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Received: 26 February 2024 | Accepted: 14 March 2024

DOI: 10.1002/ecs2.4909

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Using integrated step selection to determine effects of predation risk on bison habitat selection and movement

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Funding information
U.S. Geological Survey Natural Resources Preservation Program; U.S. Geological Survey, Fort Collins Science Center; The Grand Canyon Conservancy; Grand Canyon National Park, Science and Resource Management Division

Handling Editor: Mathew A. Mumma

Abstract

Animal movement is a fundamental mechanism that shapes communities and ecosystems. Ungulates alter the ecosystems they inhabit and understanding their movements and distribution is critical for linking habitat with population dynamics. Predation risk has been shown to strongly influence ungulate movement patterns, such that ungulates may select habitat where predation risk is lower (refugia), adjust movement rates, temporal patterns, or selection of cover variables in areas with greater predation risk. We evaluated potential predation avoidance behavior in a population of plains bison inhabiting the north rim of Grand Canyon National Park (GRCA) and adjacent Kaibab National Forest (KNF). The KNF has year-round hunting managed by Arizona Game and Fish Department, whereas hunting is not allowed in GRCA. Human-maintained water sources on the KNF are particularly important resources for bison wherein they may be exposed to higher predation risk to access these resources. We used 2-h GPS locations for three years from 31 bison ($n = 9$ males; $n = 22$ females), and integrative step selection analysis to test four hypotheses about the potential for bison to reduce their risk from human predation by avoiding areas of high predation risk; moving faster in areas with high predation risk; entering high-risk areas at night when risk is reduced; and entering high-risk areas in habitats that provide cover (coniferous forest). The highest performing model indicated bison movement was 1.3 times faster per 2-h step interval than in areas with no hunting across all vegetation classes (coniferous forest, shrub, quaking aspen, grass-forb meadow) and across all topography classes (valley, slope, ridge). Bison moved more slowly in grass-forb meadows than all other vegetation types, and in valleys relative to slopes and ridges. Several radio-collared individuals had no GPS locations in KNF for the duration of the study. Bison avoided predation risk using two strategies: moving faster while in the KNF, and fully avoiding high-risk areas by remaining within GRCA. Management that manipulates or reduces timing of hunting seasons may reduce perceived predation risk and encourage bison to distribute into the KNF and across a broader range of available habitat.

KEYWORDS
bison, *Bison bison bison*, Grand Canyon National Park, habitat selection, hunting, integrated step selection, Kaibab Plateau, predation risk, ungulate, wildlife movement

INTRODUCTION

Large grazing mammals are influential components of ecosystems they inhabit, able to affect and alter structure, function, and nutrient dynamics of vegetation communities (Augustine & McNaughton, 1998; Hobbs, 1996; Schoenecker et al., 2004). Their movement and space use, resource selection and distribution can have long-lasting effects on vegetation, and have implications for population dynamics (Morales et al., 2010; Nathan et al., 2008). Prey species in particular must select habitat and conduct movements that balance resource acquisition with predation risk. Predation risk has been shown to effect prey species' movement patterns and habitat selection (Fortin et al., 2005, 2009; Hebblewhite & Merrill, 2009; Proffitt et al., 2009). Prey species employ multiple strategies to balance predation risk with acquiring resources, such as seeking land classifications that offer refuge ("refugia"), reducing exposure by moving faster (Fortin et al., 2005; Proffitt et al., 2009), selecting habitat that offers spatial or temporal separation from predators (Lundgren et al., 2022; Seip, 1992), adjusting temporal behavior to complement a predator's daily activity and space-use patterns (Smith et al., 2019), selecting habitat that offers better cover (Fortin et al., 2005; Hernández & Laundré, 2005), forming large groups with conspecifics (Fortin et al., 2009), or altering behavior otherwise in regard to vigilance, foraging, movement, or social behavior (Gaynor et al., 2019).

The risk allocation hypothesis proposes that when predation risk is high, prey species increase vigilance and reduce foraging effort, potentially slowing movement through high-quality foraging areas but speeding up in times of high predation risk (Lima & Bednekoff, 1999). Elk (*Cervus canadensis*) move more quickly through areas with high wolf use and spend more time grazing in areas with low predicted use by wolves (Frair et al., 2005), and increase their movement rates during intensive hunting seasons (Cleveland et al., 2012). Animals also select for vegetation or terrain that provides cover, such as elk moving into dense timber in response to elevated predation risk from wolves (Winnie & Creel, 2007), and mountain sheep (*Ovis canadensis* and *Ovis dalli*) utilizing slopes ≥60° (escape terrain), that offer spatial protection from predators (Geist & Petocz, 1977; Holl, 1982; McKinney et al., 2003; Terwilliger, 2005).

Another strategy to avoid predation risk is the use of temporal refuge. When predation risk is high, prey species must allocate time to both feeding and anti-predator behaviors, however in low predation risk settings they can allocate more time to foraging (Lima & Bednekoff, 1999). In the Andes, vicuñas (*Vicugna vicugna*) exploit the temporal and space-use patterns of ambush predators (pumas; *Felis concolor*), by foraging in risky habitats at times of day when predators are least active (Smith et al., 2019). Donkeys (*Equus asinus*) in Death Valley National Park have been found to avoid water sources at night when predation risk by mountain lions is highest (Lundgren et al., 2022). Elk in southern Colorado were observed using agriculture fields at night when risk of hazing by humans was absent (R. Rivale, Colorado Parks and Wildlife, personal communication, 2006). Humans relate to and interact with prey species as predators, but also as shelter/refugia from predation. Anti-predator behavior is flexible and predator-specific, addressing the most relevant predator at a given time and space (Lima, 1992; Proffitt et al., 2009).

Humans create refuge from predators with their presence and infrastructure as well as by designating land use areas where predation risk is lower due to species management (e.g., hunting regulations). Prey species can capitalize on areas with reduced predation risk due to high human activity, or in areas considered refugia from hunting (Davidson, 2007). This can greatly alter the movement and spatial ecology of ungulates. In Canada there has been a decline in migratory behavior of elk in several herds at Banff National Park, due to elk adopting more resident strategies near human developments, which offer predation refuge from wolves (*Canis lupus*; Hebblewhite et al., 2005, 2006; Robinson et al., 2010). By switching to a more resident strategy, these elk have relinquished the nutritional benefits of migration (Hebblewhite & Merrill, 2009). Further, moose (*Alces alces*) in Yellowstone, birthed calves near roads to minimize risk from traffic-averse brown bear (*Ursus arctos horribilis*; Berger, 2007), and mule deer (*Odocoileus hemionus*) acclimated to human settlements to avoid predators in Canada (Darlington et al., 2022). Animals may even use anthropogenic refugia to avoid predation risk by humans, such as elk using non-hunted private-lands during hunting seasons (Burcham et al., 1999; Gude et al., 2006; Proffitt et al., 2009).

Plains bison (*Bison bison bison*) are large grazers that currently inhabit the Kaibab Plateau of Arizona, USA, specifically on the north rim. Bison were not historically abundant in this ecosystem; itis considered the edge of historic range (Gates et al., 2010; Plumb et al., 2016; Plumb & McMullen, 2018), but they have persisted since 1926 when a small herd was acquired by the Arizona Game and Fish Department (AGFD) and managed as a game species with annual harvests (Plumb et al., 2016; Terwilliger et al., 2020). Current law prohibits hunting in National Parks unless specified by statute, but hunting is permitted on the adjacent United States Forest Service lands within KNF (Figure 1). Bison hunting is delineated by a boundary between two contiguous but different land management jurisdictions. Bison hunting on the KNF is regulated and managed by AGFD, which established nearly continuous bison hunting seasons to provide abundant hunting opportunities for recreational hunters. Mountain lions are the only natural predator in the area and have not been documented predating bison (Ironside et al., 2017; Stortz et al., 2018). Humans are thought to be the primary predator of bison in this system.

Step selection analysis is a tool to facilitate investigations of animal movement and distribution (Duchesne et al., 2015). We sought to assess potential effects of hunter harvest on bison movement by applying step selection analysis to GPS locations of 31 individually marked bison. Step selection functions are a mechanistic movement model (a biased correlated random walk; Duchesne et al., 2015), in which habitat selection parameters are estimated with bias because the observed movement process is confounded by habitat selection (Forester et al., 2009). Integrated step selection analysis (iSSA) overcomes this by estimating two independent processes: a "movement-free habitat selection kernel" and a "selection-free movement kernel." The resulting movement model is the product of these two independent kernels. The "movement-free habitat selection kernel" represents the habitats an animal would select or avoid if it were not constrained by movement. The "selection-free movement kernel" represents how the animal would move if it were not constrained by habitat. The power of iSSA is that it estimates these two processes using a simple regression model (conditional logistic regression) that is widely implemented in statistical software. To accomplish that, it requires the user to sample available steps from a "tentative" theoretical distribution. The estimated parameters either belong to the habitat selection or the movement process (and they can interact with each other). The habitat selection parameters are interpreted as the logarithm of relative selection strength (log-RSS), and the movement parameters are used to update the tentative distribution to the estimated selection-free movement kernel (Fieberg et al., 2021, appendix C). Our objective was to assess how human predation pressure (hunting) influenced movement patterns and habitat selection of bison on the Kaibab Plateau, Arizona. We tested the following hypotheses: (1) bison are avoiding areas of high predation risk by selecting areas that provide predation refuge; (2) bison are moving faster in areas where they experience high predation risk; (3) bison are entering high predation risk areas more frequently at night when predation risk is reduced; (4) bison are entering high predation risk areas more frequently in habitats that provide cover (e.g., coniferous forest) to reduce predation risk. We tested these hypotheses over a three-year period between 2019 and 2022, at an individual- and population-level to evaluate effects of predation risk on bison movement patterns and habitat selection.

METHODS

Study area

We conducted our study on the Kaibab Plateau in Coconino County, Arizona, USA, from September 2019 to January 2022 (Figure 1). The Plateau encompasses approximately 2980 km^2 with elevations ranging from 1830 to 2800 m (Rasmussen, 1941), and is bordered on the south by the steep walls of Grand Canyon's North Rim. The National Oceanic and Atmospheric Administration (NOAA) maintains the Bright Angel weather station on the Plateau at an elevation of 2560 m (NECI, 2022). Average annual snowfall during 1925–2021 was 4.7 m, and during our study period was 5.1 m (NWS, 2023). Snow can accumulate on the Plateau during winter to a depth of 2.3 m, with February having the greatest snow accumulation (Rasmussen, 1941). Snow typically melts by mid-June and dry conditions can persist during the summer and autumn months. Mean annual precipitation on the Kaibab Plateau (Bright Angel Ranger Station) was 538.5 mm during 1925–2021. During our study period, annual precipitation ranged from 657 mm (2019) to 218 mm (2020). Winter (December, January, February) precipitation ranged from 100 mm (2019–2020) to 138 mm (2020–2021) Average precipitation during the summer months (June, July, August) of our study period ranged from 33 mm (2020) to 109 mm (2021). There are a few natural springs that are productive during summer and although the landscape is characterized by steep drainages, there is no flowing water on the Plateau. Monsoon occurrence and significance varies by year but typically occurs from July through early September. During heavy monsoon seasons, water can pool on the landscape in karst sinkholes.

Much of the Plateau is covered in mixed-conifer forest dominated by ponderosa pine (*Pinus ponderosa*), Douglas

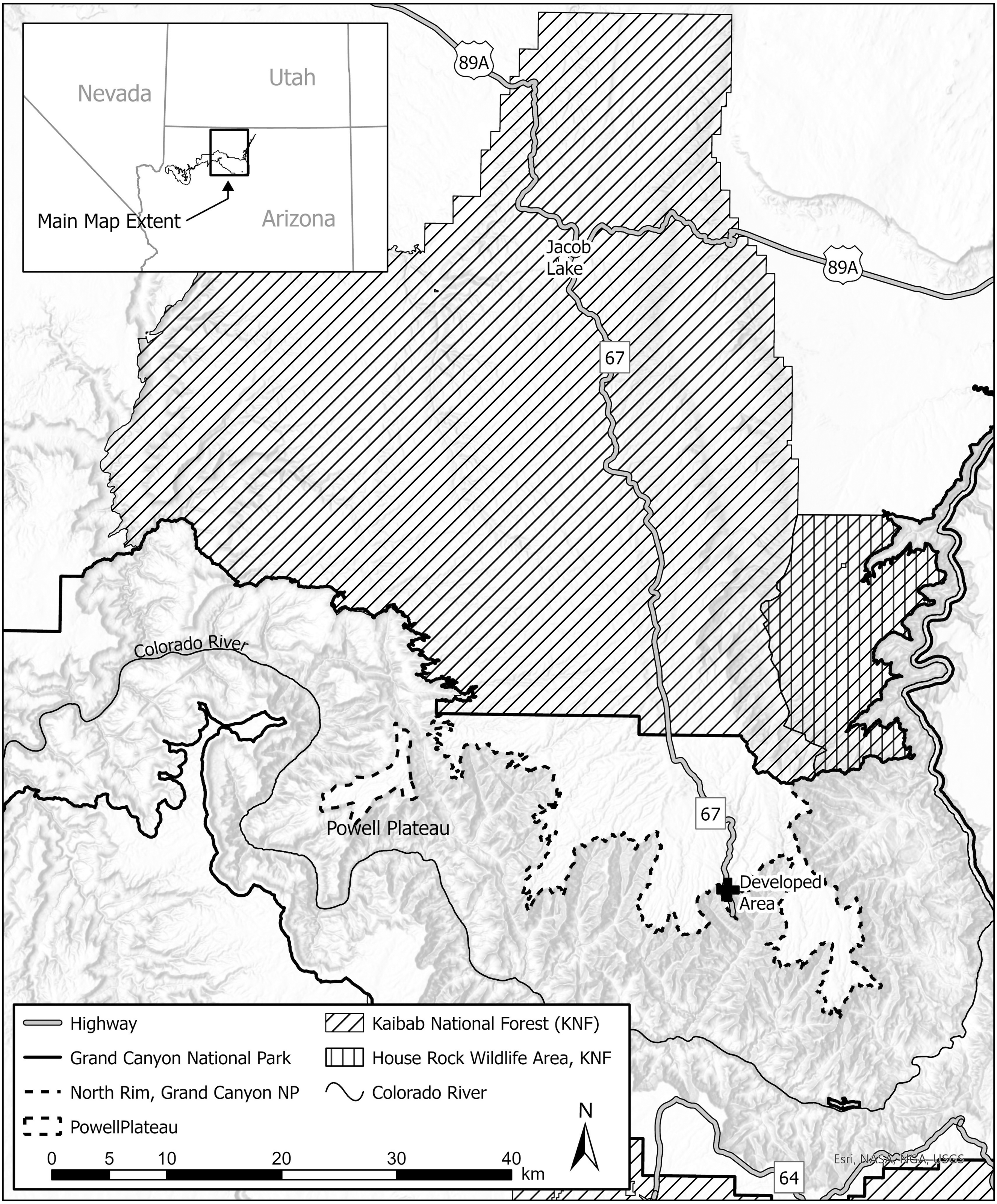

FIGURE 1 Study area map showing the Kaibab National Forest (KNF; hatched) and Grand Canyon National Park (GRCA), Arizona, USA for a study of bison space use and movements relative to predation risk from 2019 to 2021. The boundary between areas with high predation risk (KNF) and low predation risk (GRCA) is shown by a bold line. The corral trap where bison were captured and fitted with GPS collars was located ~3 km south of the GRCA/KNF boundary.

fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and blue spruce (*Picea pungens*), or quaking aspen (*Populous tremuloides*) (White & Vankat, 1993). Grass and forb meadows occur along drainage bottoms. Some areas along the edge of the Canyon are characterized by shrubs and/or sparse herbaceous vegetation.

The study area is comprised of public lands managed by the U.S. Department of Interior, Grand Canyon National Park (GRCA), and the U.S. Department of Agriculture, Kaibab National Forest (KNF). The AGFD manages plains bison (*Bison bison bison*) as a wildlife species within the KNF, whereas hunting is not permitted in GRCA. Bison first started moving to the Kaibab Plateau from the House Rock Wilderness Area in the late 1990s and became full time residents by 2010 (AGFD, 2022; Terwilliger et al., 2020). The bison population was estimated at 175–509 in 2019, 285–365 in 2020, 296–483 in 2021, and 187–313 in 2022 (M. Terwilliger, NPS data).

Most hunting activity and harvests occur within 2 km of the GRCA/KNF boundary (AGFD, 2022). State managers maintain multiple water sources, salt blocks, and blinds within 400 m of the GRCA/KNF boundary on the KNF (AGFD, 2022). Water is a limiting resource for bison in summer months when many ephemeral water sources on the Kaibab Plateau dry up. Bison hunts are broken into nine seasons spanning January 1–December 31 (Appendix S1: Table S1) with one seven-day no-hunting period in October. Breaks between hunting seasons are typically a single day, and this day is often used for camp set up and scouting by hunters, resulting in nearly continual year-round human presence and perceived predation risk for bison along the GRCA/KNF boundary.

Capture and collaring

We captured bison annually for three years using a baited corral trap located near the GRCA/KNF boundary (Figure 1) on September 14, 2019, September 2, 2020, and August 30, 2021. We employed low-stress handling techniques (Hibbard, 2021) and immobilized adult bison aged 4+ years old using a hydraulic squeeze chute; then fitted 31 bison ($n = 9$ male and $n = 22$ female) with GPS tracking collars (Telonics, Mesa, AZ, USA; model TGW-4477 Iridium). Bison were released from the capture facility immediately following collaring. Collars were programed with a two-hour fix rate and a timed-release mechanism to fall off after two years. All capture and handling of bison was conducted in accordance with an approved U.S. Geological Survey institutional animal care and use protocol (FORT IACUC 2018-14), a National Park Service Animal Research Protocol Concurrence (IMR-GRCA-Schoenecker-Bison-2018.A2), and a scientific collecting permit from the State of Arizona (LIC# SP407081), and the National Park Service (GRCA-2021-SCI-0031).

Data analysis

For analysis we combined data from males and females and used location data from September 15, 2019 to January 15, 2022. We omitted data from the first five days following each animal's capture to avoid bias of animal movement following capture events. We censored GPS tracking collar data to exclude fixes with low accuracy (<30 m; 13% of all locations; DeMars et al., 2013; Frair et al., 2010). We used location data from all seasons except winter; we omitted winter locations because 95% kernel density estimates of bison indicated they move to and remain near the edge of the Canyon during winter (Salganek et al., 2022), far from the hunt/no-hunt (GRCA/KNF) boundary which was the variable of interest in our study (Appendix S1: Figure S1). Further, an analysis of step lengths between winter and all other seasons indicated bison move less during winter months (Appendix S1: Figure S2) and this seasonal difference in movement rate would confound analyses. For our final analysis we used a total of 39,415 bison locations.

We applied iSSA to investigate the spatio-temporal effects of human predation risk (hunting) on bison movement patterns and habitat selection. iSSA was developed for the simultaneous inference of habitat-dependent movement and selection to test ecological hypotheses (Avgar et al., 2016; Fortin et al., 2005; Prokopenko et al., 2017; Signer et al., 2019). iSSA builds on the foundation of the resource selection function (RSF) and similarly uses animal relocation data to estimate the strength of selection of resources, and compares animal relocations to randomly sampled available habitat in a used:available design (Johnson et al., 2004). While RSF attempts to sample available habitat from the animals' estimated home range, iSSA incorporates movement into the assignment of available habitat (Thurfjell et al., 2014). For each GPS relocation, iSSA samples available steps from parametric theoretical distributions (e.g., the gamma distribution for step lengths and the Von Mises distribution for turn angles; Appendix S1: Figures S3 and S4). In the used:available study design, used steps are compared with available steps generated at each discrete temporal period (Boyce et al., 2002; Boyce & McDonald, 1999; Manly et al., 2002). With the advancement of animal tracking collars (i.e., iridium GPS), animal relocations are taken frequently and often create large datasets. Using data with such high temporal resolution requires using techniques that relax assumptions about spatial and temporal independence of samples. By sampling available habitat from the theoretical distributions of step length and turning angle, iSSA techniques avoid some of the spatial autocorrelation problems common to RSFs. We used iSSA formulations to test our alternative hypotheses both at an individual- and population-level to learn about the effects of hunting pressure on bison movement patterns and habitat selection. For analysis using iSSA, consecutive locations are needed. Thus, we evaluated GPS data from 31 bison to ensure that all movement tracks represented an uninterrupted series of movements (Signer et al., 2019) using the package "amt" in R (R version 4.3.0, R Core Team, 2021). We used the "amt" function step-length to calculate distance traveled for each 2-h movement. Using the gamma distributed step length distribution and the Von Mises distributed turn angle distribution from our steps, we generated 50 available steps for each step derived from consecutive bison relocations.

The "amt" function time_of_day was used to assign each step a day or night designation (factor with two levels), using the positional and temporal data relative to sunset and sunrise. Bison generally move more during the day than night; however, during the hottest times of years they have been demonstrated to increase nighttime movement (McMillan et al., 2021). Similarly, we assigned each step a season (factor with four levels). To delineate winter from other seasons, we used peak phenology, snow depth, temperature range, and timing of bison migration to determine when they left the summer range (Appendix S1: Figures S1 and S2).

We fit conditional logistic regression models to individual movement tracks using movement metrics, habitat covariates, and interactions between them. We tested four alternative models based on the expectation that bison are responding to predation risk and adopting movement and resource selection strategies to reduce predation risk.

Core model covariates

We established a core model that included environmental covariates that were expected to influence movement and resource selection of bison (Bastille-Rousseau et al., 2010; Schoenecker et al., 2015) regardless of the effects of hunting pressure. This core model served as the foundation of the four models that were designed to test our hypotheses on effects of predation risk.

Normalized Difference Vegetation Index (NDVI) at the spatial and temporal end of the step (end of each bison movement) was included in the core model. NDVI, an index for live green vegetation, has proven extremely useful in predicting herbivore distribution, and has been used as a reliable predictor of forage biomass (Hebblewhite & Merrill, 2009; Pettorelli et al., 2011). We used Terra Moderate Resolution Imaging Spectroradiometer (MODIS) surface reflectance data (NASA, 2022, MOD09GA product) to calculate NDVI from red and near-infrared light bands using the "raster" package in R. MODIS satellite data have been used widely and praised for sensitivities in discriminating land surface characteristics (Huete et al., 2002; Pettorelli et al., 2011). MODIS data are collected over an eight-day interval; therefore, we produced an NDVI raster dataset for each day that satellite data were available over the period of our study. We matched each data point collected from bison tracking collars to the NDVI raster that most closely matched the date and extracted the NDVI value for the spatial location. Values for NDVI range from 0 to 1, with values closer to 1 representing greater greenness. We acknowledge that in forested landscapes NDVI may not be correlated to herbaceous biomass, particularly with conifers. We chose to include NDVI in base models anyway because forage biomass was not a primary interest of our study, and it improved model performance.

Water sources were gathered from the National Hydrography Dataset (USGS, 2008) in combination with locations of man-made tanks maintained by the State (AGFD, 2022). Due to the arid conditions present in our study area relative to most plains bison ranges, we wanted to consider distance to water as a habitat covariate in our models. Because water is not available year-round at most springs in our study area, we created a subset of water sources for each biological season. Distance to water raster datasets were created using the path distance tool in ArcGIS Pro (version 2.6).

We used a digital elevation model (DEM) at a 10-m resolution (USGS, 2021, USGS 1/3 arc second) to construct a Topographic Position Index (TPI) raster. We used the raster calculator and model builder tools in ArcMap PRO to construct a TPI tool based on the formula "%cell_elevation% − %elevation_mean%." We used ±SD of our index to then reclassify slopes as "valley," "slope," or "ridge," in which valley ≤ -1 SD; -1 SD < slope < $-1/2$ SD; 1/2 SD < slope < 1 SD, $-1/2$ SD < ridge < 1/2 SD, ridge ≥ 1 SD, and exact values we used were: valley [−85.00, −0.97], slope [>−0.97, −0.485] and [>0.485, 0.97], ridge [>−0.485, 0.485] and [>0.97, 48.87].

We used mid-scale vegetation classification data from INREV (USDA FS, 2022) to have continuous data for vegetation classes across the two separately managed land authorities in our study area. We reclassified data from this source into four categories: "coniferous forest," "quaking aspen," "grass-forb meadow," or "shrub or sparse vegetation" (Appendix S1: Table S2). Vegetation categories were broad but intended to represent categories of vegetation that bison would move through similarly. For example, bison may move through spruce-dominant forest at a similar rate to ponderosa pine-dominant forest relative to their movement rate through a sedge-dominated area where they would likely be foraging. We expected to find bison selecting for "grass-forb meadows" frequently during the duration of our study season (spring–autumn) because they have been found to select for grasslands in a semi-arid ecosystem during all seasons (Schoenecker et al., 2015). We used log-transformed step length (hereafter LogStepLength) in the core model. We assumed the scale parameter of the tentative gamma distribution was identical to the scale parameter of the updated (estimated) gamma distribution, thus we did not include StepLength in our model, only LogStepLength. We expected that movement rates would differ depending on distance to water, vegetation classification, and topography classification; and we included an interaction term for LogStepLength and these covariates in our models. The cosine of turn angle (hereafter CosTurnAngle) is a measure of −1 to 1 that describes the direction of an individual's movement based on the previous location (Avgar, et al., 2016; Prokopenko et al., 2017). If the mean of the distribution of CosTurnAngle is a positive value, this indicates a tendency to continue straight, whereas if the mean of the distribution is a negative value, it can be interpreted as a tendency to turn around. If the mean of the distribution of CosTurnAngle is zero, there is no correlation and this can be interpreted as a random walk (Benhamou, 2006).

Predation risk covariate

We created four statistical models to quantify the specific behavioral responses of bison to areas where hunting occurs. This predation risk covariate was categorical, a factor with two levels, hereafter PredRisk. Values of 0 represented GRCA and 1 represented KNF. In models that involved the interaction between two categorical variables (e.g., veg and PredRisk) we, instead, created an indicator variable to account for the interaction and avoid having an overabundance of interaction combinations.

Individual and population-level model evaluation

We evaluated individuals on a yearly basis, hereafter bison-year. After fitting each iSSA model to individual bison-years, we attained population-level beta coefficients and CIs by applying bootstrapping to the individual beta coefficients (Fieberg et al., 2021; Prokopenko et al., 2017). For each bison-year, we evaluated models and compared Akaike information criterion (AIC) to evaluate model performance and find the best-ranking model for each bison-year. The model with the lowest AIC was tallied for each bison-year to infer population-level model performance (Appendix S1: Table S1; e.g., Prokopenko et al., 2017). When delta AIC between models was less than 2 for a particular bison-year, we tallied all bison-years within 2 AIC.

RESULTS

During non-winter months between 2019 and 2021, 93.97% of GPS fixes occurred in GRCA and only 6.03% of GPS fixes occurred on KNF (Figures 2 and 3). With respect to year, 83.99% (2019), 94.52% (2020), and 97.16% (2021) of GPS fixes occurred within GRCA and 16.01% (2019), 5.48% (2020), and 2.84% (2021) of GPS fixes occurred in KNF. Seven of 48 bison-years had no intervals that included a relocation in KNF (either at the start of the step or at the end of the step).

Core model covariates

Beta coefficients of covariates from the core model were similar in all four models (Table 1), thus we restrict

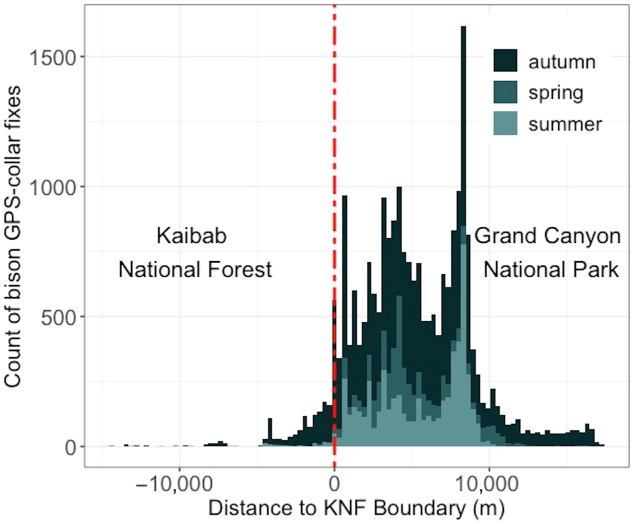

FIGURE 2 Histogram showing the number of bison locations (count) within the Kaibab National Forest (KNF), a high predation risk area, compared to the number of bison locations in Grand Canyon National Park (GRCA), a low predation risk area, and the distance of all locations to the KNF-GRCA boundary in spring, summer and fall, on the Kaibab Plateau, Arizona, USA. Data are from relocations of 31 GPS collared bison from 2019 to 2021. Negative values represent locations within KNF, and positive values represent locations within GRCA. The KNF-GRCA boundary is located at $x = 0$.

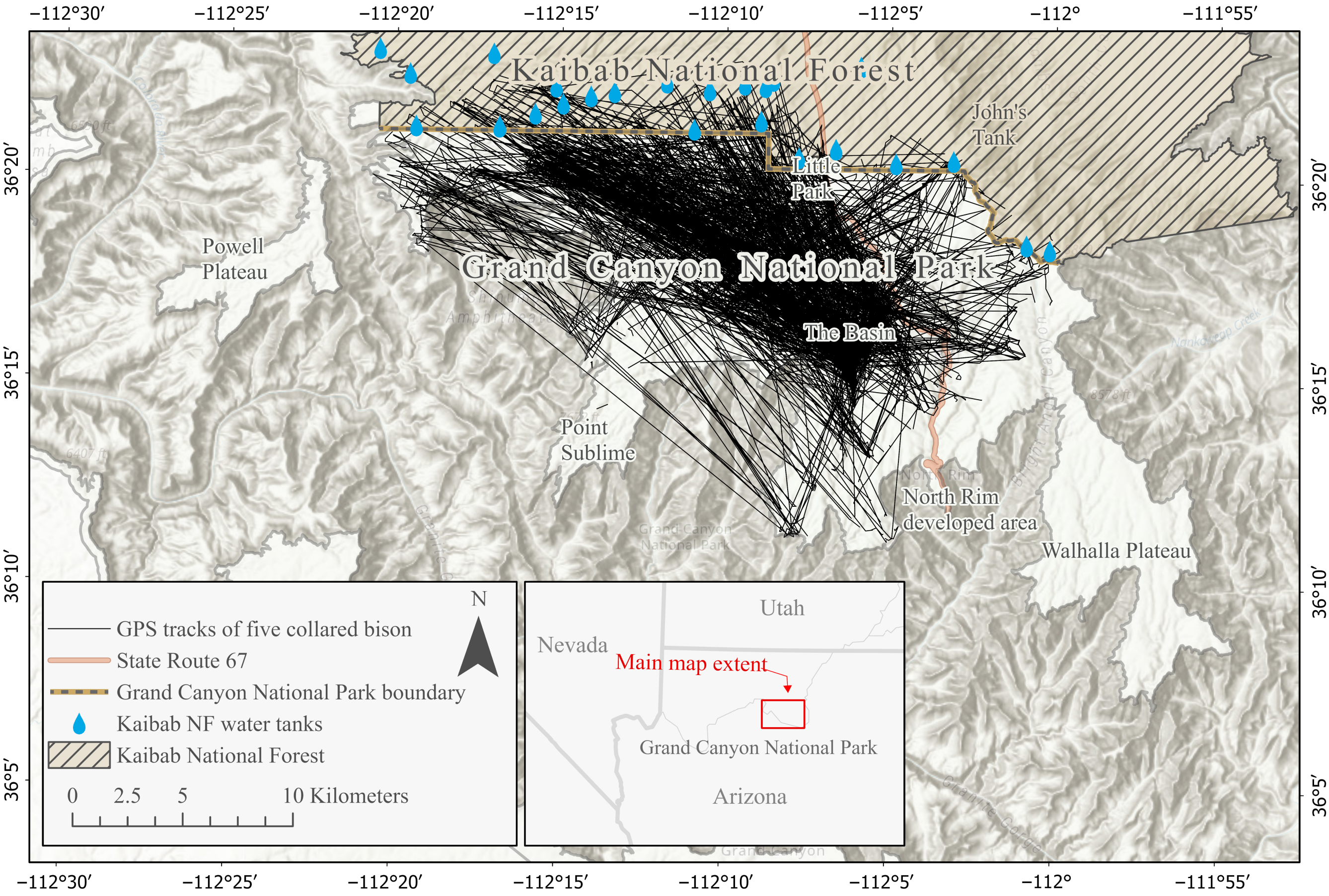

FIGURE 3 Movement track of five bison during spring, summer and fall over a three-year period from 2019 to 2021 on the Kaibab Plateau, Arizona, USA. Only five individuals are shown to enable viewing details of movements; however, these individuals were randomly selected and are representative of the 31 GPS collared bison. The boundary between Grand Canyon National Park and Kaibab National Forest (KNF) represents a political jurisdiction only; there is no physical barrier.

discussion of population-level results to the top model, Model 2. The population mean for the beta coefficient for NDVI was negative (mean coefficient value = −0.5725, 95% CI = [−0.6570, −0.4880]), and 100% of individual bison-year models had negative coefficients, meaning bison were selecting for grass-forb meadows that had lower NDVI (NDVI = 0.30) than coniferous forest (NDVI = 0.60) and quaking aspen forest (NDVI = 0.59) but higher than sparsely vegetated areas (NDVI = 0.10). It is possible that due to the low spatial resolution of the remotely-sensed MODIS imagery we used for NDVI calculations, greenness in grass-forb meadows was underestimated due to residual snow in these areas. The population mean for the coefficient of cos(TurnAngle) was not significantly different from zero (mean coefficient value = −0.0016, 95% CI = [−0.0425, 0.0394]), indicating that the true selection-free movement kernel had a turn angle distribution that was not significantly different from our tentative distribution and there was little directional persistence in bison movements.

The interaction between WaterDist and log(StepLength) yielded a coefficient that was significantly positive (mean coefficient value = −3.55e−05, 95% CI = [−0.0001, 2.32e−05]), indicating that the shape parameter, and therefore the mean of the gamma distribution of step-lengths, increased in the movement-free selection kernel. Approximately 63% of individual bison-years indicated that bison movement was quicker when moving towards water sources.

Movement rate (i.e., mean of the model-adjusted gamma step-length distribution) was variable between topographic position types and also variable between vegetation classes. The interaction between log(StepLength) and the categorical variable TPI compared step length interactions with the topographic position categories “slope” and “ridge” against the reference level “valley.” Both “slope” and “ridge” produced positive population-averaged beta coefficients indicating that the mean of the gamma distribution of step length increased (mean coefficient value “slope” = 0.0367, 95% CI = [0.0167, 0.0567]; mean coefficient value

TABLE 1 Mean beta coefficient values and 95% CIs (in brackets) for a study of bison movement and habitat selection relative to predation risk from hunting, 2019–2021, Arizona, USA.

Movement parameter	Model 1	Model 2	Model 3	Model 4
Total bison-years used in model	41	41	48	48
cos(TurnAngle)	−0.0021 [−0.0618 0.191]	−0.0019 [−0.0601, 0.0211]	−0.0021 [−0.0630, 0.0193]	−0.0020 [−0.0615, 0.0207]
log(StepLength): WaterDist	1.44e−05 [−4.45e−05, 7.11e−05]	−3.55e−05 [−0.0001, 2.32e−05]	1.45e−05 [−4.41e−05, 7.11e−05]	1.40e−05 [−4.39e−05, 7.13e−05]
log(StepLength): TPI_slope (relative to “TPI_valley” index)	0.0387 [0.0184, 0.0590]	0.0367 [0.0167, 0.0567]	0.0386 [0.0183, 0.0589]	0.0400 [0.0196, 0.0603]
log(StepLength): TPI_ridge (relative to “TPI_valley” index)	0.0852 [0.0678, 0.1027]	0.0828 [0.0650, 0.1005]	0.0846 [0.0673, 0.1020]	0.0862 [0.0681, 0.1042]
log(StepLength): veg_meadow (relative to “veg_conifer” index)	−0.0350 [−0.3000, 0.2299]	−0.0357 [−0.3018, 0.2303]	−0.0341 [−0.3012, 0.2330]	−0.0364 [−0.3050, 0.2322]
log(StepLength): veg_aspen (relative to “veg_conifer” index)	−0.0316 [−0.0553, −0.0079]	−0.0332 [−0.0574, −0.0090]	−0.0316 [−0.0552, −0.0079]	−0.0314 [−0.0555, −0.0073]
log(StepLength): veg_shrub (relative to “veg_conifer” index)	0.2147 [0.1934, 0.2360]	0.2139 [0.1929, 0.2348]	0.2149 [0.1938, 0.2359]	0.2137 [0.1922, 0.2352]
Selection parameters (end)				
NDVI	−0.3633 [−0.4331, −0.2935]	−0.3596 [−0.4295, −0.2897]	−0.3658 [−0.4363, −02953]	−0.3624 [−0.4316, −02934]

Note: Models are as follows: (1) Influence of hunting pressure on selection; (2) Influence of hunting pressure on movement; (3) Influence of hunting pressure and time-of-day on selection; (4) Influence of hunting pressure and vegetation type on selection. Shown are beta coefficients from the core model used in the four models to control for baseline selection and movement. Population means and CIs were calculated by bootstrapping coefficients for individual bison-years. Note that “:” indicates an interaction. Total bison-years represents bison-years used to estimate coefficients. Models 1 and 2 used “end of step” or “start of step” calculations, and seven bison-years could not be used in these models because bison had no locations close to the Kaibab National Forest/Grand Canyon National Park boundary.

Abbreviations: NDVI, Normalized Difference Vegetation Index; TPI, Topographic Position Index.

“ridge” = 0.828, 95% CI = [0.0650, 0.1005]). Using the signs and absolute magnitude of the coefficients for these interaction terms (Fieberg et al., 2021) we can determine that bison moved slowest while in valleys, and most rapidly when using ridges.

Using the interaction between log(StepLength) and the categorical variable veg, we compared vegetation classes “shrub and sparsely vegetated,” “quaking aspen,” and “grass-forb meadow” to the reference veg level, “coniferous forest.” In this case “shrub and sparsely vegetated” produced a relatively large positive coefficient (0.2149, 95% CI = [0.1938, 0.2359]) and “quaking aspen” and “grass-forb meadow” both produced relatively small negative population-averaged beta coefficients (mean coefficient value “quaking aspen” = −0.0316, 95% CI = [−0.0552, −0.0079]; mean coefficient value “grass-forb meadow” = −0.0341, 95% CI = [−0.3012, 0.2330]). Bison moved most rapidly in sparsely vegetated or shrubby areas, followed by coniferous forest, and quaking aspen. The slowest rates of movement were in grass-forb areas.

Predation risk

Of four alternative hypothesis, model 2 (where bison move more rapidly in areas of high predation risk) performed the best among individual bison-years, having the lowest AIC in 42.5% of bison-years (Table 2). Five of 48 bison-years had no GPS relocations in KNF and an additional two of 48 bison-years had no relocation interval in which the animal was in KNF at the end of the step. For our modeling this meant that seven of 48 bison-years could not yield

TABLE 2 Lowest Akaike information criterion (AIC) tally for individual bison-years comparing four models.

Model	Forest boundary covariates	Minimum AIC tally
1. Influence of hunting pressure on selection	Core model + PredRisk(end)	26 (33)[a]
2. Influence of hunting pressure on movement	Core model + log(StepLength):PredRisk(start)	38
3. Influence of hunting pressure and time of day on selection	Core model + PredRisk(end)_night(start)	26
4. Influence of hunting pressure and vegetation type on selection	Core model + PredRisk(end)_forest(end)	28

Note: If ΔAIC was <2 across, all qualifying competitive models were tallied. Each model contained the core model: NDVI + cos(TurnAngle) + log(StepLength):WaterDist + log(StepLength):TPI (":" signifies an interaction between the two covariates). Forty-one out of 48 individual bison-years had results for four models, however seven bison-years that were not analyzed support Model 1 results.

Abbreviations: NDVI, Normalized Difference Vegetation Index; TPI, Topographic Position Index.

[a] Indicates where seven additional bison-years support model 1.

results if models included the variable PredRisk(start) or PredRisk(end). For individual models and in population-level means of coefficients, these seven bison-years were excluded but accounted for nearly 15% of our data.

Model 1: Influence of predation risk on use of refugia

Ten bison-years or 25% of bison-years supported Model 1 as the best-performing model (Table 2). The population-level mean coefficient for PredRisk(end) covariate was negative (mean coefficient value = −0.8288, 95% CI = [−0.1688, 0.0013]) and 68% of all individual bison-years had negative coefficients. This variable was a categorical covariate, a factor with two levels, "GRCA" and "KNF." Model 1 used "GRCA" as the index value and compared "KNF" values to this index, therefore negative coefficients indicate bison were selecting GRCA over KNF. The bison-years that had no model results because the individual's range was entirely within GRCA were included in results of the use of refugia because these animals exclusively used predation refugia.

Model 2: Influence of predation risk on movement

We found strong evidence of bison moving faster in areas of high predation risk. Of four alternative hypothesis, Model 2 performed the best among individual bison-years, having the lowest AIC in 18 bison-years (42.5% of bison-years). The population-level mean coefficient (bootstrapped) for the interaction term log(StepLength):PredRisk(start) was positive (mean coefficient value = 0.4317, 95% CI = [0.1769, 0.6865]) and 68% of all individual bison-years that contributed to the population-level mean had positive coefficients. Because PredRisk(start) is categorical and uses "Park" as reference level, the positive coefficient for this variable indicates that bison are generally moving greater distances between locations (i.e., faster) in areas where there is high predation risk (KNF) than in areas that provide predation refugia (GRCA).

Bison movement rate was consistently faster across all vegetation classes where there was predation risk (Figures 4 and 5). Mean step length during a 2-h interval in coniferous forest was 224 m in GRCA ($n = 10{,}659$, range = [1–4689 m]) compared with 281 m in KNF ($n = 909$, range = [1–8553 m]). Similarly, in shrub or sparsely vegetated habitat, mean step length was 266 m in GRCA ($n = 1717$, range = [1–2971 m]) and 910 m in KNF ($n = 5$, range = [44–2938 m]). In quaking aspen habitat, mean step length was 241 m in GRCA ($n = 4231$, range = [1–4483 m]) and 329 m in KNF ($n = 495$, range = [1–6459 m]), and in grass-forb meadow mean step length was 258 m in GRCA ($n = 5105$, range = [1–5097 m]) and 523 m in KNF ($n = 105$, range = [5–3333 m]).

Movement rate was also consistently faster in all topographic position classes where there was greater predation risk (Figures 4 and 5). Mean step length during a 2-h interval in valleys was 282 m in GRCA ($n = 1257$, range = [1–4540 m]) and 485 m ($n = 61$, range = [1–6466 m]) in KNF. On ridges, mean step length in GRCA was 239 m ($n = 15{,}848$, range = [1–5097 m]) and 307 m in KNF ($n = 1178$, range = [1–8553 m]). On slopes, mean step length was 225 m in GRCA ($n = 4603$, range = [1–4689 m]) and 320 m in KNF ($n = 271$, range = [2–6459 m]).

Model 3: Influence of predation risk on temporal patterns

We did not find support for the hypothesis that bison may move into KNF more frequently at night to avoid predation risk. Model 3 ranked last among lowest-AIC tally of bison-years, performing best among only six individual bison-years (15% of bison-years). The

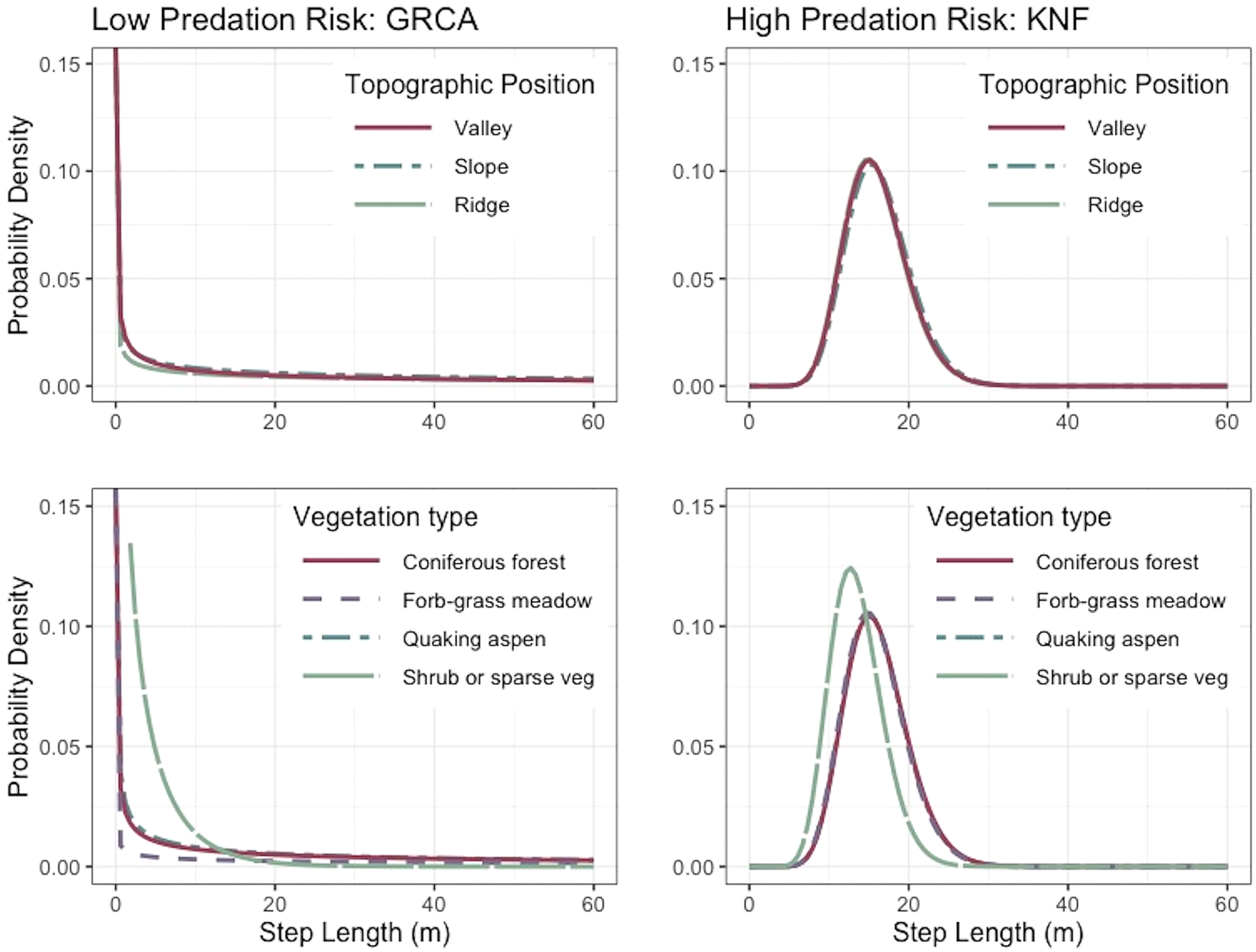

FIGURE 4 Probability density of the updated step length gamma distributions for Model 2. Bison step length increased in all topographic positions and in all vegetation types when traveling through areas where predation risk was greater. Estimated probability distributions were averaged over 48 bison-years and bootstrapped to determine how gamma distribution shape and scale were impacted by covariates and predation risk. GRCA, Grand Canyon National Park; KNF, Kaibab National Forest.

population-level mean coefficient (bootstrapped) for the indicator variable, PredRisk_night, was negative (mean coefficient value = −0.7203, 95% CI = [−1.6013, 0.1606]) and 61% of all individual bison-years that contributed to the population-level mean had negative coefficients, indicating bison moved less at night than during the day in high predation zones.

Model 4: Influence of predation risk on cover selection

Model 4 did not demonstrate strong support for the hypothesis that bison selected vegetation that offered better cover in high predation risk areas; in both GRCA and KNF bison selected for open grass-forb meadows, relative to availability of meadows (Figure 5). Model 4 performed best among 17.5% of bison-years (seven individual bison-years). Bison did not select coniferous forest in KNF (mean coefficient = −2.7712, 95% CI = [−4.6305, −0.9121]); 66% of bison-years had a negative coefficient for the indicator variable PredRisk_forest indicating bison did not select for greater cover vegetation (e.g., conifer forest) when entering high predation risk areas. We used an indicator variable for this analysis to avoid the complication of interactions between categorical variables, therefore the reference level for this factor variable was selection of all other vegetation and PredRisk(end) combinations.

DISCUSSION

Our findings indicate predation risk played a prominent role in bison avoidance of the KNF. Bison showed

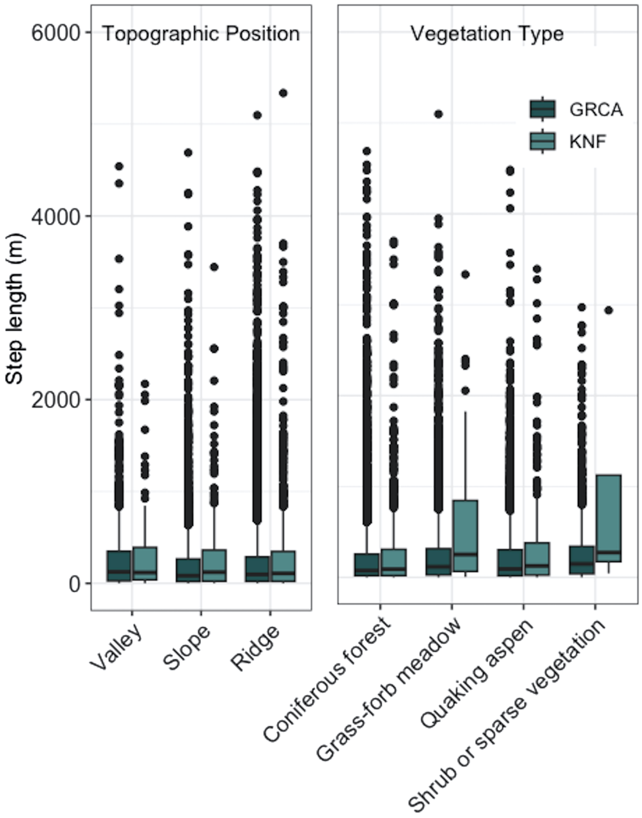

FIGURE 5 Boxplots of bison step length (in meters) across topographic types (valley, slope, ridge) and vegetation types (coniferous forest, grass-forb meadow, quaking aspen, shrub or spare vegetation) for bison GPS locations in Grand Canyon National Park (GRCA) and Kaibab National Forest (KNF), Arizona, USA. Box plots depict the minimum, first quartile, median, third quartile, and maximum, with outliers depicted as single points.

distinct differences in their movement patterns in areas with human predation pressure compared to areas without, increasing their average step length and speed of movement by 30% in higher risk locations. In seven of the bison-years we evaluated, bison avoided high predation risk areas entirely and remained completely within the park. These seven bison-years comprised 15% of our dataset, demonstrating the strong use of refugia within GRCA.

In two bison-years, bison relocations were far enough from KNF that even the available locations, generated from step length and turning angle for the individual bison-years, were not generated within KNF. Because we used a categorical variable for predation risk, rather than a gradient raster, we were unable to consider bison-years that had no KNF locations for either the start of the step, or both, the start and end of the step. We chose to represent predation risk as a two-level factor rather than a distance raster because locations that are proximal to the GRCA/KNF boundary still represent a low predation risk area. However, this highlights a shortcoming of iSSA when using coarse categorical land-cover variables. If we had generated available habitat from each animal's home range, a technique common to RSFs, our results may have demonstrated more avoidance of high predation risk areas. Although given that the GRCA/KNF boundary is nearly a straight line, it is possible that even 95% minimum convex polygons would also underestimate available habitat in KNF.

We did not observe a temporal shift in use of high predation risk areas during time periods when predation risk was lower, such as at night when hunting was not allowed. We posit human presence from recreation, or hunters preparing and staying in nearby camps was enough of a cue for bison to influence their movement behavior. Hunting in KNF during the time of our study was almost full time, so hunters preparing for the next season would still be camped near the boundary. Additionally, European bison were observed in 15 of 19 cases to rest at night and found in the morning within 100–300 m of the evening resting place from the preceding day (Caboń-Raczyńska et al., 1987). This suggests bison may simply not have high movements at night.

We expected bison would use forest cover when predation risk was high, but results did not support this hypothesis. Bison avoided forested habitat in other studies (Courant & Fortin, 2012; Kohl, 2013; Schoenecker et al., 2015) and movement through forested areas is likely slower and more arduous. Similarly, bison did not respond to wolf predation risk by increasing their use of forest cover in Wyoming (Hernández & Laundré, 2005). Bison have been shown to select for habitats with higher graminoid and herbaceous productivity (Allred et al., 2011; Courant & Fortin, 2012; Kohl, 2013; Schoenecker et al., 2015), and we found similar selection for open herbaceous meadows in this study. We considered that bison fidelity to GRCA may have been influenced by a higher availability of meadows in GRCA relative to the KNF. However, habitat conditions for bison on the KNF are considered comparable if not preferable to GRCA. The KNF had similar species richness but greater grass cover compared to GRCA (Musto, 2023; Musto et al., 2019), water was more temporally and spatially available on the KNF because it is maintained by AGFD, species composition of KNF meadows had higher cover of graminoids than forbs which is the preferred forage for these large-bodied grazers (Campbell & Hinkes, 1983; Fortin et al., 2003; Meagher, 1973; Peden, 1976; Van Vuren & Bray, 1983), and grass height was taller and bare ground was lower on KNF compared to GRCA (Musto, 2023). These conditions suggest predation risk played a prominent role in bison avoidance of the KNF.

Over time, concentrations of large grazers can degrade vegetation communities. We considered that bison remaining in the park and not distributing to available habitat in KNF may affect park meadow communities. However, Musto (2023) found increased vegetation productivity, increased nitrogen yield of grazed plants, and higher soil nutrients in high-density park meadows compared with low bison density meadows on the KNF. This indicates bison are not over-concentrating to an extent that would cause meadow community decline.

The Kaibab Plateau bison appear to treat the GRCA/KNF political boundary as a biological boundary due to predation by hunters. Thus, careful manipulation of spatial and temporal hunting seasons to provide more and longer breaks between hunting seasons has the potential to alter distribution of bison across a broader continuum of available habitat in the KNF.

ACKNOWLEDGMENTS

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. We thank B. Smith for assisting with relative selection strength figure and expertise on integrated step selection functions, and T. Bean and K. Joly for consultations on analysis. Thank you to G. Holm for his support and S. Garcia for data management, data support, and cartography assistance, particularly for creating Figure 1. This project was funded by the U.S. Geological Survey Natural Resources Preservation Program, the U.S. Geological Survey, Fort Collins Science Center, the Grand Canyon Conservancy, and Grand Canyon National Park, Science and Resource Management Division.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data supporting this research are sensitive and not available publicly. Bison location datapoints are available to qualified researchers by contacting the United States Geological Survey, Fort Collins Science Center, at the following email address: fortdatamanagement@usgs.gov or schoeneckerk@usgs.gov.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Salganek, S., K. A. Schoenecker, and M. L. N. Terwilliger. 2024. "Using Integrated Step Selection to Determine Effects of Predation Risk on Bison Habitat Selection and Movement." *Ecosphere* 15(7): e4909. https://doi.org/10.1002/ecs2.4909