 $\Delta\mathrm{AIC_c}$

lower than the Poisson model, indicating greater support for the negative binomial model and that overdispersion in depredation event counts was likely present. Also, the estimated dispersion parameter increased the variance, indicating overdispersion was present. Therefore I used a GLMM with a negative binomial distribution (natural log link function) for further modeling.

Zero inflation occurs when there are far more zeros in the response than what would be expected for a Poisson or negative binomial distribution and can lead to biases in estimated parameters and standard errors (Coxe et al. 2009, Zuur et al. 2009). While there were many zero depredation event counts, it was assumed that all zeros were true zeros. Structural zeros were excluded prior to analysis by excluding observations from non-stocked allotments, bull and/or horse-only allotments, and allotments outside of grizzly bear range because these allotments could never display a depredation count greater than 0. I also assumed that depredation counts were equally detected across allotments and years. However, it was likely that some depredations were not detected or documented, leading to false zeros. While false zeros from undocumented depredations were likely present but not accounted for, results of my analysis would produce underestimates of the effects of allotment characteristics on depredation counts, which would be preferred over Type I errors where estimates of important relationships are documented but are not actually present. With reasonable assumptions about the nature of the zero depredation event counts and the difficulties with parsing out types of zeros, I used a simpler negative binomial distribution model (natural log link function) instead of more complex zero-inflated or zero-altered negative binomial models for further analysis (Zuur et al. 2009).

Livestock stocking was not constant throughout the grazing season on some allotments. When livestock numbers or classes changed dramatically during the grazing season on an allotment (e.g., 500 yearlings from June 1–June 30 and 200 yearlings from July 1–August 31), I created multiple observations for that year, and these additional observations accounted for approximately 7 % of total observations. With these multiple observations, as well as the fact that measures were recorded for multiple years on the same allotments, I accounted for the lack of independence among the repeated measures and unbalanced numbers of observations within allotments by including allotment ID as a random intercept in a generalized linear mixed-model (GLMM) approach (Gillies et al. 2006, Bolker et al. 2009, Zuur et al. 2009). Potential temporal autocorrelation among annual depredation counts on allotments was accounted for by including recurring depredations as an explanatory variable in models. I fitted all GLMMs to the data using the statistical computing program R package “lme4” (Bates et al. 2015, R Core Team 2016). I plotted the estimates of the random effects for allotment ID for all 254 allotments in the analysis using the “lattice” package in R (Sarkar 2008, R Core Team 2016).

Multicollinearity among variables in a model will lead to inflation of the standard errors of model estimates and could lead to unstable models, described as situations where different sets of variables are chosen when modeled with similar but new information (Fieberg and Johnson 2015). Prior to model development, all potential livestock stocking and grizzly bear habitat variables were assessed for collinearity using the Spearman-rank correlation in R (Appendix C; R Core Team 2016). Because compositional variables sum to a constant or nearly so, my measures of proportion forest, grass/shrub, and riparian cover were correlated to one another (Fieberg and Johnson 2015). Based on common use of forest habitats by grizzly bears, I chose to include proportion of forest cover and exclude proportion of grass/shrub and riparian cover from further analysis. Riparian areas were approximated using the stream density metric. A significant correlation existed ($|r| > 0.7$) between the proportion of tree cover and elk security cover as well as between slope and terrain ruggedness. I chose to use the proportion of tree cover and terrain ruggedness and exclude elk security cover and slope from further analysis because tree cover and terrain ruggedness have been found to be related to grizzly bear habitat use and are used more commonly in other grizzly bear habitat studies.

Because all grizzly bear habitat attributes measured at the two spatial extents (8 km^2 or 196 km^2) were correlated to one another (Appendix C), the scale at which habitat variables were modeled was selected using Akaike information criterion adjusted for a small sample size (AIC_c) model selection in R (Burnham and Anderson 2002, R Core Team 2016). All AIC_c model selection methods were applied using the R package “AICcmodavg” (Mazerolle 2016, R Core Team 2016). For each habitat variable, two single-variable GLMMs with a negative binomial distribution and allotment ID as a random effect were fit to the response of depredation event counts at each spatial extent. For each habitat variable, the spatial extent in the model with the lowest AIC_c was considered to have more support in explaining variation in the response and was used for further modeling while the other spatial extent was removed from the analysis.

I hypothesized that the relationships between relative elevation and depredation event counts as well as between terrain ruggedness and depredation event counts would be non-linear where depredations increase with relative elevation and ruggedness to a point, then decreases. This hypothesis is based on the notion that grizzly bears select for relatively higher, rugged terrain within an area (Apps et al. 2004, Steyaert et al. 2011) but livestock are not present in these areas due to lack of quality forage and water (Roath and Krueger 1982). Similarly, I hypothesized that the relationship between proportion of forest cover and depredation event counts would be non-linear, where depredation counts would be higher at an intermediate amount of forest cover that had grizzly bear security cover but also open areas for bears and livestock to feed. I expected that depredation event counts would increase up to a certain grizzly bear density index value and then would level off when the addition of bears no longer greatly increased depredation events. Similarly, I hypothesized that the depredation event counts would increase up to a number of livestock then would level off where the addition of more animals does not greatly influence depredation events.

Hypothesized non-linear relationships between depredation event counts and explanatory variables were explored using generalized additive models (GAMs) with a Poisson distribution in the R package “mgcv” (Appendix D; Wood 2006). GAMs use smoothing parameters that allow for non-linear relationships between the response and explanatory variables and plot a smoother, or curve, showing the relationship (Zuur et al.

2009). If non-linear relationships were evident in the GAMs, such relationships were further explored by comparing full (all potential variables) GLMMs with linear, quadratic ($X + X^2$), and pseudo threshold (natural log (X); Dugger et al. 2005) terms for the explanatory variable of interest using AIC_c model selection in R (R Core Team 2016). The relationship term in the model with the lowest AIC_c was considered to have more support in explaining variation in the response and was used for further modeling.

Depredation Model Construction and Selection. To assess the relationships between grazing allotment characteristics and grizzly bear depredation, the explanatory variables of interest used in my candidate model set included: number of livestock, grazing season length, allotment size, livestock class, bull and/or horse presence (Y/N), recurring depredations (Y/N), stocked previous year (Y/N), spring grazing (Y/N), summer grazing (Y/N), fall grazing (Y/N), relative elevation, VRM, road density, stream density, relative NDVI, tree cover, distance to forest edge, WBP proportion available, annual median WBP cone production, and moth site proportion available. Allotment ID was included as a random effect and the effects were assumed to follow a normal distribution with a mean of zero (Gillies et al. 2006). Grazing seasons were included individually in order to better understand how grazing in each season was related to livestock depredations, especially for the summer season when grizzly bears are in hyperphagia and documented depredations are the highest. Year was not included as a fixed effect. While there was an increasing trend in depredation events across years, this trend was assumed to be at least partially explained by annual variables included in my models, such as grizzly bear density.

I developed a set of 27 *a priori* candidate models representing my hypotheses regarding the associations of livestock stocking attributes and grizzly bear habitat characteristics with livestock depredation event counts during 1992–2014 (Table 1 & 2). Livestock stocking and grizzly bear habitat attributes were modeled together in order to better understand how livestock management characteristics related to depredation counts when considering grizzly bear habitat and vice versa. A null (intercept only) model was included to assess the relative support for my hypothesized models. I included an interaction between livestock number and livestock class because the number of livestock stocked partially depended on the livestock class (i.e., ewe/lamb pairs can be stocked at much higher numbers than cow/calf pairs). In other words, my models allowed the relationship between livestock number and depredation event counts to differ across livestock classes (Appendix E). Based on the focus of my study and the current lack of understanding regarding relationships between depredations and public land livestock grazing, I included basic livestock stocking variables for nearly all the candidate models.

Table 1. Variables considered in competing candidate models to identify factors related to livestock depredation by grizzly bears on USFS and NPS grazing allotments in the Demographic Monitoring Area (DMA), 1992–2014.

Model variable	Description	Categorical or continuous
no. livestock	Number of livestock (or pairs) on an allotment	continuous
livestock class	Class of livestock on an allotment (cow/calf, yearling, mature cow, mixed cattle, or ewe/lamb)	categorical
season length	Number of months livestock were grazing an allotment	continuous
allotment size	Allotment area	continuous
bull/horse	Were bulls and/or horses present with other grazing livestock?	binary
spring	Were livestock grazing during the spring season of March 1–July 15?	binary
summer	Were livestock grazing during the summer season of July 16–Aug 31?	binary
fall	Were livestock grazing during the fall season of Sept 1–Nov 30?	binary
recurring depredation	Was an allotment experiencing livestock depredations in 3 or more of the last 5-year period?	binary
stocked previous year	Was an allotment stocked with livestock the previous year?	binary
stream density[a]	Average stream density in and around an allotment	continuous
elevation[a]	Average relative elevation and around an allotment	continuous
terrain ruggedness[a]	Average terrain ruggedness in and around an allotment	continuous
road density[a]	Average road density in and around an allotment	continuous
bear density[a]	Average grizzly density in and around an allotment	continuous
distance to bear range edge[a]	Average distance to grizzly bear population edge in and around an allotment	continuous
ndvi[a]	Average relative NDVI in and around an allotment	continuous
WBP presence[a]	Average proportion of whitebark pine tree presence in and around an allotment	continuous
WBP production	Annual median cone production per tree in the GYE	continuous
moth site presence[a]	Average proportion of army cutworm moth site presence in and around an allotment	continuous
tree cover[a]	Average proportion of forest cover in and around an allotment	continuous
distance to forest[a]	Average distance to forest edge in and around an allotment	continuous

[a] Average grizzly bear habitat variables in and around allotments were modeled at spatial extents representing a grizzly bear daily activity area (8 km^2) and an average annual female grizzly bear home range (196 km^2).

Table 2. Competing candidate models to identify factors related to livestock depredation by grizzly bears on USFS and NPS grazing allotments in the Demographic Monitoring Area (DMA) from 1992–2014.

Model	Model variables[a]
1	~ 1 [null model]
2	~ no. livestock × livestock class + season length + allotment size + bull/horse
3	~ no. livestock × livestock class + season length + allotment size + bull/horse + spring + summer + fall
4	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + stocked previous year
5	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation
6	~ no. livestock × livestock class + no. livestock × bull/horse + season length + allotment size + recurring depredation
7	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + summer × stream density
8	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + elevation + terrain ruggedness + road density
9	~ no. livestock × livestock class + no. livestock × bull/horse + season length + allotment size + recurring depredation + elevation + terrain ruggedness + road density
10	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + elevation + terrain ruggedness + road density + bear density
11	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + terrain ruggedness + stream density
12	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + terrain ruggedness + stream density + bear density
13	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + bear density + distance to bear range edge
14	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + ndvi + summer × stream density + bear density
15	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + ndvi + WBP presence + WBP production
16	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + ndvi + WBP presence + WBP production + bear density
17	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + summer + ndvi + WBP presence + WBP production
18	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + summer + ndvi + WBP presence + WBP production + bear density

[a] All models included a random intercept of allotment ID (1 \| Allotment ID), n=254

Table 2 Continued.

Model	Model variables[a]
19	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + WBP presence + WBP production + moth site presence
20	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + WBP presence + WBP production + moth site presence + bear density
21	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + ndvi + stream density + elevation + terrain ruggedness + road density + bear density
22	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + tree cover + distance to forest edge + elevation + terrain ruggedness + road density + bear density
23	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + tree cover + distance to forest edge + ndvi + WBP presence + WBP production + bear density
24	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + tree cover + distance to forest edge + bear density
25	~ no. livestock × livestock class + season length + allotment size + bull/horse + recurring depredation + tree cover + distance to forest edge
26	~ bear density + distance to bear range edge + elevation + terrain ruggedness + road density
27	~ ndvi + tree cover + distance to forest + WBP presence + WBP production + moth site presence + stream density

[a] All models included a random intercept of allotment ID (1 | Allotment ID), n=254

I used multimodel inference based on AIC_c to evaluate the relative support for my candidate models. Models that differed in AIC_c values by ≤2 from the best fit model were considered to have similar support and were considered parsimonious. In the case of model uncertainty, I used model averaging to obtain parameter estimates (Burnham and Anderson 2002). Standardized β-coefficients from the best model(s) were used compare the relative importance of each association between a variable and average depredation counts. Because effects of explanatory variables on the response are multiplicative when a log link function is used during modeling (Coxe et al. 2009), exponentiated standardized β-coefficients with 85% confidence intervals that did not overlap one were considered to be significant predictors of grizzly bear depredation counts on allotments.

As suggested by Arnold (2010), 85% confidence intervals were used so that the AIC model selection and parameter evaluation criteria were consistent. All $\mathrm{AIC_c}$ model selection and model averaging methods were applied using the R package “AICcmodavg” (Mazerolle 2016, R Core Team 2016).

As is often the case, managers are more interested in explaining ecological processes and mechanisms when management strategies are applied than in predicting outcomes based on given information (Fieberg and Johnson 2015). Poisson regression cannot directly assess the absolute fit of models or the proportion of variation in the response accounted for by the predictors, such as the squared multiple correlation R^2. Instead, only a measure of model fit relative to another model can be assessed (Coxe et al. 2009). Relative model fit was assessed by computing a pseudo-R^2 measure using the deviance, or poorness of model fit, of the top models(s) and the null model. The pseudo-R^2 measure of the proportional reduction in deviance by adding variables to the null model was calculated using (Coxe et al. 2009):

$$R_{deviance}^{2} = 1 - \frac{deviance\ (top\ model(s))}{deviance\ (null\ model)}$$

If there was more than one top model based on model selection criteria, the average deviance of the top models was used as the numerator in the calculation.

Results

Objective 1: Grazing Allotment Characteristics

Livestock Grazing. Livestock grazing information was collected for 316 allotments within the grizzly bear Demographic Monitoring Area from 1992–2014, including 36 on the Beaverhead-Deerlodge National Forest, 66 on the Bridger-Teton National Forest, 65 on the Caribou-Targhee National Forest, 76 on the Custer Gallatin National Forest, 68 on the Shoshone National Forest, and 5 in Grand Teton National Park. Of those 316 allotments, 295 were within grizzly bear distribution or documented outlier grizzly bear observation locations for at least part of the study period (Bjornlie et al. 2014a). Grazing allotments within study area varied in size, ranging from 2.25 ha to 44,240 ha with a median size of 2,684 ha (6,632 ac). Approximately one third of grazing allotments were inside the Yellowstone Grizzly Bear Recovery Zone (YGBRZ). As the Yellowstone grizzly bear population's distribution has expanded over the last several decades, the number of grazing allotments occupied by grizzly bears has increased from 48 in the 1970s to 295 in the 2000s, leading to more areas of potential livestock-bear conflicts (Figure 1).

Grazing allotments were stocked with cattle, sheep, horses, and combinations of these livestock types. Average livestock stocking per allotment differed across livestock classes and forests (Table 3, Appendix F). Approximately 70% of allotments throughout the ecosystem during 1992–2014 were stocked with cow/calf pairs, with most other allotments stocked with ewe/lamb pairs, yearling cattle, a mix of cow/calf and yearling cattle, or horses. A relatively few number of allotments were stocked with mature cows or bulls. Cow/calf pairs generally comprised two-thirds of stocked allotments on each forest but the proportion of other classes stocked varied by forest. Cow/calf pairs averaged approximately 300 animals per allotment and ewe/lamb pairs averaged approximately 1,100 animals per allotment when those livestock classes were stocked. Yearling cattle averaged approximately 250 animals per allotment when stocked. Mature cows, bulls, and horses, livestock classes that were generally stocked along with other classes in an allotment, averaged approximately 130, 8, and 26 animals, respectively, when stocked (Table 3).

Table 3. Livestock stocking per allotment (allot.) on all stocked USFS and NPS grazing allotments within the Demographic Monitoring Area (DMA) during 1992–2014.

Forest		Beaverhead-Deerlodge	Bridger-Teton	Caribou-Targhee	Custer Gallatin	Shoshone	Grand Teton NP	DMA-Wide
No. allots		36	66	65	76	68	5	316
Mean allot. size [ha] (SD)[a]		4,458 (5,649)	7,006 (9,131)	4,929 (4,211)	2,156 (2,265)	7272 (6,598)	1,300 (1,367)	4,947 (6,145)
Mean total no. livestock per allot. (SD)[a]		475 (572)	699 (840)	583 (431)	102 (132)	268 (267)	269 (132)	376 (521)
Mean no. cow/calf per allot. (SD)[a]		359 (520)	662 (709)	352 (361)	95 (85)	232 207)	568 (393)	307 (447)
Mean no. yearling per allot. (SD)[a]		241 (187)	326 (367)	444 (145)	109 (117)	215 (204)	290 (0)	249 (270)
Mean no. mature cow per allot (SD)[a]		112 (112)	86 (105)	-	66 (81)	223 (205)	-	128 (155)
Mean no. bull per allot. (SD)[a]		6 (5)	10 (8)	-	4 (3)	11 (10)	-	8 (7)
Mean no. ewe/lamb per allot. (SD)[a]		1,253 (160)	2,594 (1,253)	978 (198)	890 (383)	949 (258)	-	1,120 (570)
Mean no. horse per allot. (SD)[a]		13 (8)	12 (10)	1 (0)	38 (44)	32 (29)	33 (23)	26 (32)
% allots with cow/calves[b]	% allots with *only* cow/calves[b]	87 | 76	80 | 66	64 | 62	80 | 77	78 | 75	40 | 39	77 | 71
% allots with yearlings[b]	% allots with *only* yearlings[b]	13 | 4	20 | 5	3 | 1	7 | 3	13 | 10	10 | 10	11 | 5
% allots with mixed cattle[b]		9	13	2	3	3	0	5
% allots with mature cows[b]	% allots with *only* mature cows[b]	2 | 1	1 | <1	0 |0	2 | 1	2 | 1	0 | 0	1 | 1
% allots with bulls[b]	% allots with *only* bulls[b]	5 | 0	13 | 0	0 | 0	4 | <1	1 | 0	0 | 0	4 | <1
% allots with ewe/lambs[b]	% allots with *only* ewe/lambs[b]	10 | 10	4 | 4	35 | 35	1 | 1	5 | 5	0 | 0	10 |10
% allots with horses[b]	% allots with *only* horses[b]	12 | 0	29 | 12	1 | 0	18 | 14	14 | 3	51 | 51	16 | 7

[a] Mean no. livestock and standard deviations (SDs) represent stocked numbers of the livestock class indicated, even if stocked with other classes. Mean livestock #s and SDs were calculated only when the livestock class indicated was stocked. Mean and standard deviations (SD) represent the center and spread of livestock numbers from the population of all stocked allotments (with the specified livestock class) in the DMA in all years from 1992–2014.

[b] Represents the percentage of all stocked allotments in the defined area in every year from 1992–2014.

Total livestock stocked on grazing allotments in the GYE decreased during the study period (Figure 3). Total sheep numbers in 2014 were almost half of those in 1992 and cow/calf pair numbers also declined after 1992. However, livestock numbers per active allotment did not change substantially during the study period (Kruskal-Wallis Rank Sum Test, $P = 0.99$). Similarly, numbers of each livestock class per allotment did not change significantly during the study period (Kruskal-Wallis Rank Sum Test, $P > 0.05$). Therefore, decreases in total ecosystem-wide livestock numbers were caused by allotment non-use or closures rather than reductions in livestock numbers per allotment. The proportion of GYE allotments that were vacant or closed increased to approximately one-fifth of all allotments during 1992–2014 and closures occurred throughout the ecosystem (Figure 4). Throughout the GYE, approximately 20 allotments stocked with sheep closed during the study period and most closures occurred in the 1990s and early 2000s. Several allotments converted stocking from sheep to cattle in the mid-late 1990s.

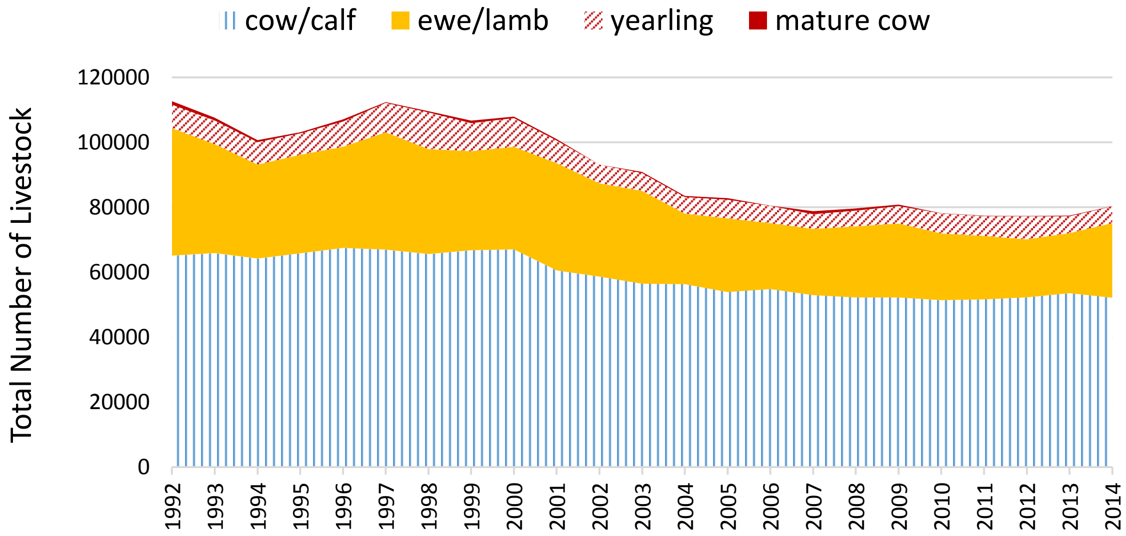

Figure 3. Total livestock numbers stocked on USFS and NPS grazing allotments in the Demographic Monitoring Area (DMA), 1992–2014. Horses and bulls are not shown. Data source: USFS and NPS.

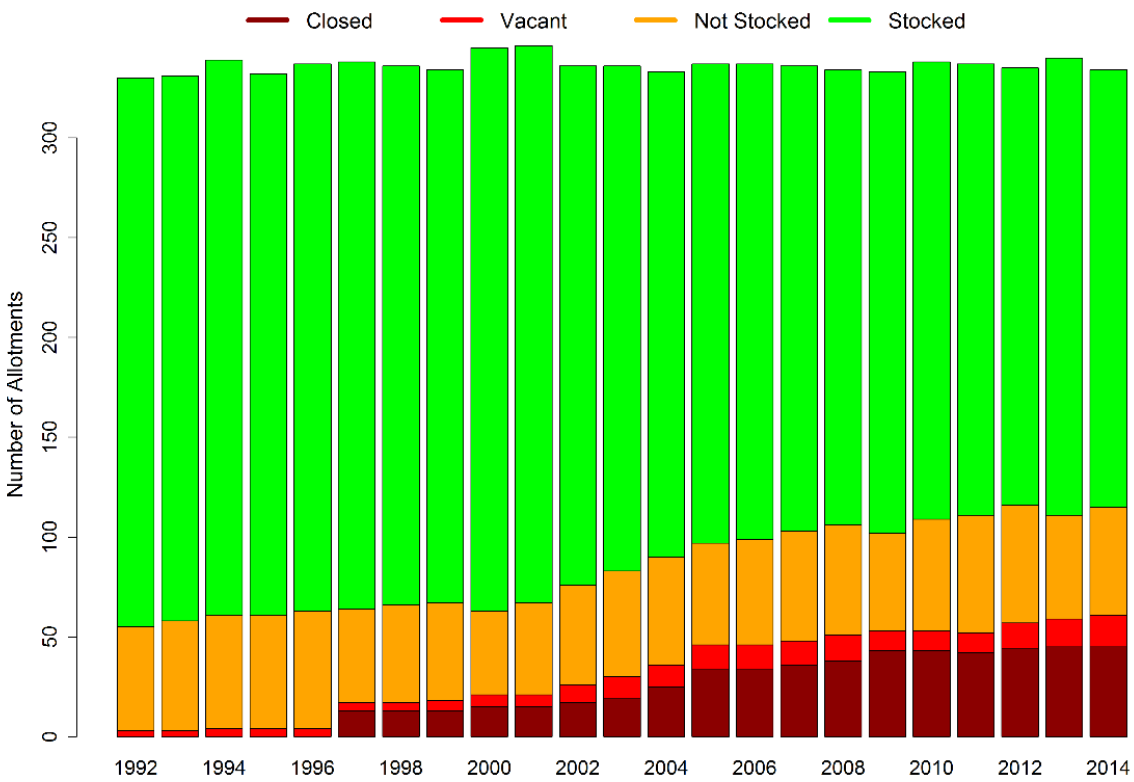

Figure 4. Livestock stocking of all USFS and NPS grazing allotments in the Demographic Monitoring Area (DMA), 1992–2014. Data source: USFS and NPS.

Livestock were generally stocked on grazing allotments in the spring (79% of allotments), summer (93% of allotments), and fall seasons (84% of allotments). Animals were stocked almost the entire summer season and were stocked for smaller proportions of the spring and fall seasons. Summer grazing on allotments in the GYE was common likely due to high quality forage availability and mild weather conditions in mountain rangelands during this time. Winter grazing was minimal and generally consisted of relatively low numbers of horses or mature cows. The average number of days livestock grazed annually varied over the study period but was similar across years (Kruskal-Wallis Rank Sum Test, *P* = 0.1).

Grizzly Bear Habitat. Habitat features that influence grizzly bear space use also showed spatial and temporal patterns (Table 4). The annual grizzly bear density index during the study period was generally highest in Grand Teton National Park, Shoshone, and Bridger-Teton National Forest allotments and lower in Caribou-Targhee, Custer Gallatin, and Beaverhead-Deerlodge National Forest allotments. However, grizzly bear densities in some allotments changed substantially over the study period. For example, an allotment in the Upper Green River area of the Bridger-Teton National Forest Pinedale District experienced an increase in the grizzly bear density index from approximately 2 in 1992 to nearly 30 in 2014. Other regions of the GYE also experienced large increases in grizzly bear density, including allotments in the Ashton/Island Park district of the Caribou-Targhee National Forest where the density index increased from <1 in 1992 to almost 13 in 2014. Generally, grizzly bear density increased for allotments in the GYE during 1992–2014. While there was little evidence of a relationship between the grizzly bear density index and number of livestock on allotments over the study period (Spearman-rank correlation, $r = -0.05$), there was some evidence that when grizzly bears were present, the grizzly bear density index was lower on allotments that were stocked compared to allotments that were not stocked (density > 0; repeated measures ANOVA, $F_{(1,5452)} = 29.1$, $P < 0.001$).

In general, annual median WBP cone production was relatively low in the mid-2000s following the mountain pine beetle outbreaks (Figure 5). However, WBP cone production was variable throughout the entire study period and several years prior to the outbreaks also had low annual cone production.

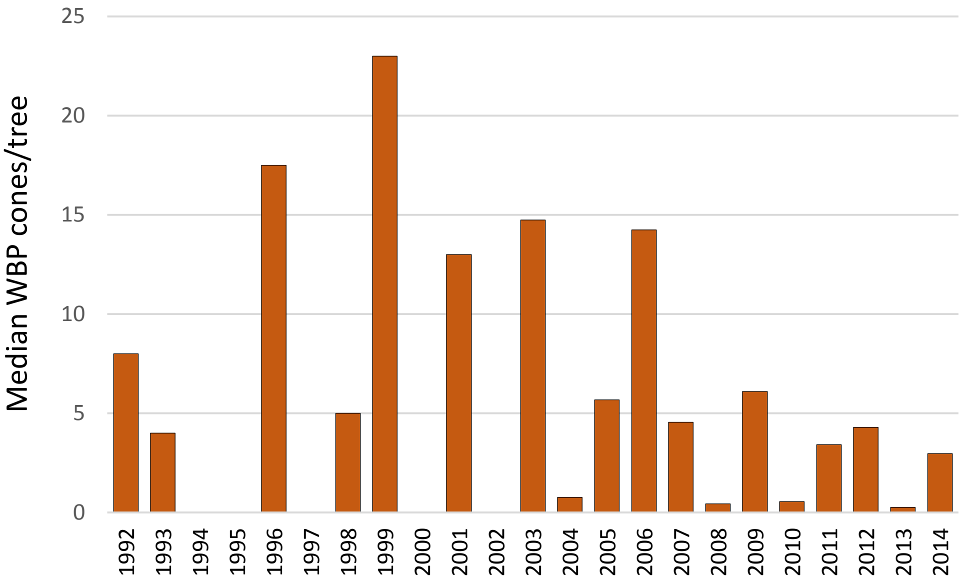

Figure 5. Annual median whitebark pine (WBP) cone production per tree adjusted for WBP tree mortality in the GYE, 1992–2014 (Interagency Grizzly Bear Study Team 2016). Years 1994, 1995, 1997, 2000, and 2002 had median cone production per tree equal to 0.

Approximately 30 army cutworm moth site complexes were located to the east and southeast of Yellowstone National Park on the Shoshone and Bridger-Teton national forests. Few moth sites were located within grazing allotments, but approximately 85 allotments were within 42 km of moth sites, the distance traveled by male grizzly bears known to use moth sites. Overall, grazing allotments throughout the GYE during 1992–2014 had variable habitat features which may have influenced grizzly bear space use and depredation on livestock (Table 4).

Table 4. Grizzly bear habitat attributes on 316 USFS and NPS grazing allotments in the Demographic Monitoring Area (DMA) during 1992–2014. Average attribute values represent habitat only within grazing allotments and not within grizzly bear daily (8 km^2) or home range activity (196 km^2) areas around the allotments.

Mean grizzly bear habitat attributes (SD)	Beaverhead-Deerlodge NF	Bridger-Teton NF	Caribou-Targhee NF	Custer Gallatin NF	Shoshone NF	Grand Teton NP	DMA-Wide
Number of allotments	36	66	65	76	68	5	316
Bear density (#/ 196km^2)[a]	1.44 (2.24)	6.53 (8.01)	2.73 (3.23)	1.85 (3.00)	8.96 (7.20)	14.17 (3.96)	4.67 (6.28)
Distance to bear range edge (km)[a]	18.67 (12.85)	22.46 (18.64)	21.41 (16.06)	18.36 (14.55)	37.34 (23.06)	26.68 (9.90)	24.16 (19.11)
WBP proportion[b,c]	0.12 (0.15)	0.11 (0.13)	0.01 (0.03)	0.10 (0.16)	0.19 (0.22)	<0.001 (<0.001)	0.11 (0.16)
Moth site proportion[b,d]	0 (0)	0.0002 (0.0006)	0 (0)	0 (0)	0.01 (0.01)	<0.001 (<0.001)	0.003 (0.008)
Forest cover proportion[a,c]	0.58 (0.20)	0.53 (0.23)	0.71 (0.20)	0.69 (0.22)	0.55 (0.19)	0.23 (0.25)	0.61 (0.23)
Elk security cover proportion[a,c]	0.29 (0.17)	0.25 (0.17)	0.26 (0.16)	0.36 (0.21)	0.24 (0.15)	0.07 (0.12)	0.28 (0.18)
Relative NDVI[a,e]	0.34 (0.51)	0.14 (0.59)	0.41 (0.41)	0.35 (0.57)	0.30 (0.48)	0.08 (0.42)	0.31 (0.53)
Stream density (km stream/km^2)[b]	0.42 (0.31)	0.60 (0.27)	0.48 (0.26)	0.54 (0.31)	0.55 (0.28)	1.07 (0.70)	0.54 (0.31)
Road density (km road/km^2)[b]	0.41 (0.38)	0.42 (0.46)	0.80 (0.52)	0.79 (0.86)	0.29 (0.28)	1.04 (0.58)	0.57 (0.60)
Relative elevation[b,e]	0.28 (0.53)	-0.23 (0.60)	0.07 (0.53)	-0.16 (0.56)	0.13 (0.57)	-0.76 (0.16)	-0.02 (0.59)
Slope (percent)[b]	28.60 (9.20)	22.33 (9.56)	20.02 (12.13)	31.27 (11.97)	30.76 (9.72)	5.57 (5.75)	26.27 (11.91)
Terrain ruggedness (index of terrain variation from 0 to 1)[b,f]	0.005 (0.002)	0.004 (0.003)	0.004 (0.003)	0.006 (0.003)	0.007 (0.003)	0.0008 (0.001)	0.005 (0.003)

[a] Temporally-explicit grizzly bear habitat attribute means and standard deviations (SD) represent the center and spread of the habitat values from the population of all allotments (stocked or not) in the specified area in all years from 1992–2014.

[b] Static grizzly bear habitat attribute means and standard deviations (SD) represent the center and spread of the habitat values from the population of all allotments in the specified area.

[c] Proportion of specified cover type within allotments

[d] Proportion of landscape within a 5,542 km^2 area (42 km radius) of an allotment delineated as moth sites

[e] Relative measures (elevation and NDVI) > 1 indicate that an allotment had a relatively high value compared to the greater 596.36 km^2 area on average and vice versa for relative measures <1.

[f] Terrain ruggedness varied from 0.000025 to 0.014 on allotments in the DMA

Livestock Depredation. Total ecosystem-wide livestock depredations by grizzly bears increased during 1992–2014 (Figure 6). The majority of depredations during the study period occurred on the Bridger-Teton National Forest and a number of depredations also occurred on the Shoshone National Forest. Other forests experienced depredations but events were variable over the study period. While the mean (SD) number of depredation events per depredated allotment increased from 3.5 (0.71) events in 1992 to 4.3 (5.07) events in 2014, the number of allotments experiencing depredation also increased (2 in 1992 to 21 in 2014).

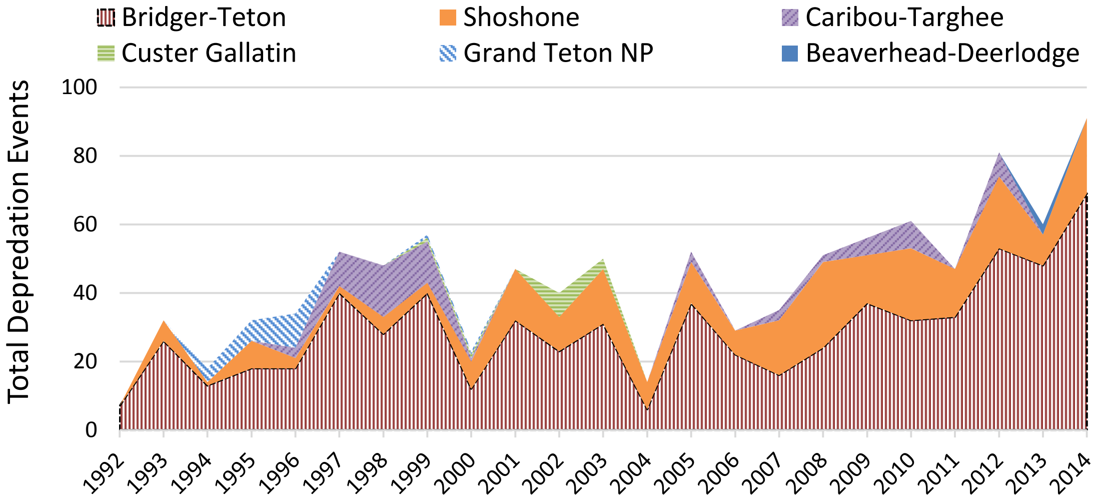

Figure 6. Total livestock depredation events attributed to grizzly bears on USFS and NPS allotments within the Demographic Monitoring Area (DMA), 1992–2014. The few documented depredation events in 2004 likely represents a year of poor depredation detection or poor recording efforts. Data source: IGBST.

Depredations differed by livestock class (Figure 7). Cow/calf pair allotments experienced the majority of depredation events during the study period (71% of all events) and sheep allotments experienced numerous depredations (18% of all events). On average (SD), 2.9 (2.7) events occurred and 3.0 (2.7) animals were killed in cow/calf allotments experiencing depredation in a given year while 6.4 (6.8) events occurred and 19.1 (19.4) animals were killed in sheep allotments experiencing conflict in a given year. Mixed cattle allotments also experienced depredation events (3% of all events) but the livestock killed in these mixed allotments were generally cow/calf pairs. A mean of 4.1 (5.6) events occurred and 4.1 (5.6) animals were killed in allotments stocked with mixed cattle classes in a given year. Fewer depredations occurred on yearling or mature cow allotments, accounting for 6% and 1% of all depredation events during the study period, respectively. If a yearling or mature cow allotment did experience depredation in a given year, a mean of 2.3 (2.2) and 1.5 (0.7) events occurred, respectively, and 2.5 (2.5) and 1.5 (0.7) animals were killed, respectively. No depredations on bulls or horses by grizzly bears were documented during 1992–2014.

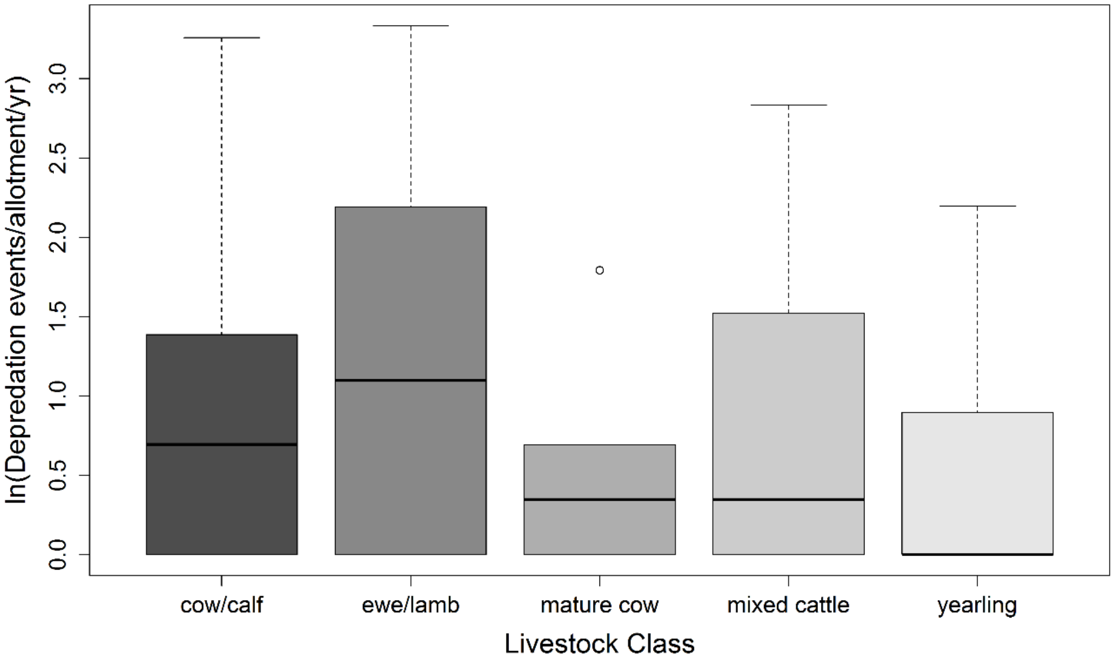

Figure 7. Livestock depredation events by livestock class on USFS and NPS grazing allotments experiencing depredations in the Demographic Monitoring Area (DMA), 1992–2014. Depredation event numbers have been natural log transformed to improve interpretation. Bull and horse allotments did not experience depredations during the study period and are not shown.

As the Yellowstone grizzly bear population’s distribution expanded during the study period, grazing allotments in previously unoccupied areas experienced livestock depredations. Over 50% of livestock depredation events in the 1990s occurred outside of the YGBRZ while nearly 75% of such events in the 2000s occurred outside of the YGBRZ. Of all the grazing allotments in the study area that experienced livestock depredation by grizzly bears in the 1990s, 93% were located in grizzly bear range not previously occupied in the 1970s and 1980s. Similarly, 98% of all depredation events in the 1990s occurred in this new grizzly bear range. Of all depredated allotments in the 2000s, 28% were located in grizzly bear range not occupied in the previous decade, accounting for 35% of all depredation events during this time period. However, nearly all depredations in the 2000s occurred in the combined 1990s and 2000s new grizzly bear range not previously occupied in the 1970s and 1980s.

There were 26 management removals of grizzly bears due to livestock depredation on public land grazing allotments documented during 1992–2014. Of those, 21 allotments had recorded depredations following a removal. The length of time until the next depredation varied, ranging from 1 grazing day to 105 grazing days, with an average of 31 livestock grazing days between a management removal and the next depredation. Of all management removals due to livestock depredation recorded over the study period, 80% occurred during 2008–2014, averaging 3 removals per year during this time. For comparison, total known and probable grizzly bear mortalities during 2008–2014 averaged 40 per year, with many mortalities attributed to site conflicts and ungulate hunting incidents (Haroldson and Frey 2014).

Characteristics of depredated allotments. Variation in livestock stocking and grizzly bear habitat attributes between depredated and non-depredated grazing allotments in the GYE during 1992–2014 was evident (Table 5). Allotments that experienced at least one depredation over the study period were, on average, more than twice the size of non-depredated allotments and had gentler terrain, more streams, and fewer roads in and around the allotments. Also, these depredated allotments had a greater presence of whitebark pine and moth sites within and around the allotment compared to non-depredated allotments. Allotments depredated in a given year were grazed for a shorter period of time than non-depredated allotments but livestock numbers did not differ after accounting for variation between allotments. Depredated allotments had more than three times the annual grizzly bear density index, on average, of non-depredated allotments. Also, these allotments experiencing depredations in a given year had less elk security cover and relatively higher NDVI within and around the allotment than non-depredated allotments after accounting for variation between allotments.

Table 5. Allotment attributes for depredated and non-depredated USFS and NPS grazing allotments in the Demographic Monitoring Area (DMA), during 1992–2014. Temporally explicit values were averaged across all years, 1992–2014. Allotment attributes are from 254 stocked allotments (excluding bull and horse-only allotments) within grizzly bear distribution. Spatial extents for each habitat variable represent values around allotments at the grizzly bear daily activity extent (8 km^2) and average annual female grizzly bear home range extent (HR; 196 km^2).

Grizzly bear habitat attribute	0 depredation events: Mean (SD)	>0 depredation events: Mean (SD)	t-statistic$_{(df)}$	P-value
Constant habitat attributes[a]				
Allotment size (ha)	3943 (4952)	8962 (8671)	-4.54$_{(85)}$	<0.001
WBP proportion$_{HR}$	0.11 (0.12)	0.16 (0.16)	-2.70$_{(98)}$	0.008
Moth site proportion$_{HR}$	0.003 (0.008)	0.006 (0.009)	-2.92$_{(108)}$	0.004
Stream density$_{HR}$ (km stream/km^2)	0.48 (0.17)	0.57 (0.16)	-4.01$_{(129)}$	<0.001
Road density$_{HR}$ (km road/km^2)	0.66 (0.40)	0.46 (0.23)	5.12$_{(213)}$	<0.001
Relative elevation$_{HR}$	0.006 (0.29)	0.002 (0.28)	0.10$_{(125)}$	0.920
Slope$_{daily}$ (percent)	28.06 (11.83)	23.80 (10.01)	2.87$_{(143)}$	0.005
Terrain ruggedness$_{daily}$ (index of terrain variation from 0 to 1)	0.006 (0.003)	0.005 (0.003)	2.47$_{(141)}$	0.015
Distance to 1990s grizzly bear range edge$_{HR}$ (km)[b]	18.34 (18.48)	14.88 (11.88)	1.24$_{(56)}$	0.221
Distance to 2000s grizzly bear range edge$_{HR}$ (km)[b]	23.57 (16.45)	27.26 (14.19)	-1.66$_{(115)}$	0.100
Distance to forest edge$_{daily}$ (m)	135.66 (74.50)	144.31 (90.52)	-0.71$_{(104)}$	0.480
Grizzly bear habitat attribute	0 depredation events: Mean (SD)[c]	>0 depredation events: Mean (SD)[c]	F-statistic (df num, df denom)	P-value
Temporal habitat attributes[d]				
Livestock number[e]	364 (475)	1034 (901)	0.23$_{(1,4035)}$	0.629
Grazing season length (months)[e]	2.78 (1.15)	2.15 (1.25)	10.40$_{(1,4115)}$	0.001
Bear density (#/ 196 km^2)[e]	4.27 (5.54)	14.66 (7.52)	42.14$_{(1,4041)}$	<0.001
Forest cover proportion$_{daily}$[f]	0.60 (0.19)	0.53 (0.19)	1.92$_{(1,4023)}$	0.165
Elk security cover proportion$_{daily}$[f]	0.28 (0.16)	0.27 (0.14)	6.75$_{(1,4030)}$	0.009
Relative NDVI$_{HR}$	0.18 (0.26)	0.21 (0.19)	7.17$_{(1,4056)}$	0.007

[a] Allotments with at least one depredation during 1992–2014 (n=60) were compared to allotments with no depredations during the study period (n=185) using a two-sided t-test accounting for unequal variances.

[b] Depredated allotments in the 1990s (n=27) versus no depredations during this decade (n=134) and depredated allotments in the 2000s (n=63) versus no depredations during this decade (n=180).

[c] Temporally-explicit attribute means and standard deviations (SD) represent the center and spread of the habitat values from the populations of all allotments in all years from 1992–2014 with and without depredations.

[d] Temporally-explicit attributes were compared using a repeated measures ANOVA with allotment ID as a random effect.

[e] The attribute was log-transformed prior to modeling to reduce violations in model assumptions

[f] Temporally-explicit proportions (forest and elk security cover) were logit transformed prior to modeling to un-bound the values

Objective 2: Livestock Depredation by Grizzly Bears

Data analysis. The relative support of the two habitat attribute spatial extents using AIC_c model selection indicated that the scale at which grizzly bear habitat attributes best explained variation in average depredation events differed across attributes (Appendix B). Terrain ruggedness, proportion of forest cover, and distance to forest edge best explained variation in average depredation events at the grizzly bear daily activity spatial extent ($8\ km^2$), while relative elevation, road density, stream density, distance to grizzly bear range edge, NDVI, proportion of WBP, and proportion of moth sites best explained variation in average depredation events at the average female grizzly bear annual home range spatial extent ($196\ km^2$). The most supported spatial extents were used in candidate model set construction and selection (Table 2).

Preliminary response screenings suggested non-linear relationships between depredation counts and relative elevation and proportion forest cover (Appendix D). However, when linear, quadratic ($X + X^2$), and pseudo threshold (natural log(X)) terms for relative elevation and forest cover were included in full GLMM model sets with all other potential variables considered, a linear relationship for both relative elevation and proportion forest cover best explained variation in the response (lowest AIC_c). Only linear terms were considered in further candidate model set construction and selection.

Depredation model construction and selection. Of the 27 competing models regarding the relationship between livestock depredation by grizzly bears and grazing allotment characteristics in the GYE during 1992–2014, five models were within 2 AIC_c

units of the top model and were considered parsimonious (Table 6, Appendix G). All five top models were at least 237.9 AIC_c units lower than the null model, indicating that all had considerable support. All top models contained the interaction between livestock number and livestock class, grazing season length, allotment size, bull/horse presence, recurring depredations, and grizzly bear density. Of the top 5 models, 3 models contained relative elevation, terrain ruggedness, road density, and NDVI, 2 models contained proportion forest cover, distance to forest edge, proportion of WBP, and WBP production, and 1 model contained stream density and summer grazing. None of the top models contained the distance to grizzly bear range edge or the proportion of army cutworm moth sites. Exponentiated model-averaged standardized estimates and associated 85% confidence intervals that did not overlap one were considered to have a significant association with grizzly bear depredation counts on allotments (Table 7). Based on these criteria, livestock number, allotment size, mixed cattle classes, the presence of bulls and/or horses, summer grazing, terrain ruggedness, road density, grizzly bear density, distance to forest edge, relative NDVI, and WBP presence had a significant association with depredation counts. Of these predictors, livestock number, allotment size, and grizzly bear density had the largest relative effects on depredation event counts.

Table 6. Akaike Information Criteria (AIC_c) values for the 5 competing top models and the null model to identify factors related to livestock depredation by grizzly bears on USFS and NPS grazing allotments in the Demographic Monitoring Area (DMA) from 1992–2014 at two spatial extents.

Model[a]	Variables[b]	K[c]	AIC_c	ΔAIC_c	AIC_c w_i	Cum AIC_c w_i	Log likelihood
22	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + tree cover$_{\text{daily}}$ + distance to forest edge$_{\text{daily}}$ + elevation$_{\text{HR}}$ + terrain ruggedness$_{\text{daily}}$ + road density$_{\text{HR}}$ + bear density	22	2576.67	0	0.22	0.22	-1266.21
21	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + ndvi$_{\text{HR}}$ + stream density$_{\text{HR}}$ + elevation$_{\text{HR}}$ + terrain ruggedness$_{\text{daily}}$ + road density$_{\text{HR}}$ + bear density	22	2576.70	0.04	0.22	0.44	-1266.23
10	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + elevation$_{\text{HR}}$ + terrain ruggedness$_{\text{daily}}$ + road density$_{\text{HR}}$ + bear density	20	2577.00	0.33	0.19	0.63	-1268.40
23	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + tree cover$_{\text{daily}}$ + distance to forest edge$_{\text{daily}}$ + ndvi$_{\text{HR}}$ + WBP presence$_{\text{HR}}$ + WBP production + bear density	22	2577.40	0.73	0.15	0.79	-1266.58
18	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + summer + ndvi$_{\text{HR}}$ + WBP presence$_{\text{HR}}$ + WBP production + bear density	21	2577.75	1.08	0.13	0.92	-1267.77
1	~ 1 [null model]	3	2815.65	239.0	0	-	-1404.82

[a] All models were a generalized linear mixed model with a negative binomial distribution and a random intercept of allotment ID (1 | Allotment ID)

[b] Spatial extents for each habitat variable represent grizzly bear daily activity area (8 km^2) and average annual female grizzly bear home range (HR; 196 km^2)

[c] Number of estimated model parameters

Table 7. Model-averaged standardized estimates of the five parsimonious models to identify factors related to livestock depredation by grizzly bears on USFS and NPS grazing allotments in the Demographic Monitoring Area (DMA) at two spatial extents. The estimates and 85% confidence intervals were exponentiated ($exp^{\widehat{\beta}_x}$) to infer multiplicative effects of variables on depredation event counts. Spatial extents for each habitat variable represent grizzly bear daily activity area (8 km^2) and average annual female grizzly bear home range (HR; 196 km^2).

Model-averaged coefficients	Est	Std. Error	Exp $^{(Est)}$	Exp (85% Confidence Interval)	
				Lower	Upper
Livestock number[a]	1.15	0.19	3.16	2.41	4.15
Grazing season length	0.05	0.13	1.05	0.88	1.26
Allotment size[a]	0.56	0.16	1.75	1.40	2.20
Ewe/lamb (baseline = cow/calf)	-0.37	0.67	0.69	0.27	1.81
Mature cow (baseline = cow/calf)	0.25	0.70	1.28	0.47	3.50
Yearling (baseline = cow/calf)	0.46	0.43	1.59	0.86	2.94
Mixed cattle[a] (baseline = cow/calf)	-1.18	0.55	0.31	0.14	0.68
Bull/horse present[a] (baseline = No)	-0.71	0.37	0.49	0.29	0.84
Recurring depredations (baseline = No)	0.008	0.20	1.01	0.75	1.35
Livestock number x ewe/lamb (baseline = cow/calf)	-0.10	0.32	0.91	0.57	1.45
Livestock number x mature cow (baseline = cow/calf)	-2.44	2.31	0.09	0.003	2.42
Livestock number x yearling (baseline = cow/calf)	-0.96	0.92	0.38	0.10	1.45
Livestock number x mixed cattle (baseline = cow/calf)	-0.12	0.39	0.89	0.50	1.56
Summer * (baseline = No)	0.61	0.29	1.84	1.20	2.80
Relative elevation$_{HR}$	0.04	0.19	1.04	0.79	1.37
Terrain ruggedness$_{daily}$[a]	-0.57	0.25	0.56	0.40	0.81
Road density$_{HR}$[a]	-0.89	0.28	0.41	0.28	0.62
Bear density[a]	1.13	0.10	3.08	2.68	3.55
Stream density$_{HR}$	0.09	0.19	1.09	0.83	1.43
Tree cover$_{daily}$	0.16	0.29	1.17	0.77	1.78
Distance to forest edge$_{daily}$[a]	0.39	0.18	1.48	1.14	1.91
Relative NDVI$_{HR}$[a]	0.33	0.16	1.40	1.11	1.75
WBP presence$_{HR}$[a]	0.30	0.15	1.35	1.09	1.66
WBP production	0.06	0.06	1.06	0.97	1.16

[a] 85% confidence interval does not overlap 1 and indicates a significant effect.

When holding the size of the allotment and the grazing season length at their mean values, expected depredation events increased more than three-fold for every 550 head of cow/calf pairs added to an allotment on average (85% CI= 2.41 – 4.15). Multiplicative effects on depredation counts become evident at approximately 2,000 animals, when estimated average depredation counts began to rise more rapidly, especially for cow/calf and ewe/lamb allotments (Fig 8a). When holding the number of livestock and the length of time they are grazing, along with all other variables, constant at their mean values, an allotment that was approximately 6,500 ha larger than another allotment was estimated to have 1.8 times as many average depredation events (85% CI= 1.40 – 2.20). Estimated average depredation counts climbed as allotment sizes grew past approximately 20,000 ha (Figure 8b). When holding the size of the allotment and the number of animals at their mean values, the length of time livestock were grazing did not have a significant effect on average depredation counts. The number of depredations generally did not differ across livestock classes when controlling for all other variables. However, there was evidence that allotments stocked with a mixture of cow/calf pairs and yearling cattle had approximately 0.3 times (85% CI= 0.14 – 0.68) the average depredation events experienced on allotments stocked with only cow/calf pairs. Allotments where bulls and/or horses were stocked were estimated to have on average 0.5 times (85% CI= 0.29 – 0.84) the depredation events experienced on allotments where bulls and/or horses were not present. On average, depredation events on allotments that were grazed for at least part of the summer season were an estimated 1.8 times (85% CI=1.20 – 2.80) the events on allotments that were grazed in the spring or fall only.

Grizzly bear density had a relatively important effect on depredation events where allotments with an approximately 6 unit increase in the grizzly bear density index had an estimated 3.1 times (85% CI= 2.68 – 3.55) as many depredation events on average. These relatively large multiplicative effects on average depredation events became evident as grizzly bear density index on allotments increased above 15 bears (Figure 8c). On average, depredation counts were associated with allotments with relatively gentle topography and fewer roads. When holding all other variables at their mean values, there were 0.4 times (85% CI=0.28 – 0.62) as many expected depredations on average for every 0.37 km/km^2 increase in road density on allotments. Average depredation events began to rise more rapidly as road densities in and around allotments decreased below approximately 1 km/km^2 (Figure 8d). Allotments with relatively high primary productivity, farther from forest edge (in or out of forest), and with greater proportions of WBP were associated with higher average depredation event counts. On average, there were 1.5 times (85% CI=1.14 – 1.91) as many expected livestock depredation events for every 80 meters farther that an allotment was (on average) from forest edge (Figure 8g). On average, there were 1.35 times (85% CI= 1.09 – 1.66) as many expected livestock depredation events for every 0.12 increase in WBP proportion in and around allotments at the grizzly bear home range extent (Figure 8h). When holding the proportion of WBP on an allotment, as well as all other variables, at their mean, median annual WBP cone production did not have a significant association with depredation events (85% CI= 0.97 – 1.16).

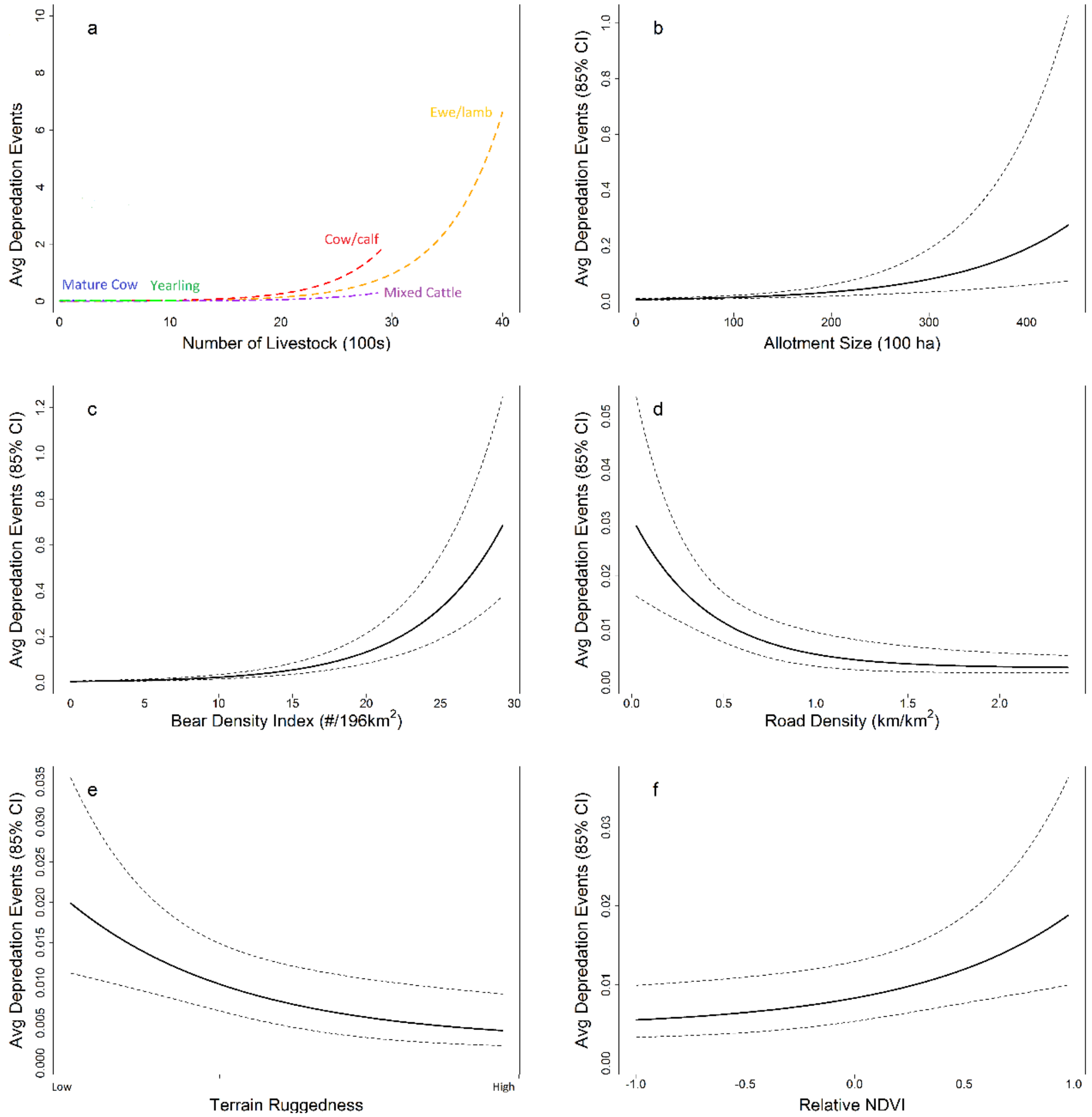

Figure 8. Effects of USFS and NPS grazing allotment attributes on livestock depredation event counts due to grizzly bears in the Demographic Monitoring Area (DMA), 1992–2014 with 85% confidence intervals. Effects and 85% confidence intervals were estimated as a weighted average of the predicted responses for the top five models using model estimates and model weights.

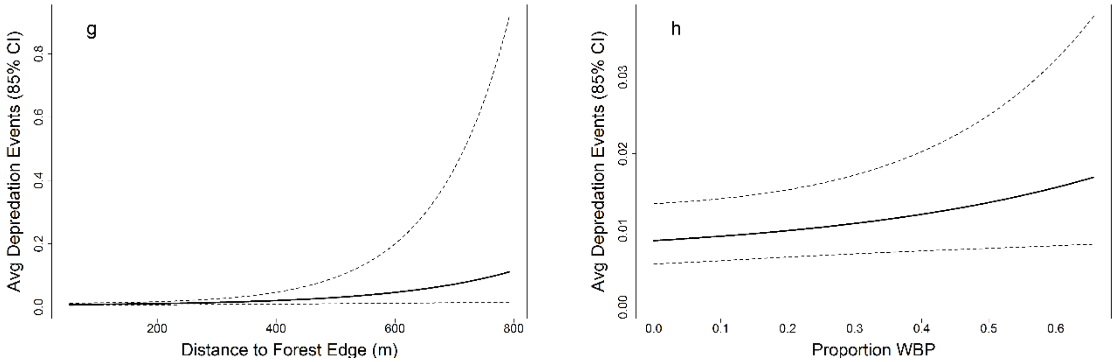

Figure 8 Continued.

The pseudo-R^2 value was 0.098, indicating that by including the predictors in the top models, the deviance was reduced by almost 10% compared to including no predictors (null model). It is important to note that this measure does not represent the proportion of variation in the response accounted for by the models but is instead only a measure of how much closer the final models are to the perfect model compared to the null model. For the single model with the most support, the estimates of the random effects of allotment ID varied from -2.5 to 6.0 at the log scale across allotments with a variance of 2.38, indicating that there was unexplained variability in depredation event counts among grazing allotments in the GYE during 1992–2014 (Appendix H).

Discussion

As the Yellowstone grizzly bear population expanded in numbers and distribution throughout the GYE in the last several decades, more federal grazing allotments were prone to potential interactions between bears and livestock. Not only were more grazing allotments becoming occupied by grizzly bears during the study period, but the majority of livestock depredations were tied to these areas of expansion, especially in the 1990s where 98% of all livestock depredation events during this decade occurred on allotments not previously occupied by grizzly bears in the 1970s and 1980s. During 1992–2014, despite the fact that approximately one-fifth of grazing allotments became vacant or closed, the number of GYE-wide livestock depredations increased. Such a trend included both an increase in the number of livestock depredation events per depredated allotment and an increase in the number of allotments experiencing depredations from the remaining open allotments. Livestock depredations were primarily on cow/calf pair and ewe/lamb pair allotments and these livestock classes were stocked on approximately 70% and 10% of all grazing allotments in the GYE from 1992–2014, respectively. Whether or not an allotment was experiencing recurring depredations did not have a measurable effect on average annual depredation counts.

Results indicated that livestock numbers and grizzly bear density on grazing allotments had relatively large positive effects on the number of annual livestock depredation events compared to the other characteristics modeled. Stocking of mixed cattle classes and the presence of bulls and/or horses with other livestock on allotments in the GYE were related to low average depredation counts while stocking in the summer season was related to high depredation counts. Depredation event counts during 1992–2014 in the GYE were related to allotments with higher bear densities, fewer roads, higher primary productivity, greater WBP presence, greater distances from forest edge, and less terrain ruggedness.

During the study period, Yellowstone grizzly bears expanded their range substantially throughout the ecosystem and the population continues to expand. The majority of depredations were in areas of population expansion, where approximately 50% and 75% of depredation events occurred outside of the YGBRZ in the 1990s and 2000s, respectively. These patterns have also been documented in grizzly bear conflict reports (DeBolt 2016, Frey and Smith 2016). It is likely that most depredations occurred in areas newly occupied by bears simply because there were more allotments on which grizzly bears would interact with cattle, leading to an increased opportunity for livestock depredation. Many grazing allotments on the periphery of the ecosystem provide habitat for bears to expand their range, except that these areas are being used for livestock grazing, leading to potential conflicts.

Livestock depredation event counts and the number of livestock killed varied among livestock classes during the study period. Depredations in the GYE consisted mainly of cow/calf pairs (mostly calves killed) and sheep, Livestock classes with a smaller body size are generally killed more often by predators than larger-bodied classes (Bjorge 1983, Mattson 1990). Previous research has suggested that a greater proportion of sheep depredation is a result of sheep being stocked in more remote areas (Horstman and Gunson 1982, Kaczensky 1999). During 1992–2014, sheep comprised only 10% of all grazing allotments but sheep depredation accounted for approximately 18% of all depredation events in the GYE, indicating disproportionate depredation on sheep relative to their availability. While cow/calf pairs experienced much greater depredations than other classes of livestock (approximately 70% of all depredation events during the study period), depredation was in proportion to their availability on the landscape since approximately 70% of allotments were stocked with cow/calf pairs. Depredation on the other classes of cattle also appeared to be in proportion to their availability on grazing allotments in the GYE.

A history of recurring depredations did not have a notable effect on allotment depredation counts during the study period. This is contrary to other studies that found amplified livestock depredation rates in agricultural areas that experienced depredation in the last year and that observed young bears learning depredatory behavior from mothers (Karlsson and Johansson 2010, Morehouse et al. 2016). My results may suggest that depredations on allotments were not attributed to a few problem bears who depredate year after year but instead that many bears in the area depredated on livestock opportunistically (Anderson et al. 2002). Alternatively, results may suggest that management efforts had been effective in relocating or removing chronic depredators from allotments.

Depredation counts during 1992–2014 were positively associated with the size of allotments and depredated allotments were on average larger than non-depredated allotments. Livestock numbers also had a relatively large positive effect on depredation counts. However, depredated allotments did not have greater livestock numbers on average than non-depredated allotments during the study period, indicating that depredations occurred on allotments with variable numbers of livestock but that higher counts of annual depredations occurred on allotments with greater numbers of livestock. Unfortunately, I was unable to evaluate relationships between livestock density and depredation counts because pastures within the allotments likely dictated livestock densities, regardless of the number of animals or size of the allotment. However, discounting pastures within allotments, for an allotment with a given number of livestock and grazing season length, increasing the size of the allotment increased the estimated number of depredation events. Similarly, for an allotment of a given size and grazing season length, increasing the number of livestock increased the estimated number of depredation events.

Instead of being a specific measure of livestock stocking on grazing allotments, livestock numbers and allotment size may be more related to the amount of human presence and supervision (per head or per hectare) on allotments. Documented cattle depredations by bears and wolves were higher on large, forested pastures in northwestern Alberta with unintensive management and little human supervision compared to pastures with intensive human management including fencing and herd supervision (Bjorge 1983). Research has shown that in general, grizzly bears select for more remote areas with less human presence, including some large grazing allotments (Ciarniello et al. 2007, Steyaert et al. 2011). The presence of bulls and/or horses with other livestock on grazing allotments may have also signified more intensive livestock management and lead to fewer depredations by grizzly bears, as seen by the approximately 50% fewer average annual depredation events on grazing allotments when these classes were present. Although the large body size of bulls and horses may have acted as a deterrent for grizzly bears with depredatory behavior (Mattson 1990), it is more likely that continuous livestock management during the grazing season associated with bulls and horses increased human presence and limited grizzly bear use of those allotments because bears generally avoid areas of human activity (Apps et al. 2004). Although not evident in historic USFS and NPS grazing records, it should be noted that bulls and/or horses may have been grazing pastures separate from other livestock on allotments for at least part of the grazing season due to breeding management or accessibility reasons. However, in general, overall human presence and management intensity on grazing allotments where bulls and/or horses were present was likely greater than on allotments without these livestock classes.

Depredated grazing allotments in the GYE during 1992–2014 had on average fewer roads compared to non-depredated allotments. Also, lower road densities in and around allotments at the grizzly bear home range extent (196 km^2) were related to greater numbers of depredation events. Grizzly bears generally avoid areas near roads due to increased human activity, which could influence potential interactions with livestock within allotments (Mace et al. 1999, Mattson and Merrill 2004, Ciarniello et al. 2007, Northrup et al. 2012). Average depredation events increased substantially as road densities in and around allotments decreased below approximately 1 km/km^2, which is similar to previous work in northwest Montana and northern Idaho that found grizzly bear space use was greatest at road densities below 1.1 km/km^2 (Mattson and Merrill 2004). Fewer roads in and around allotments may also limit access to bear managers and the strategies they can use to manage conflict bears. For example, capture and relocation of depredating bears in remote areas is logistically difficult. Restricted management of conflict bears on allotments with low road densities could have also explained higher average depredation events.

Grizzly bear avoidance of human activity, including livestock grazing, could also explain the evidence that bears were less numerous in grazing allotments that were stocked with livestock compared to grazing allotments that were not used for grazing in a given year (Servheen and U.S. Fish and Wildlife Service 1993, Apps et al. 2004). However, this relationship between livestock presence and bear density is not causal and other characteristics of stocked grazing allotments could also be related to bear densities. Also, allotments with high grizzly bear densities could have not been stocked to prevent likely depredations on those allotments.

The length of time livestock were grazing on allotments, or the time the animals were exposed to depredation by grizzly bears, did not have a notable effect on depredation counts. Because almost 60% of livestock depredations have been documented during the relatively short summer season when grizzly bears are in early hyperphagia, the additional time that livestock grazed outside of this season may not have greatly increased the number of depredation events (Gunther et al. 2004). My results are consistent with other research on livestock-bear conflicts in the GYE that documented spatial associations between cattle and grizzly bears throughout the grazing season but with depredations concentrated during a discrete time period, usually from July to August (Murie 1948, Knight and Judd 1983, Anderson et al. 2002). Differences in daily habitat use between grizzly bears and livestock may limit interactions and subsequent depredations during the spring and fall seasons, even when both species are present on an allotment. During spring and early summer, grizzly bears are generally consuming over-winter ungulate carcasses and new elk calves and often select for areas closer to streams;

whereas free-ranging cattle often select for quality herbaceous forage available in upland areas (Gunther et al. 2004, Steyaert et al. 2011). Later in the grazing season (late August-September), grizzly bears generally use relatively higher elevations with more rugged terrain and further from streams where foods including whitebark pine, army cutworm moths, and berry-producing shrubs are available; whereas livestock generally use relatively lower elevations with milder slopes near water sources and with less forest cover (Roath and Krueger 1982, Steyaert et al. 2011, Costello et al. 2014).

Estimated annual grizzly bear density had a large positive effect on depredation counts on grazing allotments during the study period; average depredation events tripled for every 6 unit increase in the grizzly bear density index. These results were consistent with higher documented cattle losses in pastures with greater numbers of predators in northwestern Alberta (Bjorge 1983). Also, results indicated that allotments experiencing at least some depredations in a given year had a higher annual bear density index, on average, than non-depredated allotments. Intuitively, more bears using an allotment could increase the likelihood of bear-livestock interactions and subsequent depredations. However, because the grizzly bear density index was estimated at a broad spatial extent (196 km^2), it is impossible to discern the actual number of bears using allotments that fell within the larger spatial extent from which bear density was measured. Nevertheless, the density of bears within the greater landscape of an allotment could be related to competition for resources and could explain the bear density-depredation relationship observed. At high bear densities, older bears, especially adult males, may dominate the most productive feeding sites around an allotment and subordinate juveniles and females with cubs are constrained to use suboptimal habitat, such as areas with increased human activity in the form of public land livestock grazing (Stringham 1983, Wielgus and Bunnell 1994, van Manen et al. 2016). Because social behaviors and habitat use differ between ages and sexes of grizzly bears (Stringham 1983, Ciarniello et al. 2007, Costello et al. 2014), consideration of livestock depredations separately for each bear cohort may give better insight as to how allotment characteristics relate to depredations. However, it is often difficult to identify specific bears responsible for depredations so such an evaluation may not be feasible. While it is unknown how many individual bears are responsible for depredations at high bear densities, the positive relationship between bear density and depredation event counts suggests that as more grizzly bears become spatially associated with livestock, they kill livestock at a higher levels, which could indicate that bears depredated on livestock opportunistically rather than a few problem bears repeatedly depredating (Anderson et al. 2002). Or conversely, higher numbers of grizzly bears could increase the probability of bears with depredatory behavior being present.

Higher average annual depredation events were related to quality grizzly bear habitat in and around allotments, as reflected in relatively high NDVI values, areas far from forest edge, and greater proportions of whitebark pine. Green vegetation productivity, often measured as NDVI, is selected for by grizzly bears at broad, home-range scales in a variety of ecosystems, especially during peak production times, which are in mid-July on average across the GYE (Mace et al. 1999, Apps et al. 2004, Ciarniello et al. 2007, Steyaert et al. 2011, U.S. Geological Survey 2016). Similar to my results, the risk of a free-ranging cattle-grizzly bear encounter was greater in areas with higher NDVI in Sweden (Steyaert et al. 2011).

While grizzly bears select areas of high forest productivity at broad spatial extents, the majority of grazing allotments in the GYE are forested, averaging 60% forest cover, and daily movements are instead more influenced by areas of closed and open canopy cover (Apps et al. 2004). The distance metric used in analysis did not specify the distance outside or inside of forest patches. However, because cattle and sheep generally avoid dense forest habitats with sparse understory herbaceous vegetation (Roath and Krueger 1982, Gillen et al. 1984), it is likely that the large average distances from forest edge on allotments that were related to higher depredations were best represented by allotments with large patches of open, non-forested areas. During the day, grizzly bears generally use forested areas for bedding or foraging for forest understory foods such as berry-producing shrubs; whereas during the night and crepuscular periods, bear movements are influenced by open, productive areas within forests that provide herbaceous forage value (Apps et al. 2004, Steyaert et al. 2011). Similarly, cattle and sheep generally select meadows and open grassland communities with relatively abundant and quality herbaceous forage and avoid mixed conifer forests if more preferable open grasslands are available while grazing forested rangelands, leading to potential interactions with grizzly bears, especially at night (Roath and Krueger 1982, Gillen et al. 1984). Johnson and Griffel (1982) found that sheep depredations by grizzly bears in Yellowstone occurred at night in open grasslands or meadows used as sheep bed grounds.

Whitebark pine was present throughout the ecosystem, comprising an estimated 18% of the land cover in the GYE (Macfarlane et al. 2013), except at lower elevations, especially to the west and southwest of Yellowstone National Park on the Custer Gallatin and Caribou-Targhee National Forests. Grizzly bears in regions where WBP is present will select for WBP habitats from approximately August 15 to September 30, even in years of poor cone production (Costello et al. 2014). Median annual ecosystem-wide cone production did not have a marked effect on depredation counts, when controlling for the amount of WBP present in and around allotments, likely because many documented livestock depredations occurred prior to the peak of WBP foraging season or because estimates of annual WBP cone production were ecosystem-wide and allotment-level relationships between cone production and depredations could not be evaluated. Grazing allotments within areas of relatively high primary productivity, with open herbaceous forage patches, and with whitebark pine habitat likely provided ample foraging opportunities as well as daytime cover for grizzly bears, especially during the summer season when bears were consuming large amounts of food to prepare for hibernation, leading to potential interactions with livestock present on those allotments.

Variation in livestock stocking characteristics on grazing allotments in the GYE during the study period could be have been due to differences in range productivity and timing of precipitation, administrative and management strategy differences, or historic stocking patterns. It should be noted that livestock operators that primarily run cow/calf pairs on public land grazing allotments often include some heifers (yearlings) as part of their herd but report stocking as simply cow/calf. Based on these complexities of livestock stocking, it is possible that allotments with cattle classes such as cow/calf pairs have an unknown number of other cattle classes such as yearlings. Therefore caution should be used when making inferences about the effects of livestock classes on depredation events, especially for cattle classes. It should also be noted that detailed livestock management strategies on allotments, such as range riders that increase the amount and timeliness of depredation reports and conflict management actions, were not recorded, which may also limit inferences about allotment stocking effects on depredations.

My analysis identified ecological relationships and potential mechanisms regarding livestock depredation by grizzly bears during the study period in the GYE, and information can be used to inform management strategies in the region. Nevertheless, including all the identified livestock stocking and grizzly bear habitat predictors in the model improved model fit by only 10% over a null model, indicating that there was still room for improvement in model fit and that other predictors not considered may have also been related to depredation counts. The GYE is a complex system and it is likely that other factors not considered in my *a priori* hypotheses were also important in predicting depredation counts during the study period. Other possibly important predictors of depredation events could have been detailed management strategies on allotments such as range riders, livestock protection dogs, carcass removal programs, and fencing (Kaczensky 1999), or could have been grizzly bear habitat factors not considered including fine-scale or spatially-explicit habitat variables. It is also important to note that this was an observational study and the relationships between allotment characteristics and depredation counts identified were not necessarily causal. The livestock stocking and grizzly bear habitat attributes identified were associated with livestock depredation counts but it is possible that other factors not considered were also part of those relationships and could have helped explain depredations. Also, differences in allotment attributes between depredated and non-depredated allotments do not show causal relationships and it is likely that other allotment factors combined to influence the relationship between a single allotment characteristic and the presence or absence of livestock depredations.

My results indicate large variation in average depredation counts among grazing allotments. While some variation was explained by the livestock stocking and grizzly bear habitat variables included in the models, some variation was left unexplained and was modeled by the random allotment ID effects (Appendix H). Detailed allotment management strategies and/or spatially-explicit habitat characteristics not considered in my analysis could have accounted for some of the unexplained variation across allotments.

Management Implications

The increasing trend in human-grizzly bear conflicts in the Greater Yellowstone Ecosystem, including livestock depredations, is largely a function of growing bear numbers and their distribution into areas more intensively used by humans, including public land grazing allotments. This study summarized baseline ecological and management information associated with public land grazing allotments in the GYE, along with grizzly bear depredation of livestock over a 23-year period. The perspectives gained from analyses provide context for long-term, landscape-level planning to accommodate livestock production on public lands while meeting grizzly bear conservation goals. While bear-livestock conflicts in the ecosystem will likely never be completely eliminated, cooperation, flexibility, and tradeoffs among public land users, local agriculture and conservation organizations, and state and federal agencies could lead to effective, long-term management strategies to minimize conflicts.

Public land managers could use results to adapt livestock management approaches and long-term planning with an aim to minimize depredations. Managers could potentially manipulate the components of stocking without necessarily changing the AUMs allotted to permittees (e.g., reduce livestock numbers and increase grazing season length, shift grazing into spring and fall seasons if feasible). Also, if human presence and supervision is suspected to be related to depredations, management approaches such as range riders could be employed to improve timely conflict management actions, including management of grizzly bears with depredatory behavior. Detailed livestock management strategies such as range riders, carcass removal programs, and grazing systems (i.e. pasture rotations) were not considered in this analysis due to the lack of information in grazing records and data collection time constraints. However, if feasible, their relationships with depredations should be explored to better identify other management aspects related to the amount of annual livestock depredations by grizzly bears.

Public land managers may consider grizzly bear habitat characteristics of grazing allotments and their relationships with depredations when developing management plans and preventative measures as the grizzly bear population continues to expand. For example, managers may identify grazing allotments with high bear densities, few roads, or relatively high vegetative production and then may further consider long-term management actions on those allotments, such as increased carnivore management or phasing out livestock use when practical. Similarly, future grizzly bear population management by states (i.e., hunting seasons) may reduce bear densities and increase human activity in some areas, which could limit potential depredations, and therefore these areas may be most suitable for livestock grazing. However, evidence of this sort of response is limited and may only be effective if depredatory bears are selectively taken. Currently, 27% of the Yellowstone grizzly bear population distribution is outside of the DMA and many human-bear conflicts have been and continue to be tied to these areas of expansion (DeBolt 2016, van Manen and Haroldson 2017). If grazing areas in the periphery of the ecosystem outside of the DMA have similar livestock management, grizzly bear habitat attributes, and grizzly bear population growth, managers could use these results to support the development of livestock management plans and identify grazing areas with characteristics less related to depredations in preparation for more grizzly bears on the landscape. However, livestock grazing areas outside of the DMA are likely to have increased human use and contain more marginal grizzly bear habitat (not deemed suitable habitat), and therefore relationships between allotment characteristics and livestock depredations may be different in these peripheral areas not considered in this study.

The Greater Yellowstone Ecosystem is a large, diverse system with many land uses and complex ecological processes. While this study could not completely explain ecological processes involved in livestock depredation by grizzly bears on grazing allotments in the GYE, some potentially important factors relating to depredations were identified. Considering grizzly bear habitat attributes and their relationships with livestock depredations at various spatial extents may offer more insights into complex, hierarchical ecological processes influencing depredations and may provide the most relevant spatial extents at which to consider management decisions. Results of this analysis, as well as the base information collected, may provide an impetus for future wildlife-livestock studies in the GYE.

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APPENDICES

APPENDIX A

GRIZZLY BEAR HABITAT GEOSPATIAL DATA LAYERS

Table A1. Geospatial data sources used to derive grizzly bear habitat attributes on USFS and NPS grazing allotments in the GYE, 1992–2014.

	Habitat attributes	Units	Min resolution	Data source	Comments
Physical	Elevation	meters	30 × 30 m	USGS Digital Elevation Model (DEM)	
	Slope	percent	30 × 30 m	Derived from USGS DEM	Slope ArcGIS 10.3.1 spatial analyst tool using elevation input (ESRI 2015)
	Vector Ruggedness Measure (VRM)	index	30 × 30 m	Derived from USGS DEM	Benthic Terrain Modeler ArcGIS 10.3.1 terrain tool, neighborhood of 3 cells; (Sappington et al. 2007)
	Stream density	km stream/km^2	30 × 30 m	Derived from USGS National Hydrography Dataset (NHD), perennial streams	Line Density ArcGIS 10.3.1 spatial analyst tool, search radius of 1,600 m (ESRI 2015)
	Road density	km road/km^2	30 × 30 m	Derived from IGBST road data	Line Density ArcGIS 10.3.1 spatial analyst tool, search radius of 280 m (ESRI 2015)
	Distance to grizzly bear range edge	kilometers	30 × 30 m	Derived from Bjornlie et al. (2014a)	For 1990s and 2000s GB range; absolute distance values
	Grizzly bear density index	individuals/ 196km^2	14 × 14 km	(Bjornlie et al. 2014b)	
Biotic	Distance to forest edge	meters	30 × 30 m	National Land Cover Database (NLCD) provided by IGBST	Absolute distance values
	Vegetation cover	proportion of area	30 × 30 m	LANDFIRE	Consolidated to forest, grass/shrub, and riparian cover classes; used 2001, 2008, 2010, and 2012 versions
	Elk security cover	proportion of area	30 × 30 m	Derived from LANDFIRE	Defined as areas with ≥40% forest canopy cover in patch sizes ≥ 26 hectares
	Whitebark pine presence	proportion of area	30 × 30 m	(Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee 2011)	Excluded LAS scores of 888 and 999 (burned WBP)
	Whitebark pine cone production	median cones per tree	N/A	(Interagency Grizzly Bear Study Team 2016)	Estimated annually from appx. 20 WBP transects across the GYE, median adjusted for tree mortality
	Moth site presence	proportion of area	30 × 30 m	Derived from IGBST moth site locations	Focal statistics ArcGIS 10.3.1 spatial analyst tool, search radius of 42 km (ESRI 2015)
	Normalized Difference Vegetation Index (NDVI)	index	1 × 1 km	USGS AVHRR NVDI 14-day composites	Annual NDVI 14-day composites for the 2nd half of July to capture peak NDVI

APPENDIX B

GRIZZLY BEAR HABITAT SPATIAL EXTENT SELECTION RESULTS

Table B1. Akaike Information Criteria (AIC_c) values for models to identify the spatial extent of grizzly bear habitat attributes that best explained variation in livestock depredation by grizzly bears on USFS and NPS grazing allotments in the Demographic Monitoring Area (DMA) from 1992–2014.

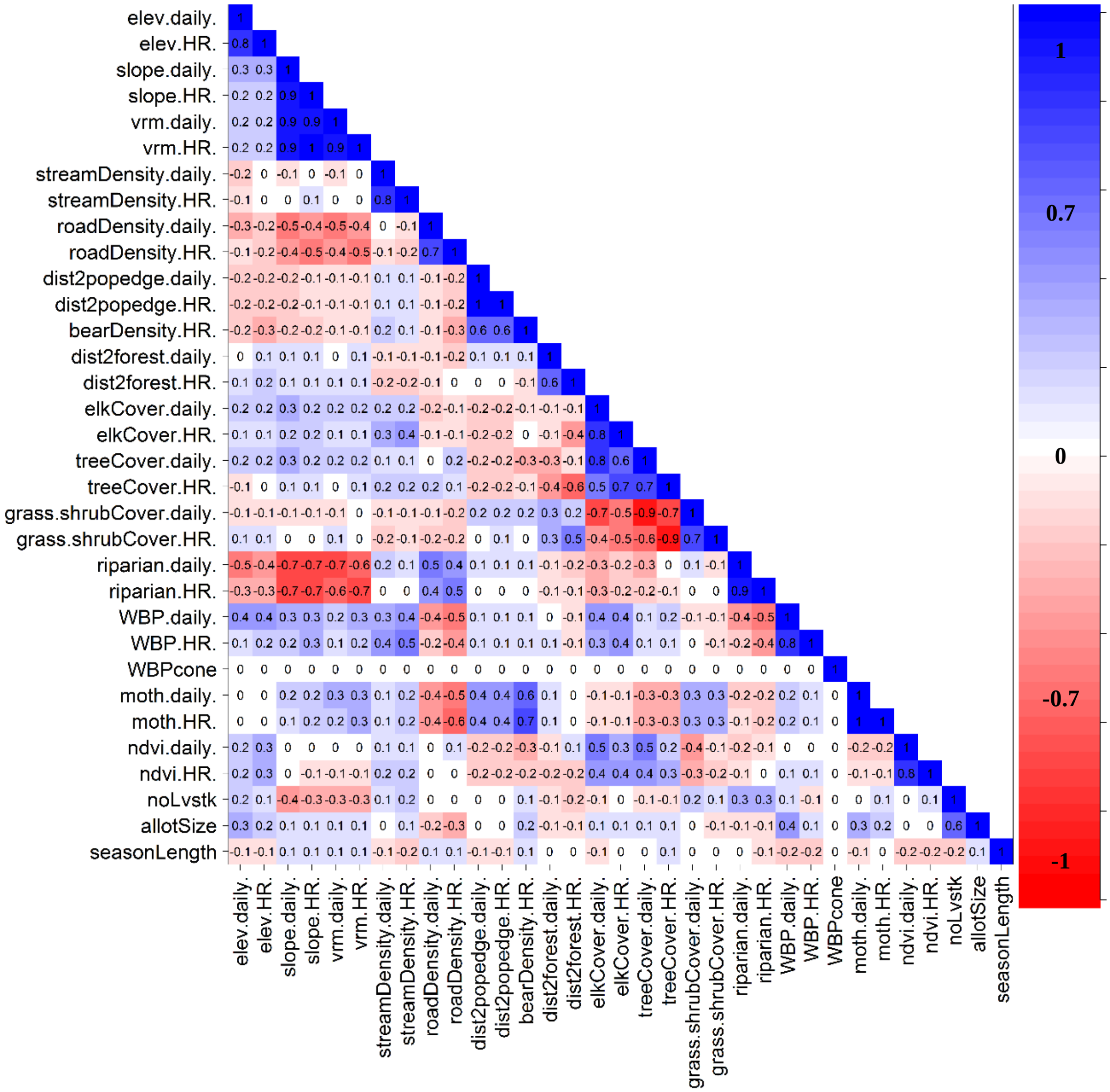
Grizzly bear habitat variable	Model[a]	AIC_c
stream density	Depredation event count ~ stream density 8 km^2	2812.87
	Depredation event count ~ stream density 196 $km^{2,b}$	2807.61
elevation	Depredation event count ~ elevation 8 km^2	2817.65
	Depredation event count ~ elevation 196 $km^{2,b}$	2817.63
terrain ruggedness	Depredation event count ~ terrain ruggedness 8 $km^{2,b}$	2814.61
	Depredation event count ~ terrain ruggedness 196 km^2	2815.32
road density	Depredation event count ~ road density 8 km^2	2813.54
	Depredation event count ~ road density 196 $km^{2,b}$	2809.29
distance to bear range edge	Depredation event count ~ distance to bear range edge 8 km^2	2754.69
	Depredation event count ~ distance to bear range edge 196 $km^{2,b}$	2754.66
ndvi	Depredation event count ~ ndvi 8 km^2	2810.88
	Depredation event count ~ ndvi 196 $km^{2,b}$	2809.44
WBP presence	Depredation event count ~ WBP presence 8 km^2	2811.22
	Depredation event count ~ WBP presence 196 $km^{2,b}$	2809.44
moth site presence	Depredation event count ~ moth site presence 8 km^2	2814.60
	Depredation event count ~ moth site presence 196 $km^{2,b}$	2814.52
tree cover	Depredation event count ~ tree cover 8 $km^{2,b}$	2810.99
	Depredation event count ~ tree cover 196 km^2	2812.06
distance to forest	Depredation event count ~ distance to forest 8 $km^{2,b}$	2816.39
	Depredation event count ~ distance to forest 196 km^2	2817.48

[a] All models were a generalized linear mixed model with a negative binomial distribution and a random intercept of allotment ID (1 | Allotment ID)

[b] Spatial extent with the lowest AIC_c and used to model the relationship between habitat attributes and livestock depredation counts

APPENDIX C

MULTICOLLINEARITY OF MODEL PREDICTORS



	elev.daily.	elev.HR.	slope.daily.	slope.HR.	vrm.daily.	vrm.HR.	streamDensity.daily.	streamDensity.HR.	roadDensity.daily.	roadDensity.HR.	dist2popedge.daily.	dist2popedge.HR.	bearDensity.HR.	dist2forest.daily.	dist2forest.HR.	elkCover.daily.	elkCover.HR.	treeCover.daily.	treeCover.HR.	grass.shrubCover.daily.	grass.shrubCover.HR.	riparian.daily.	riparian.HR.	WBP.daily.	WBP.HR.	WBPcone	moth.daily.	moth.HR.	ndvi.daily.	ndvi.HR.	noLvstk	allotSize	seasonLength
elev.daily.	1																																
elev.HR.	0.8	1																															
slope.daily.	0.3	0.3	1																														
slope.HR.	0.2	0.2	0.9	1																													
vrm.daily.	0.2	0.2	0.9	0.9	1																												
vrm.HR.	0.2	0.2	0.9	1	0.9	1																											
streamDensity.daily.	-0.2	0	-0.1	0	-0.1	0	1																										
streamDensity.HR.	-0.1	0	0	0.1	0	0	0.8	1																									
roadDensity.daily.	-0.3	-0.2	-0.5	-0.4	-0.5	-0.4	0	-0.1	1																								
roadDensity.HR.	-0.1	-0.2	-0.4	-0.5	-0.4	-0.5	-0.1	-0.2	0.7	1																							
dist2popedge.daily.	-0.2	-0.2	-0.2	-0.1	-0.1	-0.1	0.1	0.1	-0.1	-0.2	1																						
dist2popedge.HR.	-0.2	-0.2	-0.2	-0.1	-0.1	-0.1	0.1	0.1	-0.1	-0.2	1	1																					
bearDensity.HR.	-0.2	-0.3	-0.2	-0.2	-0.1	-0.1	0.2	0.1	-0.1	-0.3	0.6	0.6	1																				
dist2forest.daily.	0	0.1	0.1	0.1	0	0.1	-0.1	-0.1	-0.1	-0.2	0.1	0.1	0.1	1																			
dist2forest.HR.	0.1	0.2	0.1	0.1	0.1	0.1	-0.2	-0.2	-0.1	0	0	0	-0.1	0.6	1																		
elkCover.daily.	0.2	0.2	0.3	0.2	0.2	0.2	0.2	0.2	-0.2	-0.1	-0.2	-0.2	-0.1	-0.1	-0.1	1																	
elkCover.HR.	0.1	0.1	0.2	0.2	0.1	0.1	0.3	0.4	-0.1	-0.1	-0.2	-0.2	0	-0.1	-0.4	0.8	1																
treeCover.daily.	0.2	0.2	0.3	0.2	0.2	0.2	0.1	0.1	0	0.2	-0.2	-0.2	-0.3	-0.3	-0.1	0.8	0.6	1															
treeCover.HR.	-0.1	0	0.1	0.1	0	0.1	0.2	0.2	0.2	0.1	-0.2	-0.2	-0.1	-0.4	-0.6	0.5	0.7	0.7	1														
grass.shrubCover.daily.	-0.1	-0.1	-0.1	-0.1	-0.1	0	-0.1	-0.1	-0.1	-0.2	0.2	0.2	0.2	0.3	0.2	-0.7	-0.5	-0.9	-0.7	1													
grass.shrubCover.HR.	0.1	0.1	0	0	0.1	0	-0.2	-0.1	-0.2	-0.2	0	0.1	0	0.3	0.5	-0.4	-0.5	-0.6	-0.9	0.7	1												
riparian.daily.	-0.5	-0.4	-0.7	-0.7	-0.7	-0.6	0.2	0.1	0.5	0.4	0.1	0.1	0.1	-0.1	-0.2	-0.3	-0.2	-0.3	0	0.1	-0.1	1											
riparian.HR.	-0.3	-0.3	-0.7	-0.7	-0.6	-0.7	0	0	0.4	0.5	0	0	0	-0.1	-0.1	-0.3	-0.2	-0.2	-0.1	0	0	0.9	1										
WBP.daily.	0.4	0.4	0.3	0.3	0.2	0.3	0.3	0.4	-0.4	-0.5	0.1	0.1	0.1	0	-0.1	0.4	0.4	0.1	0.2	-0.1	-0.1	-0.4	-0.5	1									
WBP.HR.	0.1	0.2	0.2	0.3	0.1	0.2	0.4	0.5	-0.2	-0.4	0.1	0.1	0.1	0.1	-0.1	0.3	0.4	0.1	0.1	0	-0.1	-0.2	-0.4	0.8	1								
WBPcone	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1							
moth.daily.	0	0	0.2	0.2	0.3	0.3	0.1	0.2	-0.4	-0.5	0.4	0.4	0.6	0.1	0	-0.1	-0.1	-0.3	-0.3	0.3	0.3	-0.2	-0.2	0.2	0.1	0	1						
moth.HR.	0	0	0.1	0.2	0.2	0.3	0.1	0.2	-0.4	-0.6	0.4	0.4	0.7	0.1	0	-0.1	-0.1	-0.3	-0.3	0.3	0.3	-0.1	-0.2	0.2	0.1	0	1	1					
ndvi.daily.	0.2	0.3	0	0	0	0	0.1	0.1	0	0.1	-0.2	-0.2	-0.3	-0.1	0.1	0.5	0.3	0.5	0.2	-0.4	-0.1	-0.2	-0.1	0	0	0	-0.2	-0.2	1				
ndvi.HR.	0.2	0.3	0	-0.1	-0.1	-0.1	0.2	0.2	0	0	-0.2	-0.2	-0.2	-0.2	-0.2	0.4	0.4	0.4	0.3	-0.3	-0.2	-0.1	0	0.1	0.1	0	-0.1	-0.1	0.8	1			
noLvstk	0.2	0.1	-0.4	-0.3	-0.3	-0.3	0.1	0.2	0	0	0	0	0.1	-0.1	-0.2	-0.1	0	-0.1	-0.1	0.2	0.1	0.3	0.3	0.1	-0.1	0	0	0.1	0	0.1	1		
allotSize	0.3	0.2	0.1	0.1	0.1	0.1	0	0.1	-0.2	-0.3	0	0	0.2	-0.1	-0.1	0.1	0.1	0.1	0.1	0	-0.1	-0.1	-0.1	0.4	0.1	0	0.3	0.2	0	0	0.6	1	
seasonLength	-0.1	-0.1	0.1	0.1	0.1	0.1	-0.1	-0.2	0.1	0.1	-0.1	-0.1	0.1	0	0	-0.1	0	0	0.1	0	0	0	-0.1	-0.2	-0.2	0	-0.1	0	-0.2	-0.2	-0.2	0.1	1

Figure C1. Spearman-rank correlation matrix of all potential predictors in models to identify factors related to livestock depredation by grizzly bears on USFS and NPS grazing allotments in the Demographic Monitoring Area (DMA) from 1992–2014. Spearman-rank correlations of $|r| > 0.7$ were considered significant. Correlations have been rounded to one decimal place for image clarity but were evaluated at two decimal places.

APPENDIX D

GENERALIZED ADDITIVE MODELS (GAMS)

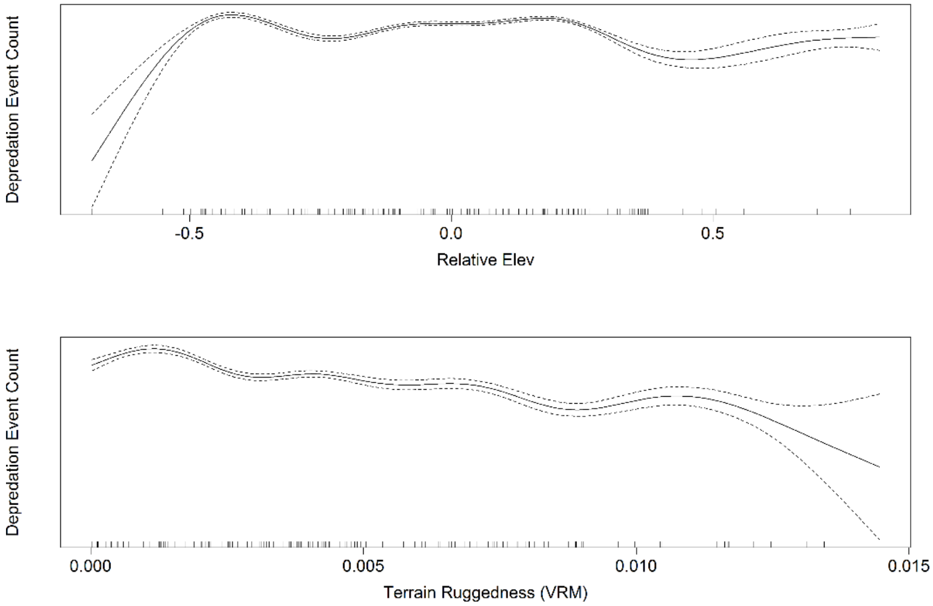


Figure D1. Predicted non-linear relationship (± 95% CI) between relative elevation and depredation event counts (top) and between terrain ruggedness and depredation event counts (bottom) on USFS and NPS grazing allotments in the GYE, 1992–2014. Other variables are not controlled for.

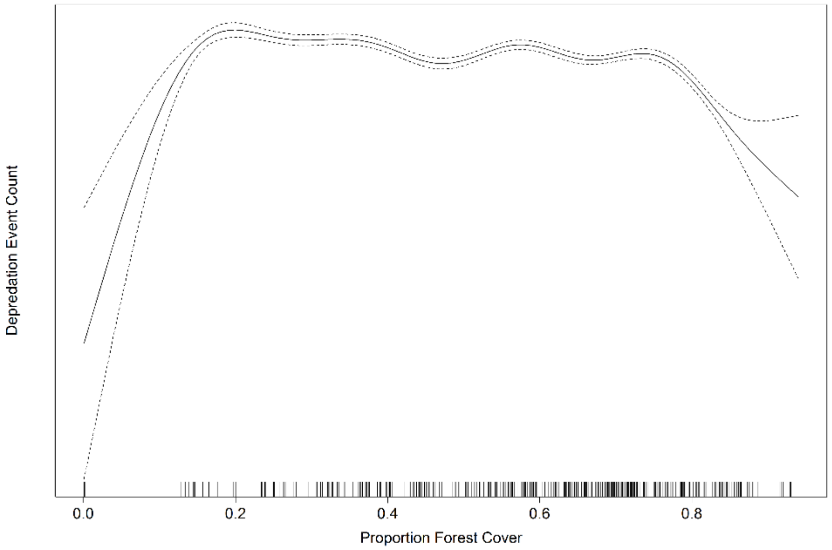


Figure D2. Predicted non-linear relationship (± 95% CI) between proportion forest cover and depredation event counts on USFS and NPS grazing allotments in the GYE, 1992–2014. Other variables are not controlled for.

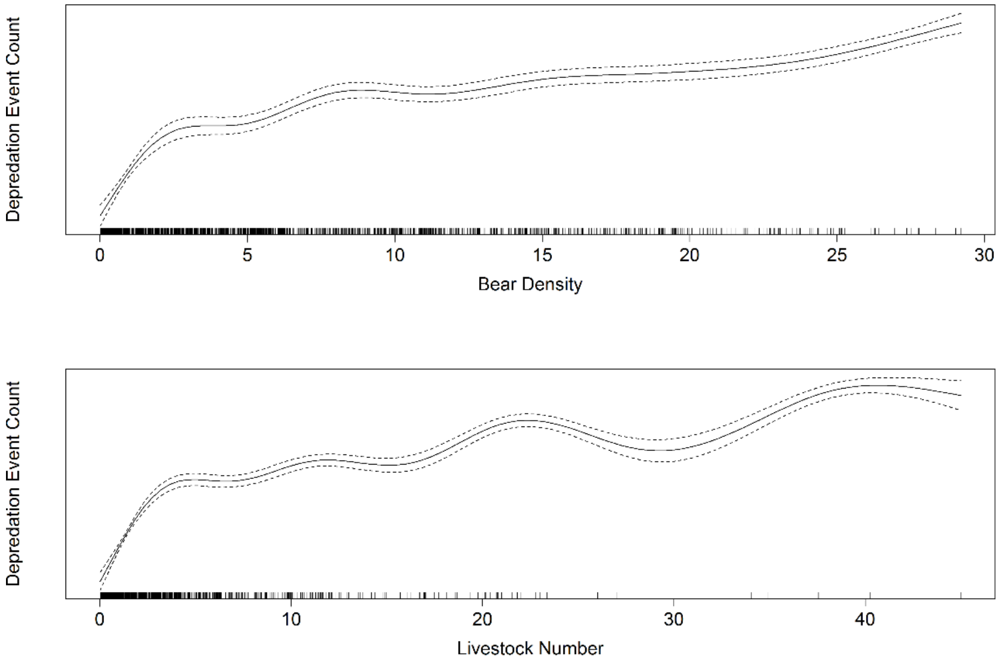


Figure D3. Predicted non-linear relationship (± 95% CI) relationship between grizzly bear density index and depredation event counts (top) and between livestock numbers and depredation event counts (bottom) on USFS and NPS grazing allotments in the GYE, 1992–2014. Other variables are not controlled for.

APPENDIX E

INTERACTION OF LIVESTOCK NUMBER AND CLASS

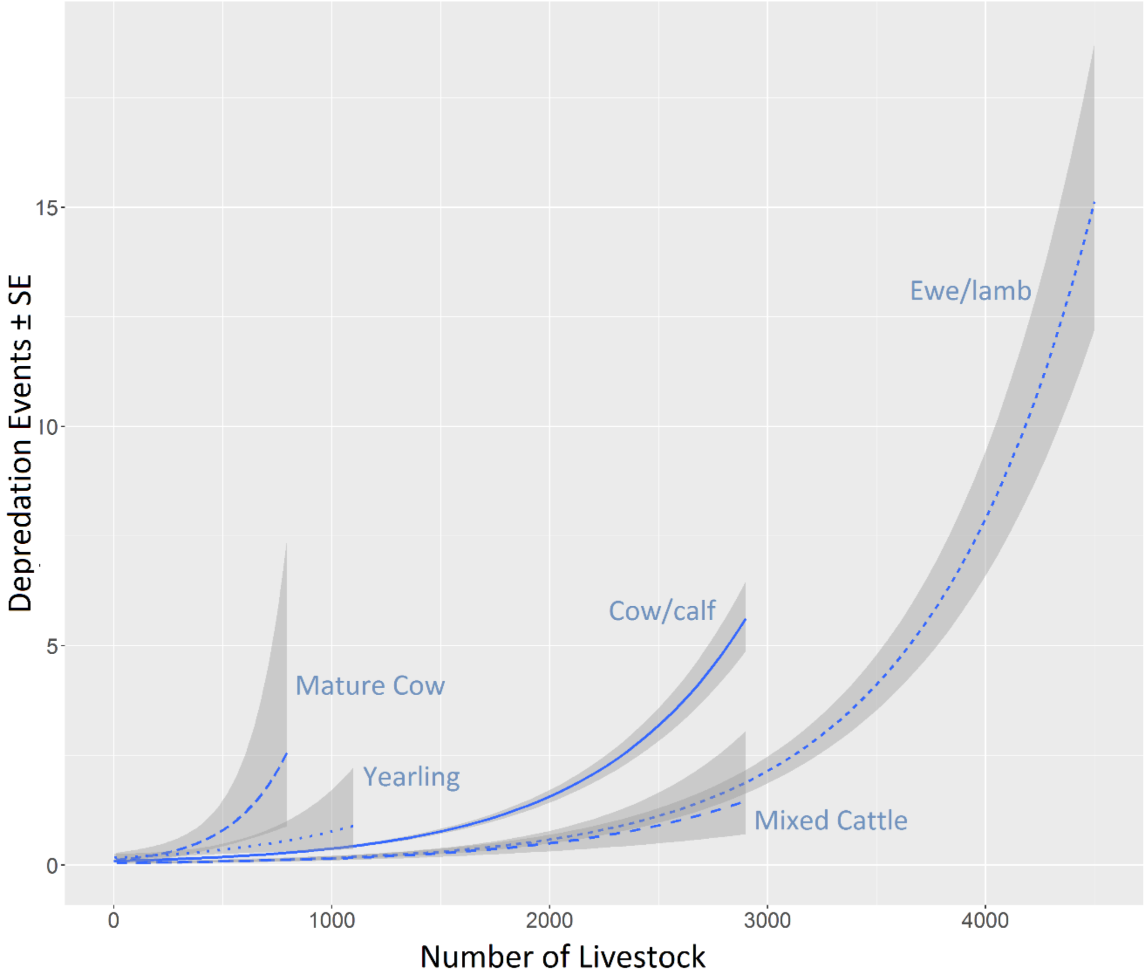


Figure E1. The effects (±SE) of livestock numbers on average depredation events per allotment per year based on livestock class in the Demographic Monitoring Area (DMA), 1992–2014. Other variables are not controlled for.

APPENDIX F

BEANPLOTS OF LIVESTOCK STOCKING BY FOREST IN THE GYE, 1992–2014

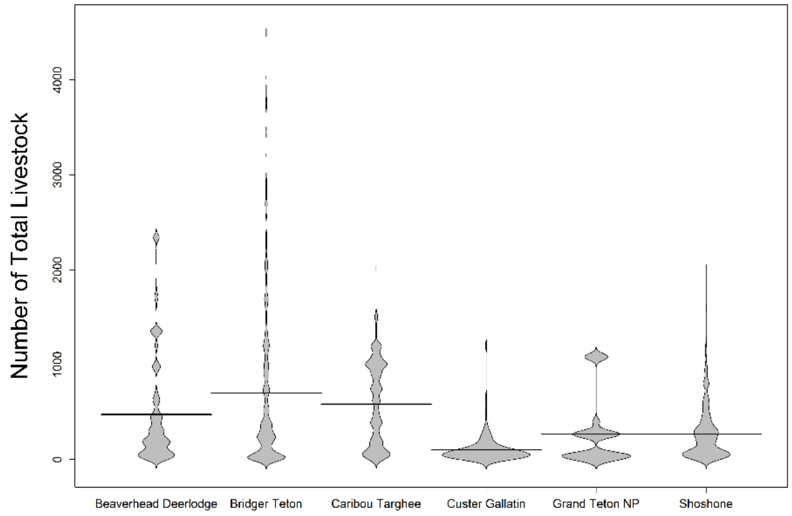


Figure F1. Distribution (density) of livestock numbers stocked per allotment per year on each forest in the Demographic Monitoring Area (DMA), 1992–2014. Horizontal lines represent the mean number of livestock stocked per allotment for each forest during 1992–2014. Plots were created using kernel density estimation in the R package “beanplot” (Kampstra 2008).

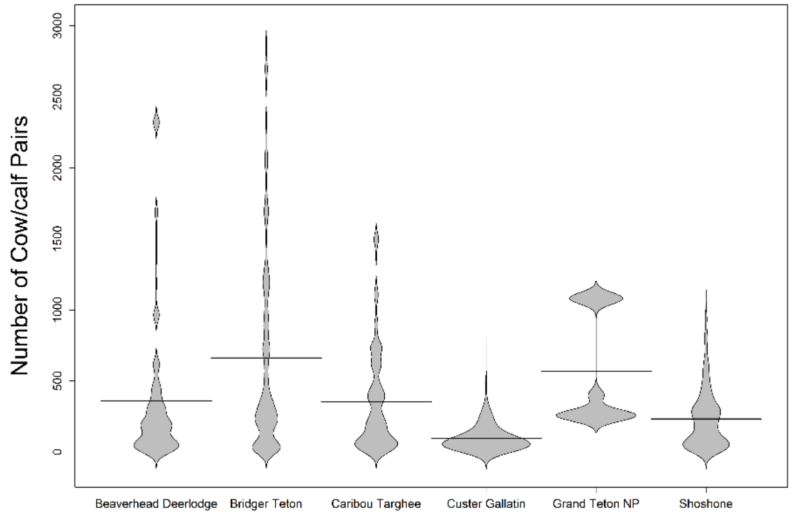


Figure F2. Distribution (density) of cow/calf numbers stocked per allotment per year on each forest in the Demographic Monitoring Area (DMA), 1992–2014. Horizontal lines represent the mean number of cow/calf pairs stocked per allotment for each forest during 1992–2014. Plots were created using kernel density estimation in the R package “beanplot” (Kampstra 2008)

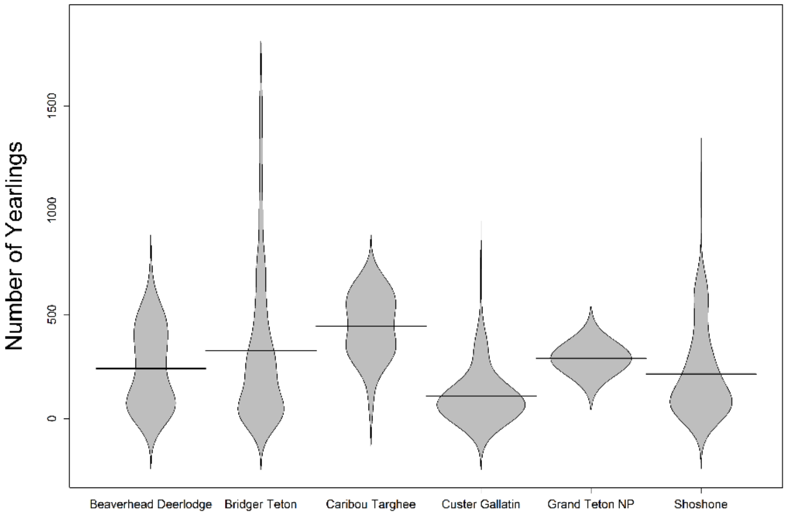


Figure F3. Distribution (density) of yearling numbers stocked per allotment per year on each forest in the Demographic Monitoring Area (DMA), 1992–2014. Horizontal lines represent the mean number of yearlings stocked per allotment for each forest during 1992–2014. Plots were created using kernel density estimation in the R package “beanplot” (Kampstra 2008).

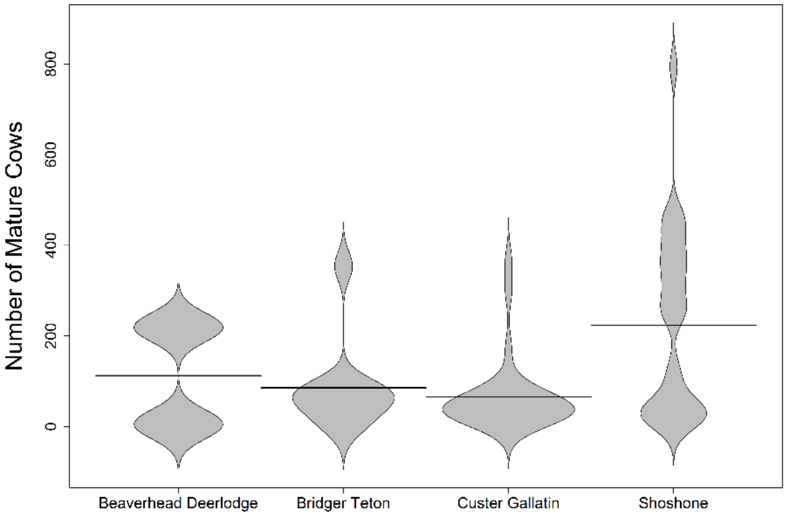


Figure F4. Distribution (density) of mature cow numbers stocked per allotment per year on each forest in the Demographic Monitoring Area (DMA), 1992–2014. Horizontal lines represent the mean number of mature cows stocked per allotment for each forest during 1992–2014. Plots were created using kernel density estimation in the R package “beanplot” (Kampstra 2008).

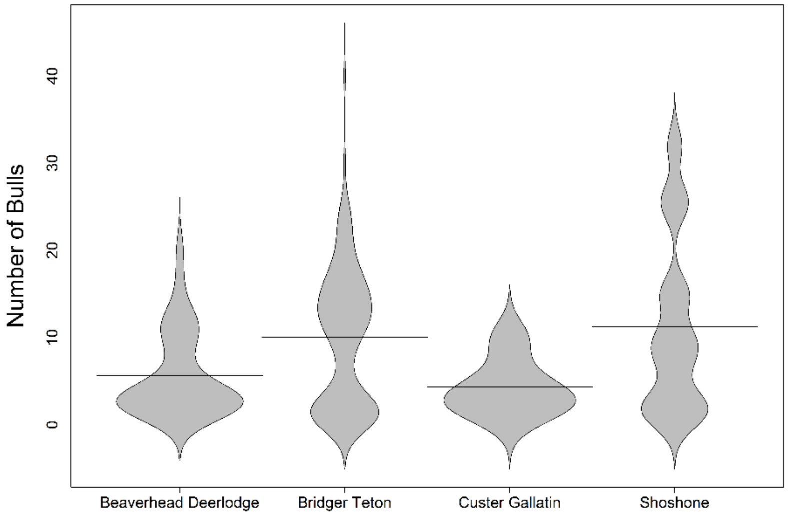


Figure F5. Distribution (density) of bull numbers stocked per allotment per year on each forest in the Demographic Monitoring Area (DMA), 1992–2014. Horizontal lines represent the mean number of bulls stocked per allotment for each forest during 1992–2014. Plots were created using kernel density estimation in the R package "beanplot" (Kampstra 2008, R Core Team 2016).

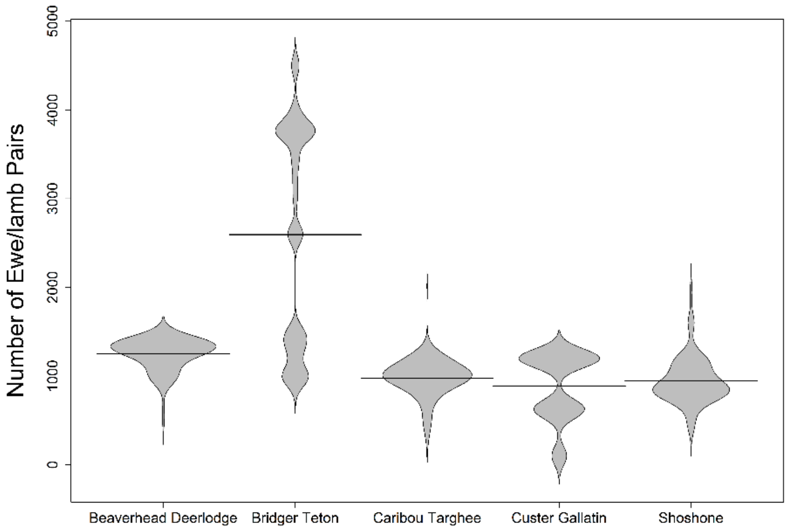


Figure F6. Distribution (density) of ewe/lamb numbers stocked per allotment per year on each forest in the Demographic Monitoring Area (DMA), 1992–2014. Horizontal lines represent the mean number of ewe/lamb pairs stocked per allotment for each forest during 1992–2014. Plots were created using kernel density estimation in the R package "beanplot" (Kampstra 2008).

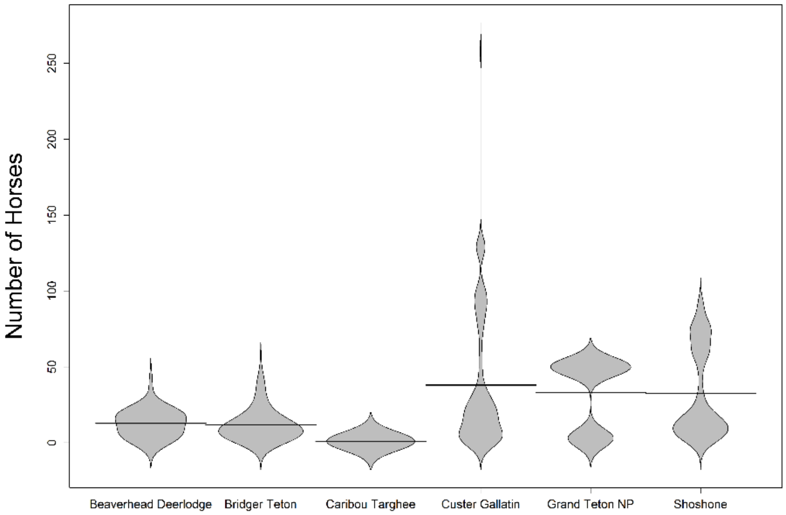


Figure F7. Distribution (density) of horse numbers stocked per allotment per year on each forest in the Demographic Monitoring Area (DMA), 1992–2014. Horizontal lines represent the mean number of horses stocked per allotment for each forest during 1992–2014. Plots were created using kernel density estimation in the R package "beanplot" (Kampstra 2008).

APPENDIX G

GENERALIZED LINEAR MIXED MODEL SELECTION RESULTS

Table G1. Akaike Information Criteria (AIC$_c$) values for the candidate models to identify factors related to livestock depredation by grizzly bears on USFS and NPS grazing allotments in the Demographic Monitoring Area (DMA) from 1992–2014.

Model[a]	Variables[b]	K[c]	AIC$_c$	ΔAIC$_c$	AIC$_c$ w_i	Cum AIC$_c$ w_i	Log likelihood
22	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + tree cover$_{\text{daily}}$ + distance to forest edge$_{\text{daily}}$ + elevation$_{\text{HR}}$ + terrain ruggedness$_{\text{daily}}$ + road density$_{\text{HR}}$ + bear density	22	2576.67	0	0.22	0.22	-1266.21
21	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + ndvi$_{\text{HR}}$ + stream density$_{\text{HR}}$ + elevation$_{\text{HR}}$ + terrain ruggedness$_{\text{daily}}$ + road density$_{\text{HR}}$ + bear density	22	2576.70	0.04	0.22	0.44	-1266.23
10	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + elevation$_{\text{HR}}$ + terrain ruggedness$_{\text{daily}}$ + road density$_{\text{HR}}$ + bear density	20	2577.00	0.33	0.19	0.63	-1268.40
23	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + tree cover$_{\text{daily}}$ + distance to forest edge$_{\text{daily}}$ + ndvi$_{\text{HR}}$ + WBP presence$_{\text{HR}}$ + WBP production + bear density	22	2577.40	0.73	0.15	0.79	-1266.58
18	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + summer + ndvi$_{\text{HR}}$ + WBP presence$_{\text{HR}}$ + WBP production + bear density	21	2577.75	1.08	0.13	0.92	-1267.77
16	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + ndvi$_{\text{HR}}$ + WBP presence$_{\text{HR}}$ + WBP production + bear density	20	2580.04	3.37	0.04	0.96	-1269.92
14	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + summer × stream density$_{\text{HR}}$ +ndvi$_{\text{HR}}$ + bear density	21	2581.06	4.39	0.02	0.98	-1269.42
20	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + mothsite presence$_{\text{HR}}$+ WBP presence$_{\text{HR}}$ + WBP production + bear density	20	2583.52	6.85	0.01	0.99	-1271.66
24	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + tree cover$_{\text{daily}}$ + distance to forest edge$_{\text{daily}}$ + bear density	19	2584.49	7.82	0	0.99	-1273.16
12	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + terrain ruggedness$_{\text{daily}}$ + stream density$_{\text{HR}}$ + bear density	19	2585.46	8.8	0	1	-1273.64
13	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + bear density + distance to bear range edge$_{\text{HR}}$	18	2585.65	8.99	0	1	-1274.75
26	~ bear density + distance to bear range edge$_{\text{HR}}$ + elevation$_{\text{HR}}$ + terrain ruggedness$_{\text{daily}}$ + road density$_{\text{HR}}$	8	2651.66	74.99	0	1	-1317.81

[a] All models were a generalized linear mixed model with a negative binomial distribution and a random intercept of allotment ID (1 | Allotment ID)

[b] Spatial extents for each habitat variable represent grizzly bear daily activity area (8 km^2) and average annual female grizzly bear home range (HR; 196 km^2)

[c] Number of estimated model parameters

Table G1 Continued.

Model[a]	Variables[b]	K[c]	AIC$_c$	ΔAIC$_c$	AIC$_c$ w_i	Cum AIC$_c$ w_i	Log likelihood
9	~ no. livestock× livestock class + no. livestock × bull/horse + season length + allotment size + recurring depredation + elevation$_{HR}$ + terrain ruggedness$_{daily}$ + road density$_{HR}$	20	2724.19	147.52	0	1	-1342.00
8	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + elevation$_{HR}$ + terrain ruggedness$_{daily}$ + road density$_{HR}$	19	2725.62	148.95	0	1	-1343.72
7	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + summer × stream density$_{HR}$	19	2732.77	156.1	0	1	-1347.29
17	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + summer + ndvi$_{HR}$ + WBP presence$_{HR}$ + WBP production	20	2733.89	157.22	0	1	-1346.85
11	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + terrain ruggedness$_{daily}$ + stream density$_{HR}$	18	2736.4	159.73	0	1	-1350.12
15	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + ndvi$_{HR}$ + WBP presence$_{HR}$ + WBP production	19	2745.69	169.02	0	1	-1353.76
25	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + tree cover$_{daily}$ + distance to forest edge$_{daily}$	18	2747.11	170.44	0	1	-1355.47
19	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + WBP presence$_{HR}$ + WBP production + mothsite presence$_{HR}$	19	2751.04	174.37	0	1	-1356.43
5	~ no. livestock× livestock class + no. livestock × bull/horse + season length + allotment size + recurring depredation	17	2753.17	176.5	0	1	-1359.51
6	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation	16	2753.79	177.13	0	1	-1360.83
4	~ no. livestock× livestock class + season length + allotment size + bull/horse + recurring depredation + stocked prev yr	17	2755.13	178.46	0	1	-1360.49
3	~ no. livestock× livestock class + season length + allotment size + bull/horse + spring + summer + fall	18	2770.11	193.44	0	1	-1366.97
2	~ no. livestock× livestock class + season length + allotment size + bull/horse	15	2783.2	206.53	0	1	-1376.54
27	~ WBP presence$_{HR}$ + WBP production + mothsite presence$_{HR}$ + tree cover$_{daily}$ + distance to forest edge$_{daily}$ + ndvi$_{HR}$ + stream density$_{HR}$	10	2789.84	213.17	0	1	-1384.89
1	~ 1 [null model]	3	2815.65	239.0	0	1	-1404.82

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[a] All models were a generalized linear mixed model with a negative binomial distribution and a random intercept of allotment ID (1 \| Allotment ID)

[b] Spatial extents for each habitat variable represent grizzly bear daily activity area (8 km^2) and average annual female grizzly bear home range (HR; 196 km^2)

[c] Number of estimated model parameters

APPENDIX H

PLOT OF ESTIMATED RANDOM EFFECTS

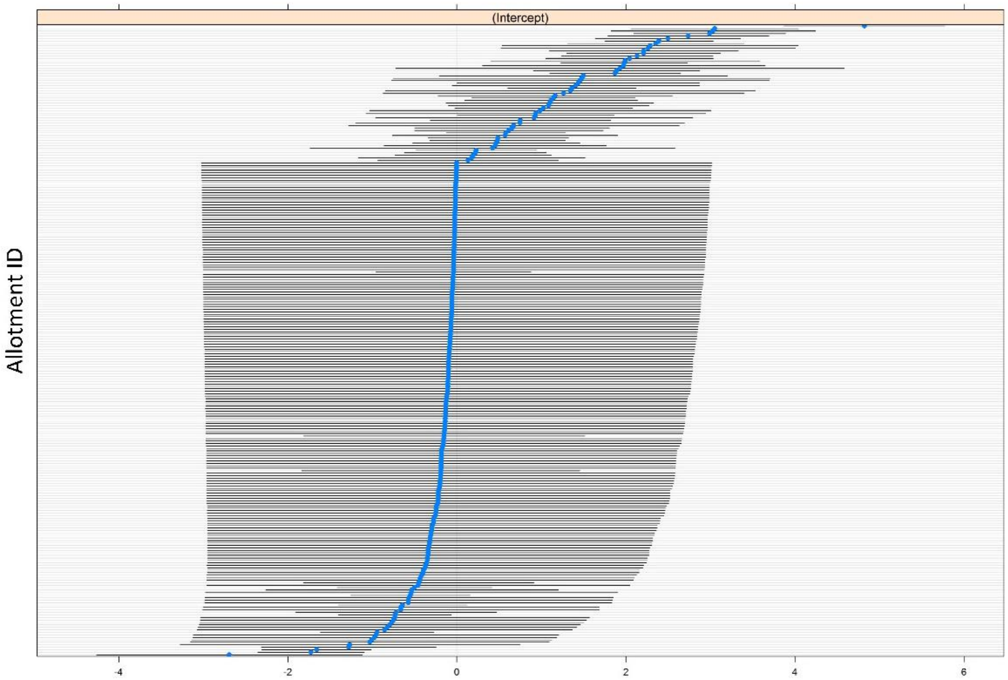

Figure H1. Estimated random effects for allotment ID from the most supported model with 95% confidence intervals for 254 USFS and NPS grazing allotments in the GYE, 1992–2014.