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RESEARCH ARTICLE

Female and male grizzly bears differ in their responses to low-intensity recreation in a protected area

Elise A. Loggers[1] | **Andrea R. Litt**[1] | **Mark A. Haroldson**[2] | **Kerry A. Gunther**[3] | **Frank T. van Manen**[2]

[1]Department of Ecology, Montana State University, P.O. Box 173460, Bozeman, MT 59717-3460, USA

[2]U.S. Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, 2327 University Way, Suite #2, Bozeman, MT 59717, USA

[3]Bear Management Office, Yellowstone Center for Resources, Yellowstone National Park, P.O. Box 168, Yellowstone National Park, WY 82190, USA

Correspondence

Elise A. Loggers, Department of Ecology, Montana State University, P.O. Box 173460, Bozeman, MT 59717-3460, USA.
Email: elise.loggers@montana.edu

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Abstract

Strategies animals use to navigate human-dominated landscapes frequently mimic anti-predator responses employed by prey species. Understanding how large carnivores respond to outdoor recreation is important for conservation, particularly in protected areas with preservation mandates. Visitation to Yellowstone National Park doubled from 1980 to 2015, increasing the need to examine potential changes in behavior of grizzly bears (*Ursus arctos*) in relation to human recreation sites (trails, backcountry campsites). We developed integrated step-selection functions to explore how recreation sites influenced the movement rate and selection by male and female grizzly bears. Further, we tested whether time of day (diurnal, crepuscular, nocturnal) and restrictions to human access (i.e., restricted, unrestricted) modified bear responses and then compared behaviors based on proximity to recreation sites. Male grizzly bears used trails to travel during crepuscular and nocturnal hours and exhibited more pronounced behavior in restricted areas compared with unrestricted areas, suggesting recreation in unrestricted areas influenced the behavior of male bears. In contrast, female bears varied their movement rate and selection of trails in restricted areas much more than in unrestricted areas, suggesting females may make security

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tradeoffs between male bears and people. Both sexes used trails, likely as energetically efficient travel corridors; however, our analyses did not indicate that bears spent time near backcountry campsites. The sex-based differences in selection and movement patterns associated with trails and campsites suggest a single management approach for recreation may not equally benefit all bears. Recreation impacts on wildlife are complex to characterize and predict, but simultaneously modeling movement and selection provides a more comprehensive assessment of strategies animals use to navigate perceived risk.

KEYWORDS

brown bear, human–bear interactions, integrated step selection, recreation, *Ursus arctos*, Yellowstone National Park

For many animal populations, humans represent a significant source of risk in several ways (Darimont et al. 2015, Wolf and Ripple 2017). The strategies animals use to navigate human-dominated landscapes frequently reflect antipredator responses used by prey species (risk-disturbance hypothesis; Frid and Dill 2002). Prey can respond behaviorally to predators by minimizing their activity during periods when predators are active (Kohl et al. 2018), changing their movement rate (Proffitt et al. 2009), or spending time in areas that provide cover and refuge (Fortin et al. 2005). These behaviors illustrate spatial and temporal responses to predation risk. Frequent, predictable exposure to people in human-dominated landscapes may allow large carnivores to adopt similar behavioral strategies that facilitate co-occurrence with people. Large carnivores that persist near urban areas reduce temporal overlap with humans by becoming more nocturnal and can change their space use to avoid people (Ordiz et al. 2011, Lamb et al. 2020). Similar responses to predictable human activity also have been documented in wildland areas with large carnivores using trails and areas near roadways during periods when human use is absent or low (i.e., crepuscular, nocturnal; Gibeau et al. 2002, Coltrane and Sinnott 2015, Anton et al. 2020).

Recreation in wildland areas often occurs at irregular time intervals (sporadically) and may not allow animals to anticipate a disturbance, leading to more extreme responses (Frid and Dill 2002, Ordiz et al. 2011). Unpredictable human activity can cause animals to move farther after an encounter and subsequently consider places with sporadic human activity as higher risk (Miller et al. 2001, Seip et al. 2007, Lesmerises et al. 2018). For example, mule deer (*Odocoileus hemionus*) respond to people hiking off-trail by traveling farther distances compared to when hikers remain on trails (Miller et al. 2001), and caribou (*Rangifer tarandus*) abandon high-quality habitat when encounters with snowmobiles are inconsistent in timing and frequency (Seip et al. 2007). Wildlife also may reduce time spent in areas deemed risky by increasing their movement rate (Scrafford et al. 2018, Ladle et al. 2019). Wolverines (*Gulo gulo*), for example, couple avoidance of roads with increased travel speeds when near roads (Scrafford et al. 2018). Simultaneously modeling movement rates and resource selection can provide more nuanced insights about the risks that animals associate with anthropogenic features in wildland areas and the strategies and behaviors they use to navigate these landscapes (Avgar et al. 2016, Scrafford et al. 2018).

Grizzly bears (*Ursus arctos*), on the southern extent of their occupied range in North America, occur largely within protected areas (e.g., national parks, wilderness areas; U.S. Fish and Wildlife Service 2022), where recreation often is limited to low-intensity activities (e.g., hiking, horseback riding; National Park Service [NPS] 2023*a*). Increases in these types of recreation have prompted questions of how these activities influence bear behavior, particularly in protected areas with mandates to preserve natural processes (e.g., NPS 1916). Yellowstone National Park is a popular location for recreation and is managed as designated wilderness. The National Park Service implements additional access restrictions in certain backcountry areas, referred to as Bear Management Areas (BMAs, Figure 1; NPS 1982). For 2 to 8 months every year, recreation in BMAs is restricted to on-trail travel, daytime use, or access is closed completely (Table S1; NPS 1982). When people cannot access these areas, grizzly bears are more likely to be near recreation sites (Gunther 1990, Coleman et al. 2013*a*), and once people are allowed access, bears spend time closer to cover (Gunther 1990). Yellowstone National Park, therefore, offers a unique setting to examine relationships between bears and low-intensity human recreation sites (i.e., trails and backcountry campsites; hereafter recreation sites).

We integrated the risk-disturbance and risk-allocation hypotheses to understand how grizzly bears respond to backcountry recreation in a protected area (Lima and Bednekoff 1999, Frid and Dill 2002). We hypothesized that 1) behaviors of bears near recreation sites reflect perceived exposure to humans (risk-allocation hypothesis; Lima and Bednekoff 1999), and 2) bears associate recreation sites with risk where and when people are active (risk-disturbance hypothesis; Frid and Dill 2002). We adapted a behavioral framework from road ecology developed by Jacobson et al. (2016) and applied to movement and selection by Scrafford et al. (2018) to infer the behavior of grizzly bears near recreation sites (Figure 2). This combined framework predicts that animals that perceived roads as high-risk environments increased their movement rate and avoided roads, whereas animals that reduced speed while avoiding roads used a pausing behavior (Scrafford et al. 2018). Thus, we assumed that bears who increased

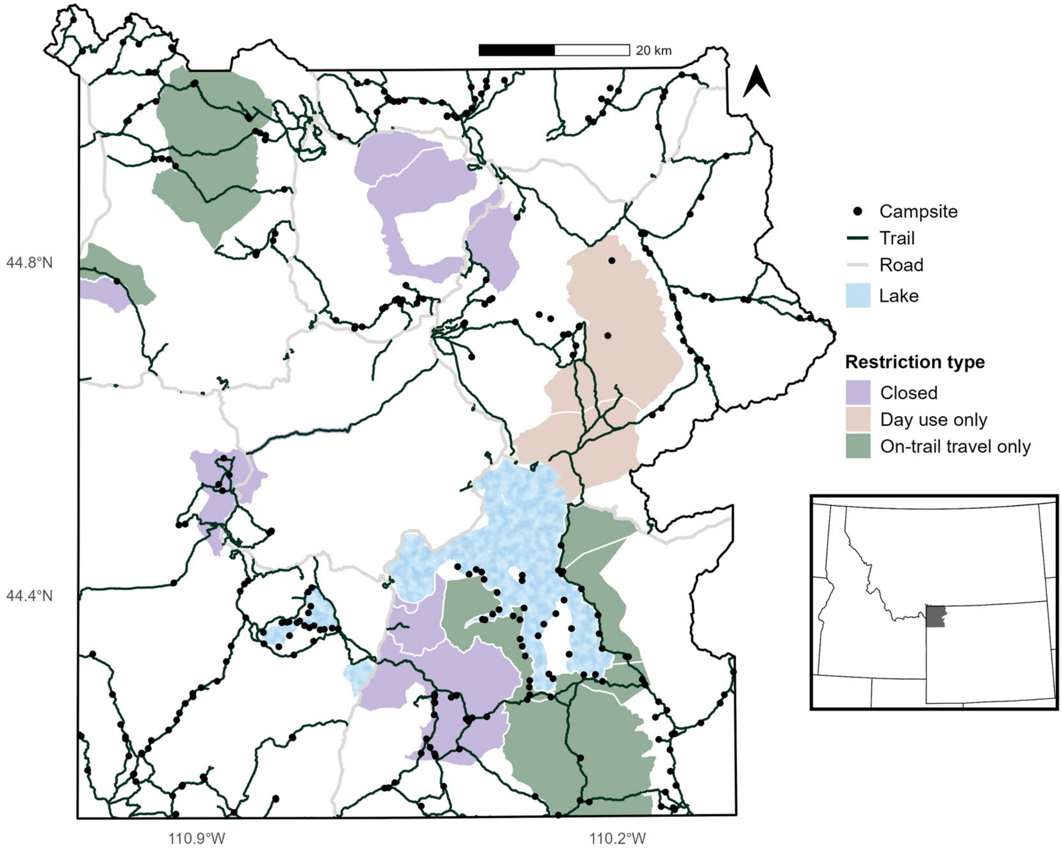

FIGURE 1 Study area, including Bear Management Areas (BMAs), access restrictions to BMAs (closed, day use only, on-trail travel only), and major roads in Yellowstone National Park, Wyoming, USA, 2004–2020.

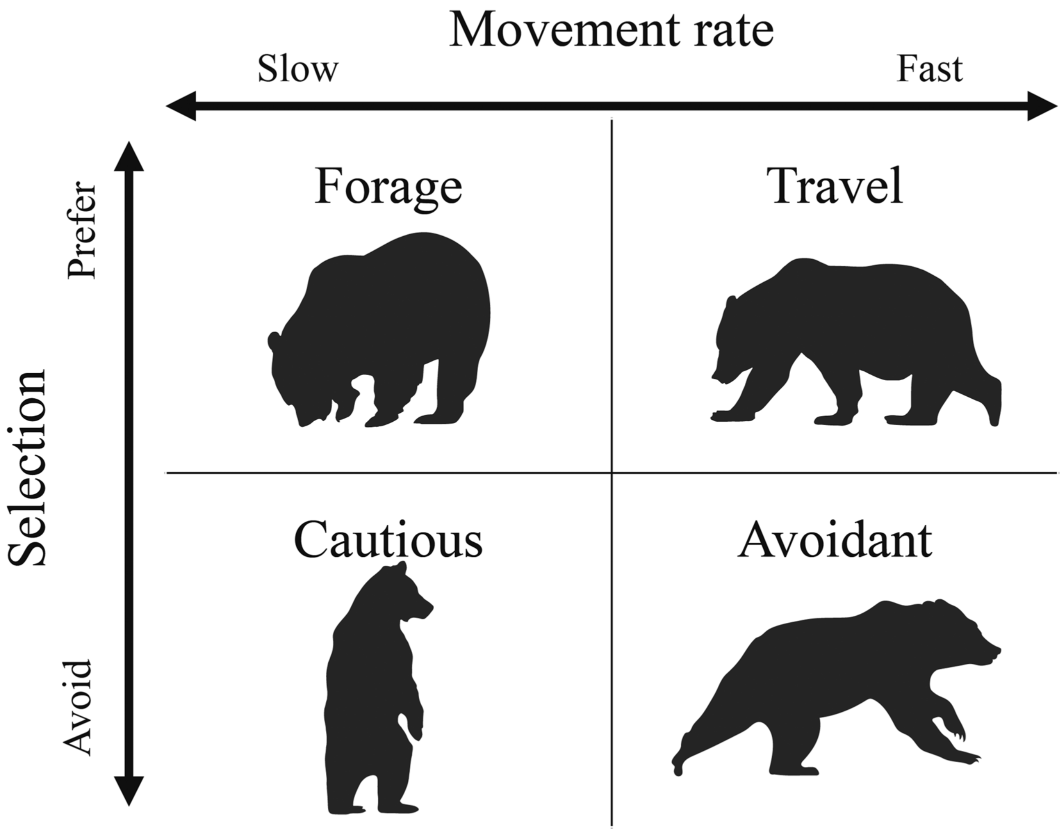

FIGURE 2 Conceptual framework characterizing behavioral responses of grizzly bears to recreation sites. We classified behavioral responses into 4 categories based on movement rate and resource selection: forage (slow movement rate, preference), travel (fast movement rate, preference), cautious (slow movement rate, avoidance), and avoidant (fast movement rate, avoidance).

their movement rate and avoided recreation sites did so because they associated these areas with high risk and therefore reduced their time near the recreation site, whereas bears that moved slowly and avoided recreation sites showed cautious behavior (Figure 2; Scrafford et al. 2018). Unlike roads that pose high mortality risk for wildlife (Moore et al. 2023), recreation sites may offer benefits for bears, so we extended this framework to reflect other ways bears may interact with recreation sites if they perceive these areas as lower risk (Gunther et al. 2014, Carnahan et al. 2021). Recreation sites often are built along streams, where food resources for bears also are available (Gunther et al. 2014). If bears reduced their movement rate and selected for recreation sites, we assumed bears used these areas to forage (Figure 2). Finally, trails optimize energy expenditure of bears (Carnahan et al. 2021); if bears increased their movement rate and selection for trails, we predicted that bears were traveling on or near trails, perhaps perceiving these areas as lower risk (Figure 2). We also explored whether bears shifted their behavior to reduce temporal overlap with recreational activities or differentiated their behavior based on whether recreation restrictions were in place (i.e., in BMAs); these comparisons allowed us to assess when and where people influenced perceived risk for bears. Therefore, in addition to behavior, we also characterized the strategy (non-responder, obligate, temporal, access; Table 1).

Previous studies have indicated that male and female brown (grizzly) bears differ in the level of risk they may associate with recreation sites (Dahle and Swenson 2003, Rode et al. 2006*a*, Ladle et al. 2019), and we therefore hypothesized they would use different strategies to navigate the potential of recreation activities. We expected

TABLE 1 Models used to test hypotheses regarding male and female grizzly bear behavior (movement and selection) in association with recreation sites (trails and campsites) with and without access restrictions (access) in Yellowstone National Park, Wyoming, USA, 2004–2020. Combination represents both movement and selection. All models included a base set of ecological variables that varied by recreation type and sex. We did not include the access variable in the analysis for the behavior of females near campsites because they had few locations within 1 km of campsites in Bear Management Areas. This limited the female model suite for campsites to 7 models.

Behavior	Strategy	Prediction	Model
No response	Non-responders	Recreation sites do not influence bear behavior	Ecological
Selection	Obligate	Proximity to recreation site influences where bears spend time	Distance to site
Selection	Temporal	Proximity to recreation site and time of day influence where bears spend time	Distance to site × time of day
Selection	Access	Proximity to recreation site and access restrictions influence where bears spend time	Distance to site × access
Selection	Temporal and access	Proximity to recreation site, time of day, and access influence where bears spend time	Distance to site × access × time of day
Movement	Obligate	Proximity to recreation site influences the movement rate of bears	Step length × distance to trail (no main effect for distance to trail and interactions only modify step length)
Movement	Temporal	Proximity to recreation site and time of day influence the movement rate of bears	Step length × distance to site × time of day (no main effect for distance to trail and interactions only modify step length)
Movement	Access	Proximity to recreation site and access influence the movement rate of bears	Step length × distance to site × access (no main effect for distance to trail and interactions only modify step length)
Movement	Temporal and access	Proximity to trail, access, and time of day influence the movement rate of bears	Step length × distance to site × access × time of day (no main effect for distance to trail and interactions only modify step length)
Combination	Obligate	Proximity to recreation site influences where bears spend time and their movement rate	Distance to site × step length
Combination	Access	Distance to recreation site and access influence where bears spend time and their movement rate	Distance to site × step length × access
Combination	Temporal	Proximity to recreation site and time of day influence where bears spend time and their movement rate	Distance to site × step length × time of day
Combination	Temporal and access	Proximity to recreation site, time of day, and access influence where bears spend time and their movement rate	Distance to site × step length × time of day × access

male bears would display greater risk-avoidant behavior where (i.e., unrestricted areas) and when (i.e., nocturnal for campsites, diurnal for trails) people recreated; however, we did not expect males to avoid these areas outside of these periods. For females, we hypothesized their behavior would reflect tradeoffs of risk associated with male bears and recreation. We expected that females would deploy risk-avoidance strategies (e.g., cautious or avoidant behavior) during crepuscular and nocturnal periods, when males were more active. Accordingly, we predicted that females would avoid trails, particularly in restricted areas, and select for areas near backcountry campsites and trails during diel periods that overlap with human recreation (i.e., diurnal for trails and crepuscular for campsites).

STUDY AREA

Our study was in Yellowstone National Park, which encompassed 8,991 km^2 of land mainly in northwest Wyoming, with some areas in Montana and Idaho, USA (NPS 2023*b*). This area ranged in elevation from 1,500 m to 3,400 m and was characterized by a large central plateau bordered by mountains to the north, south, and east. 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). In addition to grizzly bears, the national park was home to black bears (*U. americanus*), mountain lions (*Puma concolor*), coyotes (*Canis latrans*), and gray wolves (*C. lupus*). Eight species of ungulates occurred in the park: elk (*Cervus canadensis*), bison (*Bison bison*), moose (*Alces alces*), mule deer, white-tailed deer (*O. virginianus*), pronghorn (*Antilocapra americana*), mountain goats (*Oreamnos americanus*), and bighorn sheep (*Ovis canadensis*). Data collection for this study occurred during the active season (May–October) for grizzly bears from 2004 through 2020. Daily average temperatures at Yellowstone Lake 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 were cool and short, whereas winters were cold and long (Frank and McNaughton 1992).

The national park contained 1,792 km of trails for hiking and hooved stock (Figure 1; NPS 2023*c*), which often traverse stream bottoms, thermal areas, or alpine ridges (Spatial Analysis Center 2010*a*). Visitors in the backcountry could camp at one of 293 designated backcountry campsites (Figure 1; NPS 2023*d*). Trail markers denoted campsites, and all sites provided either a food pole or a metal bear box for food storage; however, specific tent locations within sites were not indicated (Coleman et al. 2013*b*). Each backcountry campsite was reserved for one group per night, with limits on the number of users per year (NPS 2023*d*).

Sixteen BMAs covered approximately 21% (188,032 ha) of the national park (Figure 1; Coleman et al. 2013*a*). Restrictions to recreation within BMAs included complete closures to human access, restricting recreation to trails and within campsites (on-trail travel only), or limiting recreation to between 0900 and 1900 hours (day use only; NPS 1982). The timing and duration of restrictions differed among BMAs, but most restrictions occurred during the spring and early summer and lasted 2–4 months (Table S1). Three BMAs near Yellowstone Lake allowed camping while restrictions were in place, but recreationists could not travel from campsites on land (NPS 2023*e*). Of the 293 backcountry campsites, 61 occurred within BMAs (Figure 1).

METHODS

We used location data collected from global positioning system (GPS)-enabled radio collars (Telonics, Mesa, AZ, USA) worn by grizzly bears during 2004–2020. We restricted our analysis period to when most overnight visitation occurred in backcountry areas of Yellowstone National Park. To identify this period, we quantified the date range during which 95% of the visits occurred at backcountry campsites. For these computations, we considered visitation data from 2000 to 2019 and calculated the median start and end date across years. We excluded visitation data from 2020 because the park was closed prior to the beginning of June because of the COVID-19 pandemic; this temporary closure would affect the temporal distribution of backcountry recreation. We conducted all analyses in R version 4.3.0 (R Core Team 2024).

Bears were captured by the Interagency Grizzly Bear Study Team as part of a long-term population research program. Capture activities followed approved protocols conforming to the United States Animal Welfare Act (see Ethics Statement). We performed all analyses on GPS data from on-board memory downloaded after collar retrieval. We excluded 3-dimensional and 2-dimensional GPS fixes with position dilution of precision >10 or horizontal error >125 m (D'Eon and Delparte 2005). We used the adehabitatHR package (version 0.4.19; Calenge 2006) to construct yearly 95% minimum-convex hull home ranges for each bear and only included individuals if 80% of their home ranges fell within the national park boundary (Mohr 1947). We used this value to ensure individuals included in the study had the opportunity to spend time in BMAs. We also wanted to ensure bears in our analysis had the opportunity to encounter trails and campsites. For the campsite analysis, we only included bears with at least 2 campsites within their home range; home ranges of all bears contained trails. The GPS data were collected over a 17-year period with fix intervals ranging from 13 minutes to 208 minutes, although most fixes involved 105-, 60-, 52-, or 30-minute intervals. We thinned the data to include consecutive fixes with a time interval of 105 minutes (± 15 min; i.e., 90–120 min) and further limited analyses to individuals with at least 100 fixes (equaling ~7 days of monitoring; Figure S1). Some bears were monitored for multiple years, so we classified an individual as all locations for a bear within a calendar year.

Stages of analysis

Overview

We used 2 stages of analysis. We first characterized movement and resource selection of grizzly bears and then determined how recreation sites, access restrictions, and time of day further modulated behavior. In stage I, we used ecological variables to characterize movement and resource selection with different models for each sex (ecological models). In stage II, we added variables representing proximity to recreation sites, access restrictions, and time of day to the ecological models to test our hypotheses about grizzly bear behavior near recreation sites (recreation models).

For both stages of analysis, we simultaneously assessed spatiotemporal variation in movement and selection using integrated step-selection functions (Thurfjell et al. 2014, Avgar et al. 2016). We matched 10 available locations to each used location to form a stratum (Signer et al. 2019). Following Muff et al. (2020), we fit conditional Poisson mixed models with stratum-specific intercepts and fixed the variance of the intercepts to 10,000 to avoid shrinkage. We generated available locations from distributions of turn angles (von Mises distribution) and step lengths (gamma distribution) of used locations using the random_steps function in the amt package (version 0.1.4; Signer et al. 2019). We included the natural logarithm of step length (hereafter step length) as the movement variable in all models (Avgar et al. 2016). This coefficient modifies the shape parameter from the tentative gamma distribution of step lengths (shape: male = 0.47, female = 0.56; scale: male = 1,655, female = 1,036; Avgar et al. 2016). We included random slopes for step length, proximity to recreation site, and access restrictions when included as main effects to account for variation among individuals, allow for more robust population-level estimates of these fixed effects, and reduce bias in availability (Gillies et al. 2006, Hebblewhite and Merrill 2008, Muff et al. 2020). We used package glmmTMB to fit all models (version 1.1.1; Brooks et al. 2017).

Ecological models

We included variables known or hypothesized to influence movement and selection by grizzly bears to create the ecological models tested. We constructed a binary raster of forested (i.e., deciduous, evergreen, mixed forests) and non-forested land (derived from LANDFIRE 2019) to incorporate variability in movement and selection in these areas. Bears often forage and seek refuge (e.g., daybed) near the interface between forested and open areas (Blanchard 1983, Nielsen et al. 2004), so we included distance to nearest forest edge (derived from LANDFIRE 2019). We assigned negative distance values to locations in the forest and positive values to non-forested areas (Peck et al. 2017). We accounted for bears using water sources for thermoregulation (Rogers et al. 2021), feeding on foods such as spawning trout or succulent vegetation (Haroldson et al. 2005, Teisberg et al. 2014), and traveling along streams (Wilson et al. 2005) by including distance to nearest water (lakes and rivers; Spatial Analysis Center 2010*b*). Because terrain features and topography affect movement of bears (Carnahan et al. 2021), we included topographic roughness index (TRI; Riley et al. 1999), rasterized from a digital elevation model (30-m resolution; U.S. Geological Survey 2013). Bears change their behavior near roadways and developments (Mace et al. 1996, Ciarniello et al. 2007), so we also included Euclidean distance to the nearest anthropogenic feature (i.e., roads and developments), with negative distance values associated with locations inside developments (Spatial Analysis Center 2010*c*). We measured all distances using st_distance in the sf package (version 1.0.3; Pebesma 2018) and scaled and centered continuous covariates (Schielzeth 2010).

We evaluated a suite of candidate models for each sex to select the ecological model that best explained step selection by grizzly bears. All models included a fixed effect and a random slope for step length. We determined the best-supported ecological model for each sex and recreation type by comparing all possible additive combinations of forest, distance to forest edge, distance to water, TRI, and distance to anthropogenic areas based on Akaike's Information Criterion (AIC; Tables S2–S6; Burnham and Anderson 2002). We calculated AIC values using the MuMIn package (version 1.43.17; Bartoń 2024). We used the best-supported models from this first stage of analysis as the baseline for hypothesis testing (Table 1).

Recreation models

In the second analysis stage, we included additional covariates and interactions to test our hypotheses regarding recreation sites and grizzly bear behavior. We included interactions among distance to recreation site, step length, time of day, and access restrictions to understand their influence on movement rate and selection. Access restrictions indicated whether a location occurred in a BMA closed to human access (restricted) or not (i.e., all other areas; unrestricted). We log-transformed distance to trail and distance to backcountry campsite because wildlife often show exponentially diminished responses to human presence (Avgar et al. 2017). We categorized time of day to incorporate differences in activity for humans and bears; day was defined using activity patterns of people in the backcountry (0800 to 1800 hours; Coleman et al. 2013*a*). The morning crepuscular period began at astronomical twilight, when bear activity increases at night (Schwartz et al. 2010) and ended at 0800 hours, when human activity begins (Coleman et al. 2013*a*). The evening crepuscular period began at 1800 hours, when human activity ends (Coleman et al. 2013*a*), and ended at the end of astronomical twilight. Finally, we characterized night as when the sun was lower than 18° below the horizon. We calculated the sun angle using the oce package (version 1.8-0; Kelley and Richards 2024). We used AIC to compare 13 models representing different hypotheses about how grizzly bears interact with recreation sites (Table 1; Burnham and Anderson 2002, Bartoń 2024). We analyzed backcountry campsites and trails separately and further split analyses by sex.

We grouped the 13 models into 4 sets (Table 1) to represent potential behaviors bears use near recreation sites (no response, selection, movement, and combination) and further assessed strategies (non-responder, obligate, temporal, access). The ecological model represented the no response strategy based on a prediction that grizzly bears do not change their movement or selection in response to recreation sites. We created the selection model set to represent the hypothesis that recreation sites influence where grizzly bears spend time. These models included interactions among distance to recreation site, time of day, and access restrictions. The movement set of models represented the hypothesis that recreation sites influenced the movement rate of grizzly bears. These models included interactions among step length (the movement parameter) and distance to recreation site, time of day, and access restrictions. For this model set, we did not include main effects for distance to recreation site, time of day, or access restrictions because we only were interested in assessing the influence of these factors on the movement rate, not selection, of grizzly bears (Scrafford et al. 2018, Ladle et al. 2019). Our final model set (combination) represented the hypothesis that recreation sites mediate both where grizzly bears spend time and their movement rate. Models in this set included main effects and an interaction between distance to recreation site and step length to assess the prediction that bears change their movement rate and selection based on proximity to recreation sites. These models also included additional interactions with time of day and access restrictions. For all models, we included the time-of-day variable only as an interaction with the distance and movement covariates, given that time of day did not differ between used and available locations (Street et al. 2016). Because females had few GPS locations within 1 km of campsites in BMAs (as previously noted by Coleman et al. 2013*a*, 2013*b*), we removed the restriction variable from the campsite analysis for females and only tested 7 models (Table 1). We evaluated the fit of our models using *k*-fold cross-validation for step-selection functions (Fortin et al. 2009), with 5 folds repeated for each sex and recreation site combination (Table A1).

Movement and relative selection strength

We calculated movement rates by multiplying the shape and scale parameters of the gamma distribution of step length from used locations of bears for each sex. We modified movement rates using the model coefficients for step length multiplied by the original scale parameter following Ladle et al. (2019; Avgar et al. 2016, Prokopenko et al. 2017). We estimated movement rate and relative selection strength (RSS) using 85% confidence intervals to ensure consistency between model selection and parameter estimation (Arnold 2010). We calculated the RSS for moving and stationary bears to capture potential differences in behavioral responses; we based moving bears on the average velocity of grizzly bears in Yellowstone National Park (3,843 m per GPS fix interval or 0.61 ± 0.28 m/sec; Carnahan et al. 2021). To calculate odds ratios, we conditioned selection on bears in an unrestricted area during the day, while holding ecological variables (distance to water, distance to anthropogenic, TRI, distance to forest edge, forest) at their mean standardized value (0; Avgar et al. 2017). In applying the odds ratios, we compared selection of proximity to recreation sites using 1 m (referred to as near) and 1 km (referred to as far) from a recreation site. This allowed us to compare bears near recreation sites with those in areas where recreation sites would generally not be visible to the bears. We use the terms near and far when reporting odds ratios, and we describe the trend of selection using closer to and farther from recreation sites.

RESULTS

We obtained 280,353 GPS locations from 116 bears collared during 2004–2020 (Figure S1). After standardizing fix interval among bears, reducing fixes to those occurring during the analysis period (27 June–14 September), and removing individuals with <80% of their home range within the national park, these GPS locations provided data for 18,297 used steps from 35 bear-years (19 male, 16 female).

Male and female grizzly bears in our study responded to areas humans frequented in Yellowstone National Park by varying their movements and selection. The best-supported model for each sex and type of recreation included interactions among distance to recreation site, step length, time of day, and access restrictions; we had insufficient data to explore access restrictions for females in relation to campsites (Table 2). Based on cross-validation, our models were accurate predictors of grizzly bear resource selection (r_s range = 0.90–0.97; Table A1). Within the trail and campsite recreation types, we separated results by sex and first present our findings for movement rate, followed by selection for moving and stationary bears. We provide specific parameter estimates in Table B1.

TABLE 2 Competing models (ΔAIC ≤ 4.0) describing movement and selection by grizzly bears in association with recreation sites for each sex in Yellowstone National Park, Wyoming, USA, 2004–2020. We used conditional Poisson mixed models to compare matched used and available locations (1 used:10 available). We compared 13 candidate models for each recreation type (trails and campsites) to test hypotheses about grizzly bear responses to access restrictions (restricted or unrestricted), distance to recreation site, and time of day. We did not include the access variable in the analysis for the behavior of females near campsites because they had few locations within 1 km of campsites in Bear Management Areas. This limited the campsite model suite to 7 models for females.

Type	Sex	Model structure	K[a]	ΔAIC[b]	AIC weight	Log-likelihood	n[c]
Trail	Female	Combination: temporal and access[d]	28	0.000	1.000	−103,955.9	16
	Male	Combination: temporal and access	27	0.000	0.689	−83,027.00	19
		Combination: temporal[e]	14	1.589	0.311	−83,040.80	
Campsite	Female	Combination: temporal	16	0.000	0.920	−55,888.27	9
	Male	Combination: temporal and access	27	0.000	0.987	−75,792.56	17

[a] Number of parameters in model.

[b] Difference between ranked models based on Akaike's Information Criterion.

[c] Number of individual bear–years.

[d] Distance to site × step length × time of day × access.

[e] Distance to site × step length × time of day.

Trails

Based on the best-supported model, male bears changed their movement rate and selection depending on distance to trail, step length, time of day, and access restrictions (Table 2). We also found some support for a model without access restrictions but focus our interpretation on the top model with the 4-way interaction.

Males moved at similar rates during the diurnal period regardless of their proximity to trails or access restrictions (3A; Table C1). During crepuscular and nocturnal periods, male bears increased their movement rate when they were closer to trails regardless of access restrictions; they moved fastest on trails in restricted areas during the crepuscular period (Figure 3a; Table C1).

When moving, male bears did not show preference or avoidance of trails during the diurnal period (Figure 3B; Table D1). In contrast, during crepuscular and nocturnal periods, male bears that were moving were more likely to be closer to trails in both access types. For male bears that were moving, we only observed differences between access types during the crepuscular period, with moving bears 2.2 times more likely (85% CI = 0.9–5.2; Figure 3B) to be near (1 m compared with 1 km) trails in restricted areas compared with unrestricted areas. Males that were stationary were more likely to be farther from trails in unrestricted areas during all times of day (Figure 3C). In restricted areas, stationary males did not show preference or avoidance of trails during the diurnal period but were more likely to be farther from trails during the crepuscular and nocturnal periods. When stationary, males did not differentiate selection between access types.

Females increased their movement rate slightly when closer to trails in unrestricted areas during all periods (Figure 3D; Table C1). In contrast, females in restricted areas increased their movement rate when closer to trails only during the diurnal period and reduced their movement rate when closer to trails during the crepuscular and nocturnal periods.

When moving, female bears in unrestricted areas only changed their selection of trails during the crepuscular period, when they were more likely to be closer to trails (Figure 3E; Table D1). Conversely, females that were moving in restricted areas were more likely to be closer to trails during diurnal hours and strongly avoided trails during nocturnal hours. Comparing access restrictions, females that were moving in unrestricted areas were 4.0 times (85% CI = 1.4–11.3) and 53.2 times (5.4–519.6) more likely to be 1 m from trails compared with females in

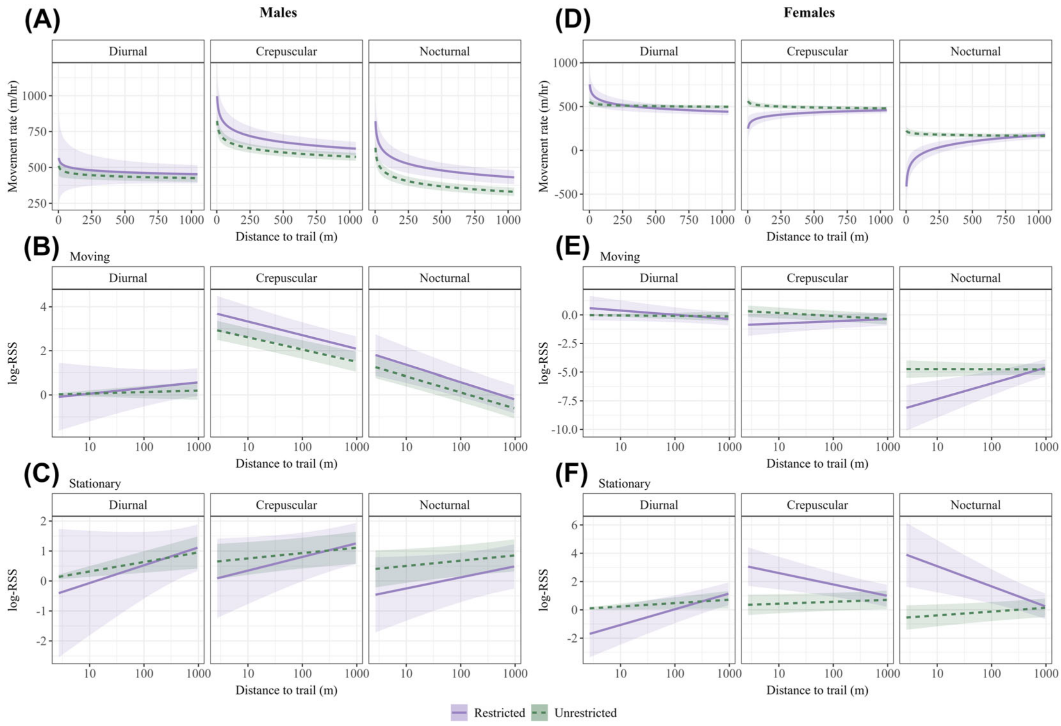

FIGURE 3 Movement rate (m/hr; A and D) and selection (log-relative selection strength [log-RSS]) by male and female grizzly bears in relation to trails in areas with (purple, solid line) and without (green, dashed line) access restrictions, based on the best-supported model for each sex, in Yellowstone National Park, Wyoming, USA, 2004–2020. We show selection for moving (B and E) and stationary (C and F) bears. All estimates (and 85% CIs) are relative to selection of 1 m from a trail in an area without recreational access restrictions during the diurnal period. We calculated moving values using the average velocity of grizzly bears in Yellowstone National Park (3,843 m/fix interval; Carnahan et al. 2021) and stationary values using 1 m/fix interval.

restricted areas during the crepuscular and nocturnal periods, respectively. When stationary, females in unrestricted areas avoided trails during diurnal and nocturnal periods but showed no difference in selection during crepuscular hours (Figure 3F). In restricted areas, females that were stationary were more likely to be farther from trails during the diurnal period but closer to trails during crepuscular and nocturnal periods. Comparing access restrictions, females that were stationary in restricted areas were 41.5 times (7.4–233.2) and 622.1 (37.2–10,408.1) times more likely to be 1 m from trails compared with females in unrestricted areas during crepuscular and nocturnal hours, respectively (Figure 3F).

Campsites

In unrestricted areas, males increased their movement rate closer to campsites during all periods, yet in restricted areas, they moved at similar rates regardless of their proximity to campsites or time of day (Figure 4a; Table C1).

When moving, male bears in unrestricted areas were more likely to be closer to a backcountry campsite during crepuscular and nocturnal periods (Figure 4B; Table D1), but they did not show preference for or avoidance of campsites in restricted areas. Additionally, males that were moving showed similar selection for proximity to campsites regardless of whether they were in restricted or unrestricted areas. Stationary male bears also did not change their selection of proximity to campsites (Figure 4C).

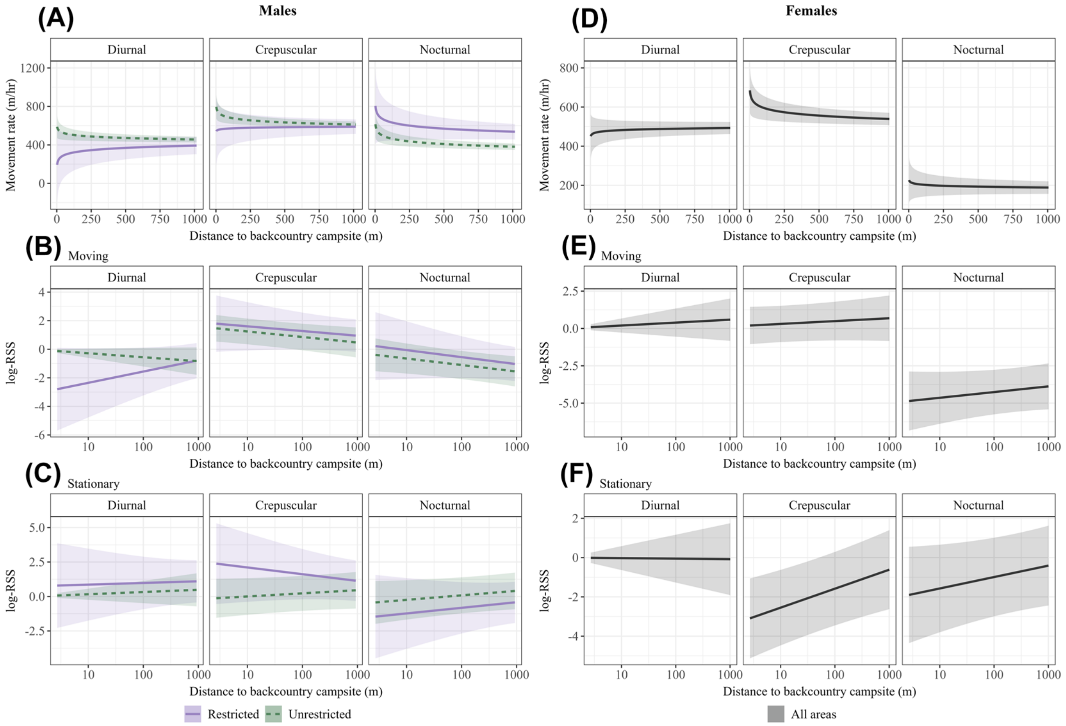

FIGURE 4 Movement rate (m/hr; A and D) and selection (log-relative selection strength [log-RSS]) by male and female grizzly bears in relation to backcountry campsites in areas with (green, dashed line) and without (purple, solid line) access restrictions, based on the best-supported model for each sex, in Yellowstone National Park, Wyoming, USA, 2004–2020. We did not include the access variable in the analysis for the behavior of females near campsites because they had few locations within 1 km of campsites in Bear Management Areas. We show selection for moving (B and E) and stationary (C and F) bears. All estimates (and 85% CIs) are relative to selection of 1 m from a trail in an area without recreational access restrictions during the diurnal period. We calculated moving values using the average velocity of grizzly bears in Yellowstone National Park (3,843 m/fix interval, Carnahan et al. 2021) and stationary values using 1 m/fix interval.

Female bears increased their movement rate closer to campsites during crepuscular hours and otherwise did not change their movement rate based on proximity to campsites (Figure 4D; Table C1). When moving, females did not change their selection of proximity to campsites (Figure 4E; Table D1). When stationary, females were more likely to be farther from backcountry campsites during crepuscular hours and otherwise did not show preference for or avoidance of campsites (Figure 4F).

DISCUSSION

Our work extends previous research in Yellowstone National Park (Gunther 1990; Coleman et al. 2013*a*, *b*; Loggers et al. 2024) by identifying potential behavioral responses of grizzly bears to recreation sites, in areas with and without people, and based on time of day. Our analyses indicated that male and female bears differed in their responses to backcountry recreation in a protected area. The variation in behavior in relation to the type of recreation (trails, campsites) and whether people were allowed to recreate in an area (access restrictions) supports previous findings that the type and frequency of recreation influence the behavior of bears (Ladle et al. 2019, Naidoo and Burton 2020). Grizzly bears likely perceive risks from afar and avoid areas they deem risky (Mace et al. 1996, Gibeau et al. 2002). Our data did not support the hypothesis that male bears perceived backcountry recreation in Yellowstone National Park as high risk because males were often indifferent to or selected for these areas while moving. However, males did show some behavioral changes when and where people could be recreating, suggesting that male bears do not perceive these areas to be completely risk-free. In contrast, females changed their movement rate and selection in areas where people were excluded; yet, where people could recreate, they showed comparatively less behavioral response to both recreation types. This finding illustrates an important distinction between males and females: males seem to use trails as movement corridors during their daily active periods, but females seemingly made behavioral tradeoffs, perhaps to navigate the potential of encountering male bears and humans in unrestricted areas.

Hiking trails provide energetically efficient movement pathways for grizzly bears (Carnahan et al. 2021). The increased movement rate near and selection for trails supports our prediction that male bears sought out these areas primarily for travel rather than foraging (Figures 2 and 3; Christianson et al. 2021), thus optimizing their energetic tradeoffs as they typically move farther distances and have larger home ranges than females. The diel pattern of travel behavior also aligned with their active period (crepuscular and nocturnal; Schwartz et al. 2010). Bears that live near more anthropogenic areas change their activity patterns to reduce overlap with human activity (Schwartz et al. 2010, Ordiz et al. 2011, Lamb et al. 2020), and male bears in our study varied their behavioral response to trails depending on access restrictions. In restricted areas, males displayed more pronounced behavioral responses (e.g., increased movement rate, stronger selection) than in unrestricted areas, supporting the risk-disturbance hypothesis (Frid and Dill 2002). For males that were moving, this pattern occurred during the crepuscular period, when people recreate on trails, but not during the nocturnal period, when human recreation rarely occurs (Coleman et al. 2013*a*). Additionally, stationary bears avoided trails during the day in unrestricted areas, when and where people could recreate. Male grizzly bears use trails to travel, yet even low-intensity backcountry recreation seemed to influence their behavior.

In contrast, the distinct behavioral differences between access restrictions we observed for female bears suggest they navigate the compounded risk of male bears and people. Females temporally changed their behavior near trails in accordance with when male bears are active and in areas where people were absent and grizzly bear density was higher (restricted areas; Loggers et al. 2024). Their reduced movement rate near and avoidance of trails in restricted areas supports our prediction that females use risk-avoidant (e.g., cautious; Figure 2) behavior when and where male bears are active. In other studies, subordinate bears (i.e., subadults, females) avoided areas where male bears spent time, potentially to reduce intraspecific interactions (Wielgus and Bunnell 2000, Ben-David et al. 2004, Rode et al. 2006*b*, Steyaert et al. 2013), and females may use cautious behaviors near areas where male bears travel to reduce the probability of an encounter. Female bears traveled on trails, indicated by their increased movement rate near and selection of trails (Figures 2 and 3), when male bears and people were not using trails (daytime in restricted areas). Daytime activity by female bears in our study area has previously been proposed as a behavioral mechanism to reduce encounters with male bears (Schwartz et al. 2010), and restricted areas provide females the opportunity to avoid male bears without also considering human activity.

In other areas, displacement of males by tourism (e.g., bear viewing) has been proposed as an asset for female bears (Nevin and Gilbert 2005, Rode et al. 2006*b*, Steyaert et al. 2016), yet our data do not support this notion. Instead, we found that female bears did not exhibit large variation in movement or selection in relation to recreation sites when people could access these areas. Female grizzly bears with cubs may be in a double-bind while trying to avoid other adult bears and people (Mattson et al. 1987). Human activity in the backcountry of Yellowstone National Park peaks during daytime hours (Coleman et al. 2013*a*), whereas male bears in our study spent time closer to trails during crepuscular and nocturnal hours. This continued occupation of trails throughout a 24-hour period in areas where people recreate constrains options for females to respond to perceived risks. Access restrictions in BMAs may provide an important reduction in the risk female bears associate with recreation sites, yet the perceived risk from male bears may still be high. Females lose more cubs during the early season (May–July) in areas with high densities of grizzly bears, potentially because of infanticide by male bears (van Manen et al. 2016). Although BMAs generally contain greater densities of bears (Loggers et al. 2024), females may have opportunities to avoid males because of the absence of people. Areas outside of BMAs that have high densities of bears and human recreation may further restrict females' options, potentially contributing to greater cub mortality. The variation in behavior between sexes supports our hypothesis that males and females associate recreation sites with different levels of risk. The probability of encountering a male bear likely further dictates the degree of risk females associate with these areas.

Our findings do not provide evidence of grizzly bears being attracted to backcountry campsites. In Yellowstone National Park, a bear-resistant food storage device is provided in every campsite. There are no energetic benefits to bears from campsites where people store food properly, aside from the frequent occurrence of campsites in areas with high-quality natural food resources (Despain 1990, Coleman et al. 2013*b*). Although backcountry campsites often occur in areas where bears spend time, of the 39 grizzly bear-inflicted human injuries that have occurred in the park since 1979, only 1 occurred at a backcountry campsite (Gunther and Atkins 2025). This further indicates that injury-related conflicts between bears and backcountry campers are rare. Grizzly bears obtained human foods in only 3 of 166 reported incidents where they entered occupied backcountry campsites during the study period (2004–2020; personal communication, K. A. Gunther, National Park Service, written, 12 May 2025). Instead, in most of these incidents, grizzly bears foraged for natural foods ($n = 30$) or traveled through the campsites without investigating or seeking human foods ($n = 80$; personal communication, K. A. Gunther, National Park Service, written, 12 May 2025). In our study, male bears were the only group that selected for campsites but only while they were moving, suggesting they displayed traveling behavior near campsites, coinciding with when they also used trails as travel corridors. This pattern occurred during crepuscular and nocturnal hours and may be a latent effect of male selection for trails, as many backcountry campsites are located near trails. Yet this pattern was not apparent in restricted areas. Coleman et al. (2013*b*) found that grizzly bears in Yellowstone National Park were more likely to be near (<200 m) backcountry campsites when humans were absent. In our study, we did not explicitly assess how the behavior of bears differed between occupied and unoccupied campsites. Areas with access restrictions may create unpredictable conditions for bears, given that occupation of backcountry campsites occurs inconsistently throughout the year.

Grizzly bears use current resources and memory cues to decide where to spend time (Thompson et al. 2022), and repeated encounters with people near recreation sites likely influence the perceived risk bears associate with these places (Hertel et al. 2019). Increasing the predictability of locations of recreational activity, particularly on established trails, may help reduce human–bear interactions. Although the probability of recreationists being injured by a bear is low overall in Yellowstone National Park, the rate of human–bear interactions that resulted in injuries was higher when people traveled off-trail compared with those recreating on trails (Gunther et al. 2024). Additionally, most (74%) bear-inflicted human injuries in the national park (1979 to 2023) resulted from surprise encounters, further supporting that bears do not seek out interactions with people (Gunther and Atkins 2025). Encounters with people can alter bear behavior for several days (Ordiz et al. 2013, 2019). This association also may be temporally acute: grizzly bears often move between restricted and unrestricted areas, so human encounters in unrestricted areas may carry over to influence the behavior of bears in restricted areas (Hertel et al. 2019, Thompson et al. 2022). Although we measured perceived recreation rather than actual recreation use, our findings support broad behavioral changes of grizzly bears in relation to recreation sites.

Recreation activities are dynamic in space and time, and different behavioral (i.e., movement, selection) responses of wildlife to recreation typically have been studied separately (Gibeau et al. 2002; Graves 2002; Coleman et al. 2013*a*, *b*). Simultaneous modeling of movement rate and selection enhanced our inference regarding behaviors of bears near recreation sites. If we had modeled selection alone and found male bears selected for trails, we could not have ruled out quality foraging opportunities as a primary mechanism of why bears spend time near these areas (Christianson et al. 2021). Additionally, separately assessing selection for moving and stationary bears allowed us to further explore differences in behaviors bears use in relation to recreation sites. For example, females that were moving in restricted areas avoided areas near trails, whereas stationary females selected for these areas (Table D1). Disentangling human-driven and innate patterns of behavior is challenging but important to further our understanding of potential causal mechanisms.

Integrating these findings with previous work focused on backcountry recreation in Yellowstone National Park provides insights into how grizzly bears navigate recreation sites in areas with and without people. Previous research indicated bears were more likely to be within 0–400 m of campsites and trails when humans were absent (Coleman et al. 2013*a*), and bears spent time in cover to avoid human presence (Gunther 1990). Our analyses support these findings and provide additional insights. Notably, male and female grizzly bears differ in their spatial selection and movement patterns relative to trails and campsites. Furthermore, including time of day allowed us to explore behavioral variation in responses to human activity and variation in diel patterns of wildlife. Collectively, these analyses suggest that male and female bears change their movement rate, more than their spatial selection, in areas where people can recreate, and they further avoid immediate interactions with people by using vegetative cover and localized movements (Gunther 1990; Coleman et al. 2013*a*, *b*). Combining inferences about these acute and long-term behaviors of bears provides a more comprehensive assessment of strategies bears use to navigate human recreational activities. Public information and outreach regarding specific behavioral patterns of bears around recreational sites can empower visitors to make informed choices that may reduce the potential for human–bear encounters that could lead to conflict.

MANAGEMENT IMPLICATIONS

Grizzly bears change their behavior to reduce spatial and temporal overlap with people near recreation sites in Yellowstone National Park. The differences between the strategies male and female bears use to navigate backcountry recreation suggest a single management approach to recreation may not equally benefit all individuals. Access restrictions in BMAs likely help preserve the natural behavioral processes of grizzly bears, particularly females that make additional behavioral changes in accordance with male bear activity. Trails and campsites that provide energy-efficient movement corridors or nearby high-quality food resources can inadvertently attract bears. Given that male bears use trails as travel corridors during their active periods, restricting recreational activities during crepuscular and nocturnal hours may enhance visitor safety, particularly in areas with high densities of grizzly bears.

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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 were approved by the Institutional Animal Care and Use Committees of the U. S. Geological Survey (U.S. Geological Survey Animal Care and Use Committee protocol #2012-01) and permitted by the United States Fish and Wildlife Service Endangered Species Permit (Section (i) C and D of the grizzly bear 4(d) rule, 50 CFR17.40(b)). Additional permits for capture and research procedures were approved by the National Park Service (research permit 0073).

DATA AVAILABILITY STATEMENT

Data either are not available or have limited availability owing to restrictions of the Endangered Species act and the National Parks Omnibus Management Act of 1998, Title II, Section 207. Contact Frank van Manen (fvanmanen@usgs.gov) for more information.

ORCID

Elise A. Loggers https://orcid.org/0009-0005-8631-424X
Andrea R. Litt https://orcid.org/0000-0002-6915-8047

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SUPPORTING INFORMATION

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APPENDIX A

We followed Fortin et al. (2009) for *k*–fold cross validation of our best supported step-selection functions for each sex and recreation type. We randomly selected stratum and split data into training (80%) and testing (20%) datasets. We built models with the training data and used fixed effects to estimate predicted values of the testing data. We ranked estimates of used locations against the random locations and calculated the Spearman rank correlation coefficient of the observed and expected frequency of used locations within each bin.

TABLE A1 Mean Spearman rank correlation (r_s) and standard deviation for 5-fold cross-validation (100 replicates) of best-supported models describing selection of Bear Management Areas by grizzly bears for each combination of sex and season, 2004–2020, Yellowstone National Park, Wyoming, USA.

Recreation site	Sex	r_s	SD
Trail	Male	0.934	0.020
	Female	0.970	0.028
Campsite	Male	0.899	0.057
	Female	0.943	0.072

APPENDIX B

TABLE B1 Parameter estimates and 85% confidence intervals from the best-supported model for each sex and type of recreation site for grizzly bears, 2004–2020, Yellowstone National Park, Wyoming, USA. We compared candidate models to test hypotheses about grizzly bear responses to recreation sites. All continuous variables were centered and scaled, and step length, distance to trail, and distance to recreation site were log-transformed.

Recreation site	Sex	Parameter	Estimate	85% CI	
Trail	Male	Terrain roughness index	−0.284	−0.315	−0.253
		Landcover–forest	0.120	0.008	0.161
		Distance to water	−0.066	−0.094	−0.037
		Step length	−0.019	−0.048	0.009
		Distance to trail	0.214	0.094	0.335
		Restricted area	0.137	−0.456	0.730
		Step length × distance to trail	−0.021	−0.036	−0.006
		Step length × restricted area	0.029	−0.036	0.094
		Distance to trail × restricted area	0.175	−0.354	0.705
		Step length × crepuscular	0.157	0.137	0.178
		Step length × night	−0.098	−0.120	−0.076
		Distance to trail × crepuscular	−0.044	−0.190	0.102
		Distance to trail × night	−0.032	0.184	0.121
		Restricted area × crepuscular	−0.049	−0.715	0.616
		Restricted area × night	−0.608	−1.336	0.119
		Step length × distance to trail × restricted area	−0.007	−0.082	0.068
		Step length × distance to trail × crepuscular	−0.041	−0.062	−0.020
		Step length × distance to trail × night	−0.055	−0.077	−0.033
		Step length × restricted area × crepuscular	0.032	−0.043	0.108
		Step length × restricted area × night	0.078	0.000	0.156
		Distance to trail × restricted area × crepuscular	0.022	−0.589	0.634
		Distance to trail × restricted area × night	−0.036	−0.639	0.566

TABLE B1 (Continued)

Recreation site	Sex	Parameter	Estimate	85% CI	
		Step length × distance to trail × restricted area × crepuscular	−0.021	−0.108	0.066
		Step length × distance to trail × restricted area × night	−0.014	−0.100	0.072
	Female	Distance to forest edge	0.100	0.072	0.128
		Distance to water	0.072	0.042	0.103
		Landcover–forest	−0.136	−0.180	−0.092
		Distance to anthropogenic	−0.145	−0.237	−0.052
		Step length	0.276	0.244	0.309
		Distance to trail	0.166	0.028	0.304
		Restricted area	0.768	0.269	1.266
		Step length × distance to trail	−0.023	−0.041	−0.005
		Step length × restricted area	−0.129	−0.186	−0.073
		Distance to trail × restricted area	0.620	0.235	1.006
		Step length × crepuscular	−0.033	−0.055	−0.011
		Step length × night	−0.561	−0.584	−0.539
		Distance to trail × crepuscular	−0.052	−0.214	0.110
		Distance to trail × night	0.018	−0.173	0.209
		Restricted area × crepuscular	−0.705	−1.264	−0.146
		Restricted area × night	−1.178	−1.927	−0.429
		Step length × distance to trail × restricted area	−0.099	−0.159	−0.038
		Step length × distance to trail × crepuscular	−0.010	−0.033	0.013
		Step length × distance to trail × night	0.000	−0.024	0.024
		Step length × restricted area × crepuscular	0.133	0.060	0.207
		Step length × restricted area × night	0.237	0.155	0.318
		Distance to trail × restricted area × crepuscular	−1.298	−1.792	−0.804
		Distance to trail × restricted area × night	−1.887	−2.538	−1.235
		Step length × distance to trail × restricted area × crepuscular	0.214	0.137	0.292
		Step length × distance to trail × restricted area × night	0.352	0.258	0.446
Camp	Male	Terrain roughness index	−0.331	−0.365	−0.297
		Landcover–forest	0.094	0.051	0.137
		Distance to water	−0.060	−0.089	−0.030
		Step length	−0.016	−0.041	0.010
		Distance to campsite	0.062	−0.092	0.217
		Restricted area	0.598	−0.015	1.212
		Step length × distance to campsite	−0.020	−0.035	−0.006
		Step length × restricted area	−0.006	−0.074	0.062

(Continues)

TABLE B1 (Continued)

Recreation site	Sex	Parameter	Estimate	85% CI	
		Distance to campsite × restricted area	−0.016	−0.394	0.363
		Step length × crepuscular	0.153	0.132	0.173
		Step length × night	−0.097	−0.119	−0.074
		Distance to campsite × crepuscular	0.025	−0.141	0.191
		Distance to campsite × night	0.063	−0.122	0.249
		Restricted area × crepuscular	−0.250	−0.963	0.463
		Restricted area × night	−1.389	−2.167	−0.610
		Step length × distance to campsite × restricted area	0.052	−0.002	0.105
		Step length × distance to campsite × crepuscular	−0.008	−0.029	0.013
		Step length × distance to campsite × night	−0.016	−0.038	0.007
		Step length × restricted area × crepuscular	0.025	−0.057	0.106
		Step length × restricted area × night	0.162	0.077	0.247
		Distance to campsite × restricted area × crepuscular	−0.259	−0.755	0.238
		Distance to campsite × restricted area × night	0.046	−0.468	0.561
		Step length × distance to campsite × restricted area × crepuscular	−0.016	−0.086	0.055
		Step length × distance to campsite × restricted area × night	−0.057	−0.132	0.018
	Female	Distance to forest edge	0.118	0.082	0.153
		Distance to water	0.063	0.024	0.103
		Landcover–forest	−0.152	−0.206	−0.097
		Step length	0.270	0.230	0.310
		Distance to campsite	−0.010	−0.225	0.206
		Step length × distance to campsite	0.010	−0.011	0.030
		Step length × night	−0.529	−0.556	−0.503
		Step length × crepuscular	0.011	−0.015	0.037
		Distance to campsite × night	0.215	−0.050	0.480
		Distance to campsite × crepuscular	0.351	0.136	0.566
		Step length × distance to campsite × night	−0.018	−0.045	0.009
		Step length × distance to campsite × crepuscular	−0.043	−0.070	−0.016

APPENDIX C

TABLE C1 Mean movement rate (m/hour), with 85% confidence interval in parentheses, of male and female grizzly bears 1 m (near) and 1 km (far) from recreation sites (trail, campsite) based on access restrictions (restricted, unrestricted) and time of day (diurnal, crepuscular, nocturnal) in Yellowstone National Park, Wyoming, USA, 2004–2020. Asterisks indicate that 85% confidence intervals did not overlap means.

Recreation site	Sex	Access restriction	Time of day	1 m from site	1 km from site
Trail	Male	Restricted	Diurnal	586.0 (217.5–954.5)	453.5 (389.4–517.5)
			Crepuscular	1,058.3 (842.8–1,273.8)*	633.7 (586.3–681.2)
			Nocturnal	888.3 (688.5–1,088)*	433.8 (385.2–482.4)
		Unrestricted	Diurnal	525.3 (447.6–603)	426.2 (399.3–453.2)
			Crepuscular	866.2 (790.0–942.5)*	575.7 (547.8–603.6)
			Nocturnal	688.3 (607.2–769.5)*	332.5 (303.2–361.8)
	Female	Restricted	Diurnal	806.9 (611.1–1,002.6)*	443.7 (403.4–484.1)
			Crepuscular	211.8 (63.9–359.7)	456.8 (423.1–490.4)*
			Nocturnal	−511.6 (−738.3 to −284.9)	172.0 (131.2–212.7)*
		Unrestricted	Diurnal	567.4 (506.2–628.7)*	497.9 (478.3–517.6)
			Crepuscular	578.3 (518.6–638.1)*	480.3 (460.7–500.0)
			Nocturnal	235.2 (169.9–300.5)*	165.6 (145.6–185.7)
Campsite	Male	Restricted	Diurnal	159.2 (−290.5–608.9)	392.4 (303.1–481.7)
			Crepuscular	533.9 (127.4–940.5)	589.4 (514–664.8)
			Nocturnal	851.4 (399.1–1,303.7)	537.5 (457.1–618.0)
		Unrestricted	Diurnal	610.7 (478.6–742.7)*	456.5 (426.5–486.6)
			Crepuscular	827.1 (688.0–966.2)*	612.3 (581.2–643.3)
			Nocturnal	654.6 (499.7–809.5)*	381.5 (347.9–415.0)
	Female	None	Diurnal	443.6 (316.8–570.4)	492.8 (461.9–523.6)
			Crepuscular	710.0 (579.2–840.9)*	539.1 (507.6–570.7)
			Nocturnal	232.7 (101.9–363.5)	188.8 (156.8–220.7)

APPENDIX D

TABLE D1 Selection of recreation sites (trail, campsite) by moving and stationary grizzly bears (male, female) among access restrictions (restricted, unrestricted) and time of day (diurnal, crepuscular, nocturnal) using coefficients from the best-supported model for each sex. We calculated relative selection strength (RSS) and 85% confidence intervals (CI) using the mean value for all continuous covariates and testing for differences in selection using 1 m (near) and 1 km (far) from recreation sites with access restriction and time of day held constant. Relative selection strength indicates the odds ratio of a bear at 1 km versus 1 m from a recreation site (avoidance) or at 1 m versus 1 km from a recreation site (preference). Indifference indicates no support for variation in selection based on distance from recreation sites; we calculated the associated RSS from the odds ratio of a bear at 1 m versus 1 km from a recreation site. Asterisks indicate evidence for difference in selection. We calculated moving values using the average velocity of grizzly bears in Yellowstone National Park (3,843 m/fix interval; Carnahan et al. 2021) and stationary values using 1 m/fix interval.

Recreation Site	Sex	Movement rate	Time of day	Restricted RSS (CI)	Direction	Unrestricted RSS (CI)	Direction
Trail	Male	Moving	Diurnal	2.2 (0.4–11.1)	Indifference	1.2 (0.8–1.9)	Indifference
			Crepuscular	6.5 (3.0–14.1)	Preference*	5.4 (3.7–7.8)	Preference*
			Nocturnal	10.5 (4.3–25.6)	Preference*	8.9 (5.6–14.1)	Preference*
		Stationary	Diurnal	0.1 (0.0–1.9)	Indifference	2.9 (1.5–5.2)	Avoidance*
			Crepuscular	6.1 (1.3–28.3)	Avoidance*	2.3 (1.3–4.2)	Avoidance*
			Nocturnal	4.9 (1.2–20.0)	Avoidance*	2.5 (1.3–4.6)	Avoidance*
	Female	Moving	Diurnal	3.0 (1.0–9.2)	Preference*	1.1 (0.7–1.7)	Indifference
			Crepuscular	1.8 (0.7–4.6)	Indifference	2.2 (1.4–3.4)	Preference*
			Nocturnal	59.8 (7.3–491.4)	Avoidance*	1.0 (0.5–2.2)	Indifference
		Stationary	Diurnal	51.9 (7.8–346.7)	Avoidance*	2.3 (1.1–4.6)	Avoidance*
			Crepuscular	16.9 (3.4–82.6)	Preference*	0.6 (0.3–1.1)	Indifference
			Nocturnal	229.3 (16.0–3292.1)	Preference*	2.5 (1.1–5.7)	Avoidance*
Campsite	Male	Moving	Diurnal	0.1 (0.0–1.6)	Indifference	2.3 (0.9–6.1)	Indifference
			Crepuscular	2.7 (0.4–18.1)	Indifference	3.2 (1.3–8.1)	Preference*
			Nocturnal	4.4 (0.4–43.5)	Indifference	3.9 (1.2–12.3)	Preference*
		Stationary	Diurnal	0.7 (0.0–12.7)	Indifference	0.6 (0.2–2.1)	Indifference
			Crepuscular	4.3 (0.3–68.6)	Indifference	0.5 (0.2–1.7)	Indifference
			Nocturnal	0.3 (0.0–5.3)	Indifference	0.4 (0.1–1.4)	Indifference
	Female	Moving	Diurnal			0.6 (0.1–2.2)	Indifference
			Crepuscular			0.6 (0.1–2.3)	Indifference
			Nocturnal			0.3 (0.0–2.5)	Indifference
		Stationary	Diurnal			1.1 (0.2–6.7)	Indifference
			Crepuscular			18.1 (3.0–111.7)	Avoidance*
			Nocturnal			0.2 (0.0–1.6)	Indifference