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Grizzly bear responses to restrictions of recreation in Yellowstone National Park

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Abstract

Avoiding humans will be more difficult and energetically costly for animals as outdoor recreation increases and people venture farther into wildland areas that provide high-quality habitat for wildlife. Restricting human access can be an attractive management tool to mitigate effects of human recreation activities on wildlife; however, the efficacy of such measures is rarely assessed. In 1982, Yellowstone National Park identified areas important to grizzly bears (*Ursus arctos*) to help protect critical grizzly bear habitat and reduce the likelihood of human injuries by bears. Referred to as bear management areas (BMAs), human access is restricted in these areas for 2–8 months each year, with timing and type of restrictions varying by area. We examined 2 datasets to evaluate grizzly bear selection of BMAs and differences of bear density in BMAs and non-BMAs. First, we used 17 years of recent global positioning system telemetry data for grizzly bears to assess their selection of BMAs during periods when human access was allowed, and when access was restricted. We used step-selection functions to test the hypothesis that bears spend time in places that allow them to avoid people and select quality food sources. There was support that grizzly bears differentially select for BMAs regardless of whether human access was restricted at the time, compared with areas outside BMAs, and that selection changed with sex and season. Only males during the summer and hyperphagic seasons

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changed their selection of BMAs based on whether access restrictions were in place, and overall, male bears preferred unrestricted BMAs (BMAs without restrictions in place). Females preferentially selected BMAs regardless of whether the area had access restrictions in place only during the mating season. Individuals varied widely in their preference for BMAs and access restrictions. Bears likely choose to spend time in BMAs based on available food resources rather than restrictions to human access. Supporting this interpretation, our analyses indicated that a greater proportion of BMA in an area was associated with higher densities of grizzly bear. Thus, restrictions to human access likely help reduce the potential for human–bear interactions, accomplishing one of the original objectives for establishing the BMAs.

KEYWORDS

access restrictions, grizzly bear, human–bear interactions, recreation, resource selection, *Ursus arctos*, Yellowstone National Park

Human activity in wildland areas can affect animals directly through human-caused mortality and indirectly by altering movement and behavior (Sinclair and Byrom 2006, Suraci et al. 2019, Nickel et al. 2020). For example, animals may respond to disturbance from recreation through increased flight and vigilance (Stankowich 2008, Naylor et al. 2009), altered habitat selection in space and time (Suraci et al. 2019, Nickel et al. 2020), increased physiological stress (Creel et al. 2002), and reduced reproductive success (Shively et al. 2005). Some forms of recreation, such as hiking and horseback riding, are often thought of as low-intensity activities and therefore compatible with wildlife conservation, yet these activities also may change wildlife behavior in cryptic, but potentially important, ways (Naylor et al. 2009, Darimont et al. 2015, Whittington et al. 2019, Naidoo and Burton 2020).

Globally, natural areas receive 8 billion human visits annually, and with wildland recreation increasing throughout the world, it is important to understand the ability of wildlife species to adapt their behaviors in response to recreational activities (Balmford et al. 2015, Larson et al. 2016). As recreation increases, people venture farther into wildland areas that often provide high-quality habitat for animals, making avoidance of humans more difficult and energetically costly (Nickel et al. 2020). Restrictions to human access can be an attractive management tool to mitigate effects of human recreation on wildlife. When managers excluded humans from areas occupied by species such as South American fur seals (*Arctocephalus australis*) and shorebirds, animals displayed fewer stress-related behaviors and expanded into areas where human activity previously occurred (Cassini 2001, Burger and Niles 2013). Despite some evidence that restrictions to human access may reduce impacts on wildlife, their effectiveness rarely is quantified (Coleman et al. *2013a*, Larson et al. 2016). Further, the few studies evaluating behavioral changes of wildlife in response to recreation restrictions have not focused on protected areas with preservation mandates, such as national parks (Cassini 2001, Larson et al. 2016, Lamb et al. 2018).

Protected areas around the world allow different intensities of human activity, from high-intensity resource extraction to low-intensity recreation (e.g., hiking, horseback riding). In the United States, the National Park Service (NPS) operates under a directive to provide enjoyment for people while simultaneously preserving species and landscapes for future generations (NPS Organic Act of 1916, 16 U.S.C. §1; Watson et al. 2014). The NPS oversees stewardship of nearly 25% of the threatened or endangered species in the United States, yet NPS lands account for only 3% of the country's land area (Ament et al. 2008, U.S. Census Bureau 2021, NPS *2023b*). On NPS lands, recreation typically is limited to low-intensity activities (NPS *2023b*). Research focused on animal responses to recreation in protected areas, such as land managed by the NPS, can provide important baseline information for comparison with areas experiencing more intense human use. For species that require large areas to roam, insights about behavioral adaptive capacity are particularly important for effective management on landscapes with an array of uses (Hebblewhite et al. 2021).

In 1982, Yellowstone National Park instituted seasonal (2–8 months) restrictions to human access (i.e., access restrictions) in areas thought to be important to grizzly bears (*Ursus arctos*; NPS 1982, Gunther 1994). These bear management areas (BMAs) were established as a response to the listing of the grizzly bear population in the Greater Yellowstone Ecosystem as threatened under the Endangered Species Act in 1975 (U.S. Fish and Wildlife Service 1975) and recommendations to protect critical grizzly bear habitat (Craighead 1980), in concert with new bear management policies intending to reduce human injuries by bears (NPS 1982, Gunther 1994). The NPS sought to meet 3 objectives with the implementation of BMAs: minimize bear–human interactions that could lead to the habituation of bears to people, prevent human-caused displacement of bears from prime bear food resources, and reduce risk of human injuries in areas with high levels of bear activity (Craighead 1980, NPS 1982). Biologists selected areas for BMA designation because they contained calorie-rich bear foods, encompassed locations that were deemed to have high densities of bears, or included places where females consistently produced cubs (Table S1, available in Supporting Information; NPS 1982).

Although BMAs were established primarily because they contained important bear foods, the distribution and timing of these foods have shifted. Since BMA establishment, fires have burned about 58% of the park's area (NPS *2023c*) and climate change increasingly mediates the distribution and abundance of seasonally available foods for bears (Kokaly et al. 2003), such as whitebark pine (*Pinus albicaulis*; Interagency Grizzly Bear Study Team 2013, Bjornlie et al. 2014, Costello et al. 2014). In terms of meat resources, the population of Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) has declined by 90% since the early 1990s (Koel et al. 2005). Additionally, the elk (*Cervus canadensis*) population fluctuated and ultimately decreased by >60%, whereas the bison (*Bison bison*) population increased (Barber-Meyer et al. 2008, White et al. 2016, NPS *2023e*). Ungulate carcasses are available year-round, following the reintroduction of gray wolves (*Canis lupus*; Gunther and Smith 2004). Since the 1980s, the grizzly bear population in the Greater Yellowstone Ecosystem expanded from perhaps fewer than 250 to around 1,000 individuals (Eberhardt and Knight 1996, Gould et al. 2023). The density of bears in Yellowstone National Park has increased since BMAs were established in 1982, though spatial variation exists (Figure S1, available in Supporting Information; Bjornlie et al. 2014, Corradini et al. 2023). Human visitation to Yellowstone National Park has doubled during this period, with >4 million visits every year since 2015 (NPS 2023*g*), except 2020 when the park implemented closures because of the COVID pandemic and 2022 when the park experienced a 500-year spring flood event. Over 90% of these visits occurred between May and September, during bears' active period (NPS 2023*g*). These changes warrant an assessment of the effectiveness of human access restrictions as a management tool in Yellowstone National Park.

Whereas many studies have characterized resource selection by grizzly bears, few studies have assessed the effectiveness of BMAs (Gunther 1990; Coleman et al. 2013*a*, *b*). These studies demonstrated that humans displaced grizzly bears from high-quality food resources and that access restrictions to recreation likely reduced human–bear interactions (Gunther 1990; Coleman et al. 2013*a*, *b*). Neither study quantified whether grizzly bears spend more time in BMAs relative to other backcountry areas and whether greater densities of bears occur in BMAs, which would provide a foundation to answer more nuanced questions regarding access restrictions and recreation sites.

We examined 17 years of recent global positioning system (GPS) telemetry data obtained from grizzly bears in Yellowstone National Park to better understand resource selection of areas with access restrictions. We tested the hypothesis that bears preferentially spend time in areas where it is easier to avoid people. Thus, the status of access restrictions (whether access restrictions are in place or not) may determine whether bears choose to spend time in BMAs. We predicted that bears would prefer BMAs when human access is restricted. Alternatively, we hypothesized that BMAs are intrinsically important for bears because of the food resources they contain. Accordingly, we predicted that bears prefer areas designated as BMAs, regardless of access restriction status, as opposed to non-BMAs. To better understand the differentiation between these 2 hypotheses, we assessed whether bears preferred BMAs associated with their intrinsic importance (i.e., regardless of whether access restrictions were in place) and whether bears chose areas based on the status of access restrictions. For the first hypothesis, we compared BMA use with areas that are never restricted (non-BMAs), and for the second hypothesis, we compared bear use of BMAs with active access restrictions (restricted BMAs), BMAs without active access restrictions (unrestricted BMAs), and areas that were never restricted (non-BMAs). Finally, given that the density of grizzly bears has increased throughout the national park, we compared an index of grizzly bear density to evaluate whether the potential for human–bear interactions was greater in BMAs than non-BMAs.

STUDY AREA

Our study area encompassed Yellowstone National Park, an area comprising 8,991 km^2 mainly in northwest Wyoming, with some areas in Montana and Idaho, USA (NPS 2023*f*). This area included several large plateaus bordered by rugged mountains in the north, east, and south. Elevations ranged from 1,500 m to 3,400 m. Spruce (*Picea* spp.)-fir (*Abies* spp.) and lodgepole pine (*Pinus contorta*) forests covered most of the area, but extensive sagebrush (*Artemisia* spp.) and grassland vegetation occurred on high-elevation plateaus and in low-elevation valleys (Despain 1990). This study focused on the active season (May–October) of grizzly bears from 2004 to 2020. During this time at Yellowstone Lake, daily average temperature ranged from −10°C to 18°C, and monthly average precipitation ranged from 0.3 cm to 15 cm (National Climatic Data Center 2010). Summers are cool and short, and winters are cold and long (Frank and McNaughton 1992).

Unlike other large carnivores, grizzly bears, black bears (*Ursus americanus*), and coyotes (*Canis latrans*) never were extirpated from the park. Mountain lions (*Puma concolor*) recolonized on their own and gray wolves were reintroduced in 1995. The populations of grizzly bears, black bears, wolves, and mountain lions have increased, whereas the coyote population has decreased since the mid-1990s (Barber-Meyer et al. 2008, White et al. 2016, Ruth et al. 2019, Haroldson et al. 2020). Eight species of ungulates also occurred in the park: elk, bison, moose (*Alces alces*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), pronghorn (*Antilocapra americana*), mountain goats (*Oreamnos americanus*), and bighorn sheep (*Ovis canadensis*). Ungulate populations in the park have fluctuated over time and management objectives limited the bison population to between 2,400 and 5,500 individuals (NPS 2023*e*).

Seventeen BMAs have been in place since 1982 and encompass approximately 21% (188,032 ha) of the park (Figure 1; Appendix A; NPS 1982, Coleman et al. 2013*a*). Biologists originally chose BMA boundaries by identifying areas with high densities of grizzly bears (Craighead 1980) and areas that held important foods for bears, such as Yellowstone cutthroat trout, bison, elk, pocket gophers (*Thomomys talpoides*), whitebark pine seeds, and diverse and productive vegetation (Table S1; NPS 1982).

In BMAs, access restrictions included complete closures, limits to the timing of activities (i.e., day-use only) or the location of activities (i.e., on-trail travel only; NPS 1982). Time-of-day restrictions limited travel to daytime (0900 to 1900) hours. In 3 BMAs, people could camp at backcountry campsites along Yellowstone Lake but could not travel away from these campsites (NPS 2023*a*). The timing and duration of BMA restrictions differed among BMAs, but most occurred during spring and early summer and lasted 2 or 4 months (Appendix A).

METHODS

Bear locations and seasons

We used GPS telemetry data obtained from grizzly bears captured by the Interagency Grizzly Bear Study Team as part of a long-term population research program (Blanchard 1985). We used locational data collected from

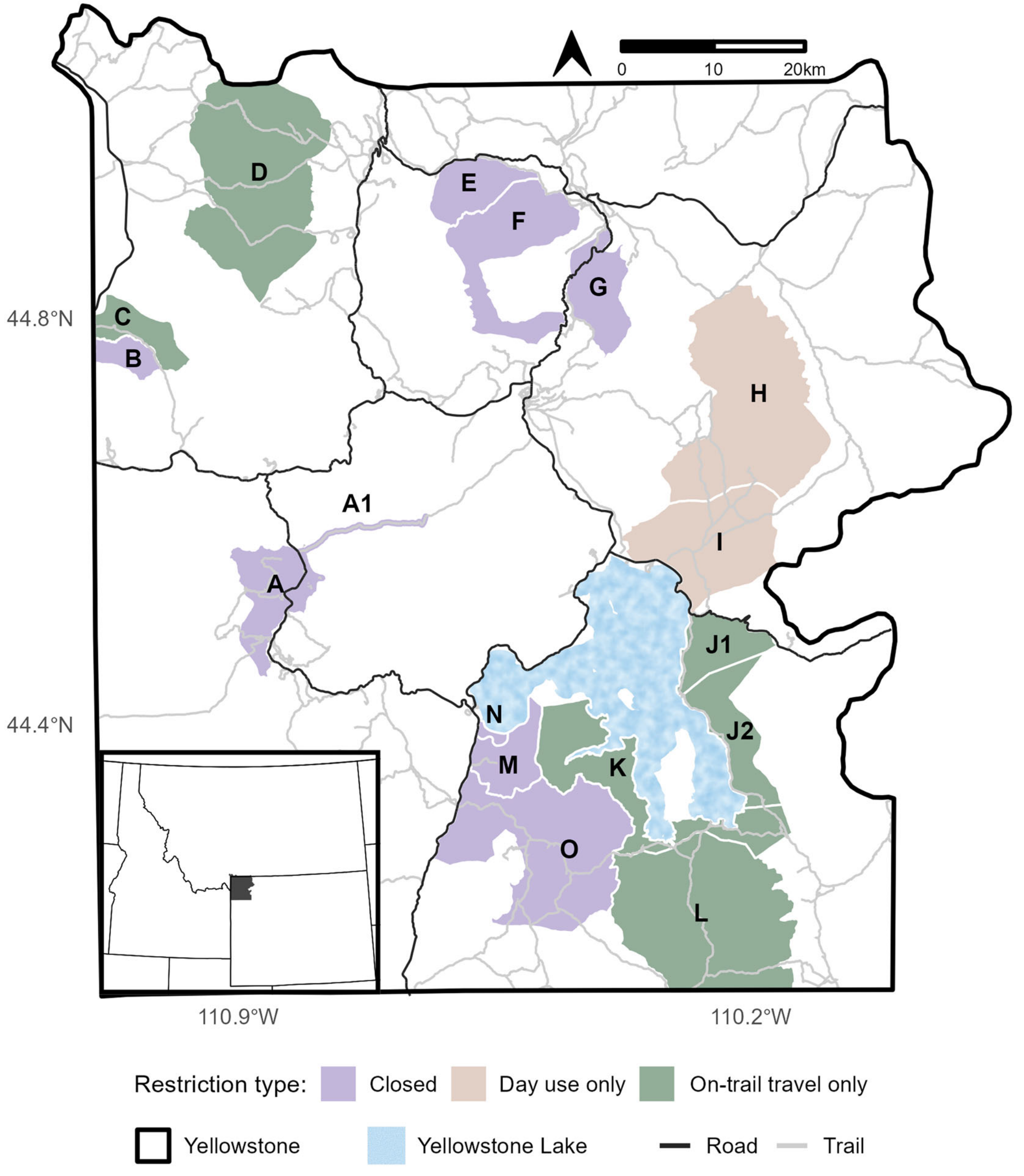

FIGURE 1 Study area, including bear management areas (BMAs), access restrictions to BMAs (closed, day use only, on-trail travel only), trails, and major roads in Yellowstone National Park, Wyoming, USA, 2004–2020.

GPS-enabled radio-collars (Telonics, Mesa, AZ, USA) during 2004–2020. We performed all analyses on GPS data from on-board memory downloaded after collar retrieval. We excluded 2- and 3-dimensional GPS fixes with a position dilution of precision >10 and horizontal error >125 m (D'Eon and Delparte 2005). Because these data were collected over 17 years, collars recorded fixes at time intervals ranging from 13 to 208 minutes, with most fixes occurring at 105-, 60-, 52-, or 30-minute intervals. We subsampled these data to only include consecutive locations with a time interval of 105 minutes (±15 min; i.e., 90 to 120 min) and only included individuals (i.e., bear-year) with at least 100 fixes (equaling 7 days of monitoring) in each season (Figure S2, available in Supporting Information). We then constructed yearly 95% minimum convex hull home ranges for each individual by using the adehabitatHR package (Mohr 1947, Calenge 2006). We included individuals in our analyses if 80% of their home ranges fell within the national park boundary; we used this value to ensure individuals included in the study had the opportunity to spend time in BMAs.

Grizzly bears select different resources throughout the non-denning period (April–October; Nielsen et al. 2004, 2010; Zeller et al. 2019; McClelland et al. 2020), so we created ecologically based seasons using methods of Basille et al. (2013; Supporting Information). This approach incorporated environmental and movement variables to account for changes in bear behavior based on food availability and life history (Basille et al. 2013). We defined the same seasons for male and female bears to enable comparisons between sexes. We delineated 6 seasons during which bears exhibited distinct movement patterns: post denning (15 March–6 April), spring (7–30 April), mating (1 May–29 June), summer (30 June–10 August), hyperphagic (11 August–3 October), and autumn (4 October–denning). For this study, we developed season-specific step-selection functions for the 3 seasons (mating, summer, hyperphagic) that coincide with highest park visitation (NPS 2023*g*). We conducted all analyses in R version 4.0.4 (R Core Team 2021).

Bear resource selection

Overview

We quantified grizzly bear responses to access restrictions using a 2-stage analysis. This multi-stage approach allowed us to first characterize and account for overall resource selection by grizzly bears and then make inferences regarding specific variables of interest. In stage I, we created resource selection functions for grizzly bears based on ecological variables, with different models for each sex (female and male) and season combination. These ecological models provided the foundation for stage II to test our predictions. To do so, we added categorical variables representing potential intrinsic importance of BMAs (intrinsic BMA; whether a location was inside or outside of a BMA, regardless of access restrictions) and access restriction status of BMAs (BMA status; whether human access was restricted at the time).

For both stages of analysis, we focused on fine-scale resource selection using step-selection functions to incorporate the varying temporal restrictions of BMAs (Thurfjell et al. 2014). The matched-point design inherent to step-selection functions pairs each used location with ≥1 available locations (collectively referred to as a stratum; Thurfjell et al. 2014). We accounted for the movement of bears in availability by simulating available locations from distributions of an individual's turn angles and step lengths (Signer et al. 2019). We classified an individual's data within a calendar year as a unique bear-year. We generated 10 available locations for each used location using the random_steps function in the amt package (Signer et al. 2019), which randomly selects locations based on a gamma distribution of an individual's step lengths and a von Mises distribution of an individual's turn angles (Signer et al. 2019). Creating available locations from an individual's movements reduces autocorrelation issues common with spatial and temporal data and allows covariate values to change as the animal moves (Avgar et al. 2016, Signer et al. 2019).

We followed the modeling approach outlined by Muff et al. (2020) and Duchesne et al. (2010). We used conditional Poisson mixed models with stratum-specific intercepts, which compare temporally correlated matched pairs. We fixed the variance of stratum-specific intercepts to 10,000 to avoid shrinkage (Muff et al. 2020). The parameter estimates and standard errors resulting from these models are likelihood-equivalent (Duchesne et al. 2010, Muff et al. 2020). We included a random intercept for each individual and included random slopes for covariates to account for variation in individual selection; this also reduces bias in availability and allows for more robust population-level estimates of fixed effects when modeling step-selection functions (Gillies et al. 2006, Hebblewhite and Merrill 2008, Duchesne et al. 2010, Muff et al. 2020). During the first stage of analysis, we determined whether to include random slopes on covariates in step-selection functions based on likelihood-ratio tests that compared iterative random coefficient structures estimated with restricted maximum likelihood (Zuur et al. 2009). During the second stage of analysis, we also included random slopes on BMA variables for each sex and season combination. We used package glmmTMB to fit all models (Brooks et al. 2017).

Ecological models

To create our initial ecological models, we included covariates known or hypothesized to influence resource selection by grizzly bears, such as land cover, terrain, and anthropogenic attributes. We measured all distances using st_distance in the sf package (Pebesma 2018). Distributions of plant species can affect where grizzly bears occur, so we included categorical variables for land cover to account for important food resources (lodgepole pine forest, wet forest, subalpine fir [*Abies lasiocarpa*] forest, whitebark pine forest, Douglas-fir [*Pseudotsuga menziesii*] forest, shrub, dry meadow, wet meadow, rock, water; LANDFIRE 2019, McClelland et al. 2020). Grizzly bears often forage and seek refuge (i.e., daybed) near the interface between forest and open areas (Blanchard 1983, Nielsen et al. 2004), so we included distance to nearest forest edge (LANDFIRE 2019); we assigned negative distance values to locations in forest and positive values to non-forested areas (Peck et al. 2017). We quantified distance to nearest water (Yellowstone National Park Spatial Analysis Center 2020) given that water sources are important for bears to thermoregulate (Rogers et al. 2021), find foods such as spawning trout (Haroldson et al. 2005), consume succulent vegetation (Teisberg et al. 2014), and travel along (Wilson et al. 2005). Terrain features and topography affect the movement of bears (Carnahan et al. 2021), so we included topographic roughness index (TRI; Riley et al. 1999), aspect, elevation, and slope rasterized from a digital elevation model (30-m resolution; U.S. Geological Survey 2013) to account for variation in landscape permeability. Resource selection by grizzly bears is influenced by anthropogenic landscape features such as roadways and developments (Mace et al. 1996, Ciarniello et al. 2007), so we included the nearest Euclidean distance to anthropogenic areas (e.g., roads and developments), with negative distance values associated with locations inside developments (Yellowstone National Park Spatial Analysis Center 2020).

Biologists move wildlife carcasses occurring near developments and along road corridors to specific carcass-redistribution sites, so we accounted for the potential influence of this concentrated, high-quality food in our models. To quantify the zone of influence of carcass-redistribution sites and account for bears who may visit a carcass opportunistically, we first delineated a buffer with a 400-m radius around the center of each of 9 carcass-redistribution sites (Ebinger et al. 2016). We classified a feeding event as beginning at the location just before the bear entered the buffered area and ending with the location just after the bear left the buffered area; a feeding event included ≥2 GPS locations within the buffered area within 24 hours. This approach allowed bears to revisit a carcass-redistribution site multiple times within a feeding event. We defined the zone of influence for each carcass-redistribution site based on the distance from the center of each site within which 90% of all feeding-event locations occurred. In our step-selection functions, we included a binary variable that identified whether a location fell within (1) or outside (0) the defined area. We examined correlations between pairs of continuous covariates and removed elevation and slope because of relationships with distance to anthropogenic areas, distance to water, and TRI ($R > 0.6$). We centered and scaled (Schielzeth 2010) all continuous covariates (distance to anthropogenic areas, distance to water, TRI, distance to edge).

To select the ecological model that best explained variation in grizzly bear resource selection, we developed model suites for each combination of sex and season. We considered models with all possible additive combinations of land cover, distance to forest edge, distance to water, TRI, aspect, distance to anthropogenic areas, and carcass-redistribution site. We compared models for each sex and season based on Akaike's Information Criterion corrected for small sample size (AIC_c), calculated using the MuMIn package (Burnham and Anderson 2002, Barton 2019). For each combination of sex and season, we used the top model from this first stage of analysis (Table S2, available in Supporting Information) as the foundation for hypothesis testing.

BMA models

In the second stage of analysis, we tested our BMA predictions by adding combinations of 4 covariates (intrinsic BMA, BMA status, abundance of whitebark pine cones, drought) to the ecological model from stage I. We added an intrinsic BMA variable (ecological model + intrinsic BMA) or a BMA status variable (ecological model + BMA status) to determine the strength of selection of BMAs by grizzly bears (Table 1). For BMAs with human access limited to on-trail travel, we divided the area into unrestricted BMA (≤200 m from a trail) and restricted BMA (>200 m from a trail). The amount of forest cover and whether a trail was motorized or non-motorized influenced the distance at which bears changed their movements and behavior in conjunction with trails (Ladle et al. 2019, Proctor et al. 2019, Parsons et al. 2020). Previous studies indicate bears change their movements 80–1,000 m from roads, depending on topography and vegetation (Proctor et al. 2019, Parsons et al. 2020). Our study occurred in an area where recreation on trails was limited to low-intensity activities (i.e., hiking, horseback riding), so we chose a lower value (200 m) as the zone of influence.

We also examined whether grizzly bears changed selection of BMAs based on other factors, namely abundance of whitebark pine cones or drought severity. We included interaction terms for these 2 factors with each BMA variable (intrinsic BMA and BMA status). Whitebark pine is a masting species and grizzly bears consume the seeds from their cones during fall (15 August–30 September; Costello et al. 2014). The abundance of whitebark pine has declined because of mortality from mountain pine beetle (*Dendroctonus ponderosae*) and white pine blister rust (*Cronartium ribicola*; Jewett et al. 2011). We categorized abundance of whitebark pine cones based on annual cone count surveys (Haroldson et al. 2004, Haroldson 2020). We classified years as abundant or scarce when the average cones per tree exceeded or were below the median value of the time series, respectively (Haroldson and Gunther 2013). Given that whitebark pine stands occurred within some BMAs, we predicted that grizzly bears would increase their selection of BMAs during years with abundant whitebark pine cones compared with scarce years (Haroldson et al. 2004).

Since BMA establishment, climate change has altered the distribution and phenology of plants in the area (Notaro et al. 2019), so we also tested whether selection of BMAs changed depending on relative drought severity. Drought conditions, for example, change the caloric content and timing of available vegetative foods (Mattson 2004, Baruch-Mordo et al. 2014). We classified drought severity based on monthly values for the Palmer drought severity index (PDSI; Palmer 1965; provided by A. Enriquez, University of Wyoming). We predicted that selection of BMAs would be greater during periods of drought, given that BMA boundaries were created to encompass important vegetative foods of grizzly bears.

We compared models for each season and sex combination (5 models for summer and mating, 7 models for hyperphagic; Table 2) to determine the model that best explained resource selection by grizzly bears. Each model suite included the ecological model without additional covariates as a benchmark model, so we could test whether the addition of BMA-related variables helped explain variation in resource selection. We only included PDSI and whitebark pine cone abundance as interactions with BMA variables, given that values for these covariates did not

TABLE 1 Description of bear management area (BMA) variables used to evaluate grizzly bear selection of BMAs, 2004–2020, Yellowstone National Park, Wyoming, USA.

Variable	Definition	
BMA intrinsic (binary)	BMA	Areas with restrictions to human access at any time during the year
	Non-BMA	Areas outside of BMAs that never have restrictions to human access
BMA status (categorical)	Restricted BMA	BMAs with restrictions to human access in place or areas within 200 m of a trail in BMAs with on-trail travel only restrictions
	Unrestricted BMA	BMAs without restrictions to human access in place or areas farther than 200 m from a trail in BMAs with on-trail travel only restrictions
	Non-BMA	Areas outside of BMAs that never have restrictions to human access

TABLE 2 Models describing selection of bear management areas (BMAs) by grizzly bears for different sex and season combinations, Yellowstone National Park, Wyoming, USA, 2004–2020. We compared 5 candidate models during the mating and summer seasons and 7 during the hyperphagic season to test hypotheses about grizzly bear responses to BMAs. We included the ecological model as a baseline for comparison, which represents resource selection without accounting for BMAs; all BMA models also include the variables from the ecological model. We used conditional Poisson regression to compare paired used and available locations (1 used:10 available).

Sex	Season	Model structure	K[a]	ΔAIC_c[b]	AIC_c weight[c]	log-likelihood	n[d]
Female	Mating	BMA intrinsic	18	0.00	0.69	−117,140.5	18
		BMA intrinsic × PDSI[e]	19	1.86	0.27	−117,140.5	
		BMA status	20	6.96	0.02	−117,142.0	
		BMA status × PDSI	22	8.29	0.01	−117,140.7	
		Ecological	17	17.81	0.00	−117,150.4	
	Summer	BMA intrinsic	19	0.00	0.65	−78,832.5	14
		BMA intrinsic × PDSI	20	1.49	0.31	−78,832.3	
		BMA status	21	6.25	0.03	−78,833.7	
		BMA status × PDSI	23	9.26	0.01	−78,833.2	
		Ecological	17	12.02	0.00	−78,840.5	
	Hyperphagic	BMA intrinsic	20	0.00	0.33	−68,502.0	14
		BMA status × WBP[f]	21	0.58	0.24	−68,501.3	
		BMA intrinsic × PDSI	21	1.08	0.19	−68,501.6	
		BMA status	22	2.15	0.11	−68,501.1	
		Ecological	18	3.46	0.06	−68,505.7	
		BMA status × PDSI	24	3.89	0.05	−68,500.0	
		BMA status × WBP	24	5.37	0.02	−68,500.7	
Male	Mating	BMA intrinsic	22	0.00	0.47	−107,866.8	24
		BMA intrinsic × PDSI	23	0.16	0.44	−107,865.9	
		BMA status	24	4.22	0.06	−107,867.0	
		BMA status × PDSI	26	5.42	0.03	−107,865.6	
		Ecological	20	35.32	0.00	−107,886.5	
	Summer	BMA status	23	0.00	0.85	−70,628.7	19
		BMA status × PDSI	25	3.48	0.15	−70,628.5	
		BMA intrinsic	21	12.18	0.00	−70,636.8	
		BMA intrinsic × PDSI	22	13.61	0.00	−70,636.5	
		Ecological	19	37.68	0.00	−70,651.6	
	Hyperphagic	BMA status	19	0.00	0.59	−49,493.3	15
		BMA status × PDSI	21	1.58	0.27	−49,492.1	
		BMA status × WBP	21	3.98	0.08	−49,493.3	
		BMA intrinsic	17	5.76	0.03	−49,498.2	

(Continues)

TABLE 2 (Continued)

Sex	Season	Model structure	K[a]	ΔAIC_c[b]	AIC_c weight[c]	log-likelihood	n[d]
		BMA intrinsic × PDSI	18	7.69	0.01	−49,498.1	
		BMA intrinsic × WBP	18	7.73	0.01	−49,498.1	
		Ecological	15	34.35	0.00	−49,514.4	

[a] Number of parameters in model.

[b] Difference between ranked models based on Akaike's Information Criterion corrected for small sample sizes.

[c] Akaike's Information Criterion weight.

[d] Number of individual bear-years.

[e] Palmer drought severity index.

[f] Whitebark pine cone production.

differ between used and available locations (Street et al. 2016). Whitebark pine cone abundance was only included in models for the hyperphagic season. We again compared model fit using AIC_c, calculated using the MuMIn package (Burnham and Anderson 2002, Barton 2019). We evaluated the fit of our models using k-fold cross-validation procedures developed by Fortin et al. (2009) for step-selection functions, using 80% of data for training and 20% for testing with 5 folds repeated 100 times for each sex and season combination.

Index of bear density

We used the index of grizzly bear density developed by Bjornlie et al. (2014) and extended by Corradini et al. (2023) to assess differences in grizzly bear density between BMAs and other areas, a proxy for the likelihood of human–bear encounters. This index used long-term capture and telemetry data, calculated for 14- × 14-km grid cells (approximate annual home-range of female bears), to hindcast and forecast estimated range extents of individuals to create a spatial-temporal reconstruction of the grizzly bear population during 1983–2020. This process uses future captures to inform the density index, so the last 5 years (i.e., 2015–2020) were projected (Bjornlie et al. 2014, Corradini et al. 2023). We examined annual index values from 1983–2020.

We tested our prediction that areas containing a greater proportion of BMA had a greater density of grizzly bears using an autoregressive mixed-effects model. We used the index of grizzly bear density in each cell as the dependent variable and included the proportion of BMA within each cell and year as covariates. The year component of this model accounted for changes in the size of the bear population. We included random intercepts for each cell to account for within-cell variation among years (Zuur et al. 2009) and accounted for temporal patterns among repeated measures of density for a cell over time with a first-order autoregressive correlation structure (Box et al. 1994). We defined and fit the model in the nlme package (Pinheiro and Bates 2023).

RESULTS

We obtained 280,353 GPS locations from 116 bears collared during 2004–2020 (Table S3, available in Supporting Information). After standardizing fix interval among bears and reducing fixes to only those occurring during the mating, summer, and hyperphagic seasons, these GPS locations provided data for 39,148 used steps from 56 bear-years (35 male, 21 female). Each season included 3,939–8,567 GPS locations from 15–24 bear-years for males and 5,441–9,312 locations from 14–18 bear-years for females. We matched the used locations with 391,480 available locations (1 used:10 available). Selection for resources changed across seasons and sexes, resulting in different ecological models (Tables S2, S4–S9, available in Supporting Information). Cross-validation demonstrated that our models were useful predictors of grizzly bear resource selection (all Spearman rank correlations > 0.75).

BMA models

There was some evidence that females selected BMAs more than non-BMAs. The intrinsic BMA variable was included in the competing models for the mating (combined AIC$_c$ weight = 0.96) and summer (combined AIC$_c$ weight = 0.95) seasons (Table 2). Based on the best approximating model, female grizzly bears were 1.3 times (95% CI = 1.0–1.8) more likely to be in a BMA during the mating season, compared with non-BMAs (Appendix B). During summer, females were somewhat (1.3 times, 95% CI = 0.8–2.1) more likely to be in a BMA compared with non-BMAs, but confidence intervals of odds ratios overlapped 1 (Appendix B). During the hyperphagic season, patterns of selection were less evident, as the benchmark ecological model was among competing models (Table 2). Although there was modest support for the intrinsic BMA variable and for an interaction between BMA status and yearly whitebark pine cone production or PDSI during the hyperphagic season (Table 2), confidence intervals of parameter estimates overlapped zero.

Male bears preferred BMAs to other areas in all seasons and changed their selection based on BMA restriction status in the summer and hyperphagic seasons (Table 2). Males were 1.8 times (95% CI = 1.3–2.4) and 1.9 times (95% CI = 1.1–3.1) more likely to be in unrestricted BMAs, compared with non-BMAs, during the summer and hyperphagic seasons, respectively (Appendix B). Males were somewhat more likely to be in restricted BMAs compared with non-BMAs during the summer and hyperphagic seasons (1.2 times for both seasons; 95% CI = 0.9–1.6), but confidence intervals of odds ratios overlapped 1 (Appendix B). During the mating season, male bears differentiated selection based on the intrinsic BMA variable (combined AIC$_c$ weight of competing models = 0.91; Table 2), but they were only 1.2 times more likely to be in BMAs compared with non-BMAs, and the confidence interval for the odds ratio overlapped 1 (95% CI = 0.9–1.6; Appendix B).

We detected substantial variation in selection of BMAs among individuals (Figure 2). For example, during the mating season, individual males were 0.8–2.7 times as likely to be in BMAs compared with non-BMAs (Figure 2).

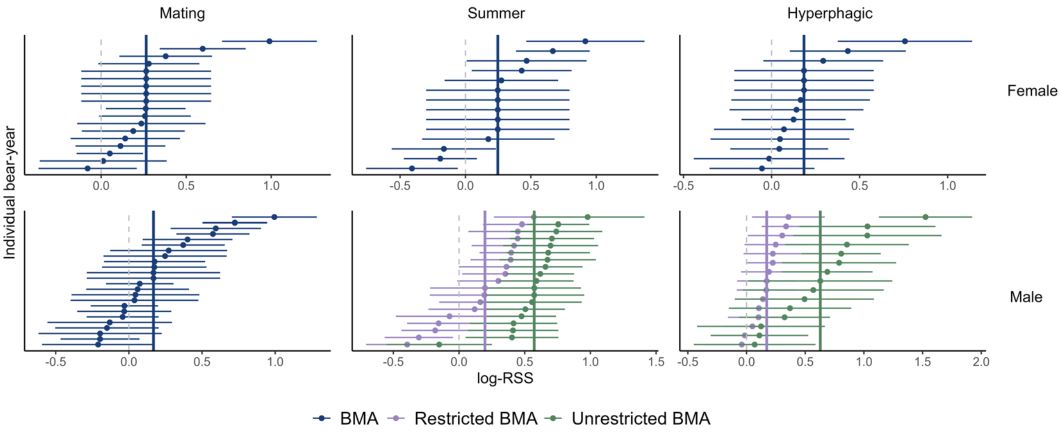

FIGURE 2 Selection patterns (log-relative selection strength [log-RSS]) by individual male and female grizzly bears of bear management areas (BMAs), based on the top model for each sex and season combination, Yellowstone National Park, Wyoming, USA, 2004–2020. All estimates are compared with selection of non-BMAs. The vertical dashed line at 0 represents equal selection and the colored vertical line represents the population-level estimate for each sex-season combination. The horizontal lines represent ±1 standard error of the individual estimate.

We did not observe clear patterns in this variation based on bear age, whether females had cubs, whether bears were known to be habituated to humans, or their spatial distribution.

Index of bear density

We detected a positive relationship between the index of grizzly bear density and the proportion of BMA in each grid cell ($P = 0.016$, $t_{56} = 2.5$). After adjusting for temporal autocorrelation, a grid cell (14 × 14 km) covered by 100% BMA would be expected to have an average of 6 additional bears (95% CI = 1.2–10.7) compared to a cell with no BMA. On a cell-by-cell basis, the density index for the national park increased over time ($\beta = 0.24$, 95% CI = 0.21–0.28, $P < 0.001$, $t_{2,145} = 13.5$).

DISCUSSION

Understanding where large mammals choose to spend time across an environment with different degrees of human use has broad implications for managing species that require large areas to live. Although grizzly bears occur throughout Yellowstone National Park, we predicted they would be more likely to spend time in areas where human access restrictions are in place because of an inherent avoidance of people. Our results reflect a more nuanced picture. Although most bears in our sample chose to spend time in BMAs, areas identified as important for bears in 1982, no clear pattern of selection emerged among sexes or seasons, and individuals varied in their degree of selection. Only male bears showed differentiation in selection based on access restrictions, and they preferred unrestricted BMAs, counter to our prediction. Further, we did not find evidence that abundance of whitebark pine cones or drought conditions influenced selection of BMAs. Bears chose to spend time in BMAs, but the absence of humans likely does not drive this phenomenon.

Across all seasons, bears in our study showed little to no preference for BMAs while human access restrictions were in place. Several factors could contribute to this finding. First, other areas of the park offered similar levels of human activity as restricted BMAs, even if these other areas lack such a management designation. Recreation in the park occurred at a low density, with only 1,704 km of trails in the 8,991-km^2 area (NPS 2023*d*). Although >4 million people visited the park annually, most of those visitors stayed within 5 km of a road, which reduced the number of recreationists in the backcountry (White et al. 2017). Snow and river conditions in many areas of the park limit human access to only 2–3 months, whereas bears reside in these areas throughout the non-denning period. Additionally, bears may not choose to completely forego foraging in areas with high-quality food resources when recreation occurs at low levels. Male bears preferred unrestricted BMAs during the summer and hyperphagic seasons, which coincided with the peak of visitation to the park (NPS 2023*f*). Bears in unrestricted BMAs may temporally and spatially alter their behavior to avoid recreationists while still accessing food resources (Gunther 1990, Rode et al. 2006, Ordiz et al. 2011, Coleman et al. 2013*b*). In Scandinavia, where brown bears are hunted, bears changed their foraging activity during times of day associated with high risk but did not change during times with lower hunting activity (Hertel et al. 2016). Lamb et al. (2020) reported that bears were not passive in shaping their encounters with people and may have tolerated some degree of human disturbance to access high-quality food resources.

Male bears' preference of unrestricted BMAs also may stem from a mismatch between the timing of human access restrictions and when bears use food resources within BMAs. Lush vegetation and ungulate carcasses were extensively used by male bears throughout the summer and hyperphagic seasons (Mattson et al. 1991, Fortin et al. 2013, Gunther et al. 2014), yet the access restrictions for BMAs containing these foods end before or during the time when bears consume them (Appendix A, Table S1; Mealey 1975, Fortin et al. 2013). Furthermore, BMAs around Yellowstone Lake were established to encompass streams where grizzly bears fished for spawning cutthroat trout, but the number of bears fishing these tributary streams has decreased in since the early 2000s because of a decline in trout (Haroldson et al. 2005, Teisberg et al. 2014). Bears use other resources to supplement the decline of this calorie-rich food resource, potentially changing when bears spend time in these BMAs (Fortin et al. 2013). Finally, changes in the predator guild in the park since BMA establishment provide bears, particularly dominant males, with year-round opportunities to scavenge wolf- or cougar-killed ungulate carcasses (Mattson 1997, Metz et al. 2012). Although carcass availability has shifted temporally, the increase in grizzly bear density (Corradini et al. 2023) may have led to increased competition for these resources. Mismatches in the timing of access restrictions and male use of calorie-rich food resources may contribute to when male bears preferred to spend time in BMAs, but the spatial distribution of calorie-rich foods also has shifted since BMAs were established.

Food resources available outside of BMAs also may have contributed to limited evidence of selection for BMAs for females (all seasons) and males (mating season). Ungulate carcasses have become available throughout the year in the northern range (Metz et al. 2012), the area with the highest densities of wolves and cougars within the national park (Smith and Bangs 2009, Ruth et al. 2019); however, few BMAs were designated in the northern range (Figure 1). Bears may now spend time outside of BMAs in this area to capitalize on the shifted spatial distribution of calorie-rich carrion. Additionally, bears may spend time outside BMAs to consume high-quality food resources that have always existed (Knight 1975, Mealey 1975, Bjornlie et al. 2014). For example, Hayden Valley does not have BMA designation but contained high-quality food resources (Knight 1975) and was noted as an important area for grizzly bears as early as the 1960s (Hornocker 1962). Bears may have made short-term tradeoffs to avoid people while accessing quality food resources wherever they occur, within or outside of BMAs.

Although several BMAs were established because they contained whitebark pine stands, there was little evidence that variation in whitebark pine cone production was associated with grizzly bear selection of BMAs. Previous work supports this finding: bears do not change their movements to access whitebark pine stands during years with abundant cones (Costello et al. 2014). As opportunistic omnivores, foraging plasticity of grizzly bears allows individual bears to use alternate foods if whitebark pine stands do not occur within their home ranges or if cone production is low (Schwartz et al. 2014). In addition to whitebark pine productivity, we investigated whether bears changed their selection of BMAs based on drought conditions. Support for this interaction was limited, likely because the spatial and temporal resolution of the index we used was relatively coarse. Exploring changes to the distribution and timing of important food resources, particularly those found in BMAs as a function of spatiotemporal variation in climate will be important, given that the region is expected to become increasingly warmer and drier (Notaro et al. 2019).

Intraspecific interactions may have contributed to sex-based differences in selection of BMAs. Male bears often outcompete females for high-quality food resources (Rode et al. 2006, Fortin et al. 2013, Steyaert et al. 2013) and survival of male bears has increased since BMAs were established (van Manen et al. 2016). Females, particularly those with cubs, often avoid areas where male use is high, likely to reduce risk of intraspecific predation (Mattson and Reinhart 1995, Støen et al. 2005, Rode et al. 2006, Steyaert et al. 2013). This avoidance may be particularly pronounced where the density of bears is high. In a salmon-subsidized environment in Alaska, for example, energy intake by females with cubs was reduced when large males were present but increased when large males were absent and people were present (Rode et al. 2006). Limited evidence of female selection for BMAs in our study may thus have been mediated by their avoidance of areas with high-quality food resources to minimize intraspecific competition (Nevin and Gilbert 2005). Because of sample size limitations, we could not conduct separate analyses for females with cubs and lone females. Sex-based differences in selection for BMAs may also have been a function of spatial scale. Male grizzly bears generally range widely, and, in our study, their home ranges typically encompassed a substantial area of BMA and non-BMA, whereas females have smaller home ranges. The probability that males encounter BMAs and learn about resources available in these areas (Blanchard and Knight 1991, Thompson et al. 2021) is thus greater compared with females; some individual females may have had little opportunity to learn about BMAs.

As a solitary, long-lived species, individual bears differ in their diets, patterns of resource selection, and tolerance of people (Hertel et al. 2017, 2019; Ordiz et al. 2020; Thompson et al. 2021), which likely contributes to spatiotemporal tradeoffs. When we examined individual variation among our sampled bears in their selection of BMAs, a few bears exhibited no selection of BMAs, whereas most showed some degree of selection for these areas (Figure 2). Bears, particularly females, learn from their mothers and display similar selection patterns (Nielsen et al. 2013, Morehouse et al. 2016). Differences in selection could create lineages of bears that learn a tradition of spending time in BMAs or not using them (Servheen and Gunther 2022). Of course, bears continually learn about the environment and change their behavior based on current conditions and spatial memory (Thompson et al. 2021), which likely also accounts for individual variation in BMA selection. Although estimating population-level selection helps us understand overall trends, further exploration of individual variation in BMA selection can provide important insights, particularly given the demonstrated potential for cascading effects on reproduction and survival (Gardner et al. 2014, Morehouse et al. 2016). Substantial variation in BMA selection between sexes and among individuals may have had an outsized influence on our findings, requiring that we better understand the factors driving such differences. This may be especially relevant in a large, protected area that is fully occupied by grizzly bears and within which density-dependent effects on demographic processes (van Manen et al. 2016) and body composition of individuals (Corradini et al. 2023) have been documented.

Given that the density of grizzly bears was higher in areas with a BMA designation and that areas with higher caloric availability are linked with greater densities of bears (Hilderbrand et al. 1999, Mowat et al. 2013), our results indicate that BMAs still contain important food resources for bears. Further, our study provides evidence that BMAs with restrictions in place likely reduce the potential for human-bear encounters that could lead to negative interactions. Over the study period, human visitation to Yellowstone National Park increased substantially (NPS 2023*f*) as did the density of bears throughout the park, suggesting the probability of human–bear encounters simultaneously increased. Whereas the probability of human–bear encounters throughout the national park is greater now than when BMAs were established, the potential for such encounters is compounded in areas with a greater proportion of BMA because of even higher bear densities. Worldwide, the number of bear attacks increased during 2000–2015 with areas of higher bear density explaining most of the variation (Bombieri et al. 2019). This trend is also apparent in our study area. For example, Hayden Valley (a non-BMA) has one of the highest index values for grizzly bear density in the Greater Yellowstone Ecosystem and is the site of 3 of the last 5 human fatalities due to bear attacks in Yellowstone National Park (Gunther and Haroldson 2020). Restrictions to recreation in areas with high densities of bears likely increase the safety for recreationists.

Our study provides evidence that BMAs still meet some of their intended objectives, based on 2 lines of evidence. First, human–bear interactions are more likely within BMAs because these areas have higher densities of bears. These interactions could lead to human injury and to the habituation of bears to people. Limiting access can improve human safety by reducing the potential for human–bear interactions in areas with high bear densities (Bombieri et al. 2019). Second, even with some model uncertainty, BMAs still contain important areas because most bears chose to spend time there. Additionally, cross-validation provides support that these results reflect the population-level selection of BMAs by bears. When access restrictions are in place, the potential for bears to be displaced from high-quality food resources by people is reduced. Although our results did not indicate that bears select for BMAs specifically to avoid people, access restrictions likely improve human safety in these high-density areas and reduce the need for bears to make short-term tradeoffs to access quality food resources while avoiding human disturbance (Ciuti et al. 2012).

MANAGEMENT IMPLICATIONS

The BMA system in Yellowstone National Park was implemented in 1982, with area boundaries delineated primarily based on bear density and distributions of important foods. Our results indicate that BMAs generally encompass areas that grizzly bears select, suggesting they offer valuable food and other resources. In addition, high densities of bears occur in BMAs and access restrictions reduce the potential for human–bear interactions, bear-inflicted human injuries, and habituation of bears to people in backcountry areas. As currently implemented, the timing of access restrictions may not match when bear selection for BMAs is high, given that selection typically was not aligned with when restrictions were in place. Objectives of the BMA program may be enhanced by modifying the timing of access restrictions, a periodic evaluation of BMA placement and boundaries, and examining temporal variation of BMA use between males and females.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Procedures for capturing, sampling, and instrumenting grizzly bears conformed with the Animal Welfare Act and were approved by the Institutional Animal Care and Use Committees of the United States Geological Survey (number 201201) and permitted by the United States Fish and Wildlife Service Endangered Species Permit. Additional permits for capture and research procedures were approved by the National Park Service (research permit number 0073).

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article. Grizzly bear location data represent sensitive information and are withheld from public distribution (National Parks Omnibus Management Act of 1998, Title II, Sec 207).

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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APPENDIX A

Table A1

TABLE A1 Types and dates of access restrictions in bear management areas (BMA) in Yellowstone National Park, Wyoming, USA, 1982–2023.

Type of access restriction	BMA	Label	Start date	End date	Area (km^2)
Complete closure	Firehole	A1	10 Mar	Friday before Memorial Day	78.0
	Richard's Pond	B	10 Mar	Friday before Memorial Day	22.1
	Blacktail	E	10 Mar	30 Jun	49.9
	Gneiss Creek	C	10 Mar	30 Jun	39.5
	Mary Mountain Trail	A1	10 Mar	31 Jul	3.1
	Antelope	G	10 Mar	10 Nov	65.3
	Heart Lake	O	1 Apr	30 Jun	228.0
	Pelican Valley	I	1 Apr	3 Jul	143.2
	Riddle/Solution	M	30 Apr	14 Jul	47.7
	Grant Village	N	20 Jun	Road opening date	4.2
	Lake Spawn	K	15 May	14 Jul	132.7
	Washburn	F	1 Aug	10 Nov	121.5
On-trail-travel only	Two Ocean	L	14 Mar	14 Jul	279.9
			22 Aug	10 Nov	
	Clear Creek #2	J2	1 Apr	14 Jul	69.4
	Clear Creek #1	J1	1 Apr	10 Aug	51.1
	Gallatin	D	1 May	10 Nov	270.1
	Gneiss Creek	C	1 Jul	10 Nov	39.5
Day use only	Mirror Plateau	H	15 May	10 Nov	269.0
	Pelican Valley	I	4 Jul	10 Nov	143.1
Off-trail with special permit	Two Ocean	L	15 Jul	21 Aug	279.9
By special permit	Washburn	F	10 Mar	31 Jul	121.5

APPENDIX B

Table B1

TABLE B1 Parameter estimates and 95% confidence intervals from the best-supported model for the bear management area (BMA) model suite for grizzly bears, by sex and season, 2004–2020, Yellowstone National Park, Wyoming, USA. We compared candidate models to test our hypotheses about grizzly bear responses to different levels of restrictions to human access. All continuous variables were centered and scaled.

Sex	Season	Parameter	Estimate	95% CI	
Female	Mating	TRI[a]	0.200	0.170	0.230
		Aspect-north	−0.235	−0.310	−0.159
		Aspect-east	−0.188	−0.259	−0.117
		Aspect-west	−0.181	−0.254	−0.109
		Land cover-wet forest	0.209	0.107	0.312
		Land cover-shrub	0.184	0.108	0.260
		Land cover-dry meadow	0.284	0.175	0.392
		Land cover-subalpine fir	−0.041	−0.156	0.074
		Land cover-Douglas-fir	0.155	0.044	0.265
		Land cover-wet meadow	0.213	0.081	0.345
		Land cover-rock	−0.260	−0.485	−0.036
		Land cover-water	−0.909	−1.083	−0.734
		Land cover-WBP[b]	0.084	−0.059	0.226
		Distance to anthropogenic	−0.303	−0.559	−0.048
		CRS[c]	0.257	0.020	0.494
		BMA	0.265	−0.035	0.564
	Summer	Distance to forest edge	0.099	0.048	0.149
		Aspect-north	0.140	0.049	0.231
		Aspect-east	−0.009	−0.098	0.080
		Aspect-west	0.073	−0.007	0.153
		Land cover-wet forest	0.419	0.293	0.544
		Land cover-shrub	0.181	0.079	0.282
		Land cover-dry meadow	0.380	0.263	0.497
		Land cover-subalpine fir	−0.006	−0.136	0.125
		Land cover-Douglas-fir	0.339	0.175	0.503
		Land cover-wet meadow	0.721	0.588	0.855
		Land cover-rock	0.355	0.137	0.573
		Land cover-water	−1.188	−1.695	−0.682
		Land cover-WBP	0.082	−0.066	0.230

TABLE B1 (Continued)

Sex	Season	Parameter	Estimate	95% CI	
		Distance to anthropogenic	−0.291	−0.617	0.036
		CRS	0.383	0.051	0.716
		BMA	0.247	−0.23	0.724
	Hyperphagic	Distance to forest edge	0.110	0.045	0.176
		TRI	0.044	0.006	0.083
		Distance to water	0.054	−0.005	0.113
		Aspect-north	0.122	0.028	0.216
		Aspect-east	0.084	−0.006	0.174
		Aspect-west	−0.093	−0.189	0.003
		Land cover-wet forest	0.468	0.337	0.598
		Land cover-shrub	−0.100	−0.216	0.016
		Land cover-dry meadow	0.115	−0.028	0.259
		Land cover-subalpine fir	0.127	0.021	0.233
		Land cover-Douglas-fir	−0.061	−0.323	0.200
		Land cover-wet meadow	0.515	0.353	0.677
		Land cover-rock	−0.140	−0.416	0.137
		Land cover-water	−0.308	−0.649	0.034
		Land cover-WBP	0.251	0.125	0.378
		Distance to anthropogenic	−0.163	−0.359	0.034
		CRS	0.796	0.383	1.209
		BMA	0.184	−0.253	0.621
Male	Mating	Distance to forest edge	−0.040	−0.077	−0.003
		Distance to water	−0.039	−0.074	−0.005
		TRI	−0.126	−0.161	−0.092
		Aspect-north	−0.170	−0.247	−0.093
		Aspect-east	−0.113	−0.183	−0.042
		Aspect-west	−0.205	−0.275	−0.136
		Land cover-wet forest	0.418	0.307	0.529
		Land cover-shrub	0.238	0.153	0.323
		Land cover-dry meadow	0.172	0.074	0.271
		Land cover-subalpine fir	−0.087	−0.203	0.029
		Land cover-Douglas-fir	0.320	0.202	0.438
		Land cover-wet meadow	0.313	0.197	0.428
		Land cover-rock	0.446	0.255	0.637
		Land cover-water	−0.050	−0.216	0.116

(Continues)

TABLE B1 (Continued)

Sex	Season	Parameter	Estimate	95% CI	
		Land cover-WBP	0.047	−0.100	0.194
		Distance to anthropogenic	−0.030	−0.311	0.251
		CRS	0.429	−0.108	0.966
		BMA	0.168	−0.112	0.448
	Summer	Distance to water	−0.112	−0.161	−0.062
		TRI	−0.260	−0.313	−0.207
		Aspect-north	0.164	0.070	0.258
		Aspect-east	0.044	−0.048	0.136
		Aspect-west	0.025	−0.068	0.117
		Land cover-wet forest	0.636	0.521	0.751
		Land cover-shrub	0.114	0.011	0.216
		Land cover-dry meadow	0.234	0.114	0.354
		Land cover-subalpine fir	0.142	0.016	0.267
		Land cover-Douglas-fir	−0.063	−0.330	0.203
		Land cover-wet meadow	0.555	0.441	0.670
		Land cover-rock	−0.142	−0.379	0.095
		Land cover-water	0.004	−0.213	0.22
		Land cover-WBP	0.253	0.100	0.407
		Distance to anthropogenic	0.272	−0.408	0.952
		CRS	0.405	−0.405	1.215
		Restricted BMA	0.197	−0.093	0.487
		Unrestricted BMA	0.572	0.259	0.885
	Hyperphagic	TRI	−0.249	−0.312	−0.187
		Aspect-north	0.017	−0.094	0.128
		Aspect-east	0.109	0.004	0.215
		Aspect-west	−0.196	−0.312	−0.081
		Land cover-wet forest	0.225	0.073	0.377
		Land cover-shrub	−0.352	−0.478	−0.226
		Land cover-dry meadow	−0.273	−0.435	−0.110
		Land cover-subalpine fir	0.201	0.077	0.325
		Land cover-Douglas-fir	0.053	−0.180	0.287
		Land cover-wet meadow	0.331	0.177	0.484
		Land cover-rock	−0.939	−1.314	−0.565
		Land cover-water	−0.028	−0.257	0.201
		Land cover-WBP	0.059	−0.087	0.205

TABLE B1 (Continued)

Sex	Season	Parameter	Estimate	95% CI	
		CRS	0.584	0.144	1.025
		Restricted BMA	0.172	−0.115	0.459
		Unrestricted BMA	0.629	0.139	1.118

[a] Terrain roughness index.

[b] Whitebark pine.

[c] Carcass redistribution site.