

ARTICLE

Animal Ecology

What does the fox select? Spatial ecology of Rocky Mountain red fox during peaks and troughs of human recreation

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Abstract

Understanding animal behavior at the population level can be challenging, especially in the presence of intraspecific variation in behavioral tactics. Individuals within a population often vary with respect to resource exploitation and use, which may be associated with individual states (e.g., male or female) or extrinsic variation (e.g., temporal variation in food). Explicitly accounting for interindividual variation can aid ecological insights, especially for species that exhibit high behavioral flexibility. Here, we evaluated how seasonal fluctuations in resources influenced individual-level habitat use and selection of Rocky Mountain red fox (*Vulpes vulpes macroura*) within Grand Teton National Park, Wyoming. Rocky Mountain red fox is a high-elevation subspecies of the common red fox (*Vulpes vulpes*), and native to North America. From 2016 to 2021, we captured and GPS-collared 18 individuals (11 males, 7 females) and evaluated spatiotemporal shifts in home range characteristics and habitat selection. We observed high individual variation in home range size, with generally larger home ranges in the winter months ($\bar{x} = 72.92 \text{ km}^2$ [minimum convex polygon—MCP], 83.65 km^2 [Kernel], 27.20 km^2 [Local Convex Hull]) than in the summer ($\bar{x} = 22.23 \text{ km}^2$ [MCP], 23.01 km^2 [Kernel], 11.11 km^2 [Local Convex Hull]). Similarly, we observed substantial individual variation in habitat selection across environmental gradients. Some foxes altered their selection for habitat types between summer and winter indicating behavioral plasticity with respect to seasonal resources. Distance to human features was the primary driver for habitat selection for both seasons across foxes, and on average, foxes had stronger selection for human features in the summer. These findings might indicate some foxes are concentrating on the temporal and spatial resource pulse of anthropogenic food, while others exhibited more natural tactics. Our work advanced the spatial ecology of Rocky Mountain red fox, identified variation in space use tactics associated with humans and natural resources among red foxes in a heavily

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recreated area, and demonstrated how human activity can influence the spatial behavior of a carnivore within a national park.

KEY WORDS

canid, carnivore, Greater Yellowstone Ecosystem, human disturbance, human food provisioning, interindividual variation, mesocarnivore, recreation, *Vulpes vulpes macroura*

INTRODUCTION

Resources often fluctuate temporally and spatially across a landscape, and animals must adjust their movement behavior in response to survive and reproduce. Behavioral changes with respect to resource exploitation are a primary mechanism linking questions in movement ecology, habitat selection, and space use (Charnov, 1976; Mitchell & Powell, 2004; Powell & Mitchell, 2012). Canada lynx (*Lynx canadensis*), for example, demonstrated increased home range sizes immediately after population crashes of their primary prey, the snowshoe hare (*Lepus americanus*; O'Donoghue et al., 2010), indicative of increased search effort in pursuit of food. Intrinsic factors like sex, age, and reproductive status (Araújo et al., 2011; Bolnick et al., 2011; Lesmerises & St-Laurent, 2017; Polis, 1984; Shine, 1989), and extrinsic factors like intraspecific competition (Rosenzweig, 1991), predation risk (Gosselink et al., 2007; Heithaus, 2001), and temporal changes in food resources can influence behavioral tactics regarding resource exploitation. These state dependencies among individuals, coupled with variation in extrinsic factors, can lead to high levels of among-individual variation within a population when considering tactics of resource exploitation. Explicitly evaluating behavioral responses across a sample of individuals can provide finer grained insight relative to the alternative of summarizing at a population level (Bastille-Rousseau & Wittemyer, 2019; Muff et al., 2020). This is particularly true for species that are known to exhibit high behavioral flexibility, like generalist carnivores.

A terrestrial carnivore that expresses vast behavioral flexibility is the red fox (*Vulpes vulpes*). Red foxes occur on every continent except Antarctica, and their dietary and behavioral flexibility allows them to thrive in a variety of environments from tundra ecosystems (Gomo et al., 2021; Savory et al., 2014) to large metropolises (Bateman & Fleming, 2012; Soulsbury et al., 2010). Indeed, red foxes have demonstrated high individual variation within populations concerning their behavior relative to extrinsic and intrinsic factors (Hradkysy et al., 2017; Walton et al., 2017). For example, of the red foxes that frequently visited anthropogenic feeding sites,

females visited the most in the spring because they had dependent young, whereas feeding sites in autumn had the lowest visitation from either sex because natural food resources were more abundant ameliorating the need for human food (Fawcett et al., 2017). Understanding how different state dependencies can influence animal space use and behavior can help aid managers tasked with conservation of foxes as well as help inform management of human–fox conflicts. Much of the current research on red foxes, however, has occurred in urban landscapes, and thus additional work is needed in less human-impacted areas such as nature preserves. Some nature reserves receive seasonal pulses in human visitation or recreation, which provides a natural experiment to evaluate questions regarding how animals alter their spatiotemporal behavior during peaks and troughs of human visitation.

Over the last 20 years, Rocky Mountain red foxes (*Vulpes vulpes macroura*) have become increasingly common within Grand Teton National Park, Wyoming (hereafter Grand Teton), leading to an increase in human–fox conflicts. The Rocky Mountain red fox is a lesser understood subspecies of red fox, endemic to North America, and tends to occupy higher elevation habitats (Quinn et al., 2022; Smith et al., 2022; Statham et al., 2012). Rocky Mountain red foxes consume a wide variety of food items (Burkholder, Stephenson, Hegg, Gustine, Robinson, et al., 2024; Cross & Crabtree, 2021), use an array of habitats (Fuhrmann, 1998; Van Etten et al., 2007), and have demonstrated seasonal shifts in behavior based on fluctuations in natural resources (O’Malley et al., 2018). Knowledge regarding the spatial behavior of Rocky Mountain red fox, as well as the impact of human activity on their spatial behavior, is lacking and thus new work is needed regarding questions on interindividual variation in seasonal movements, habitat selection, and space use of this subspecies.

Our goal was to evaluate habitat selection and space use of red foxes within Grand Teton, which were genetically confirmed as the Rocky Mountain subspecies (Quinn et al., 2022). We sought to assess how seasonality and human disturbance influenced individual-level habitat use and selection. Grand Teton received marked seasonal (i.e., winter and summer) fluctuations in human

visitors throughout our study, which generated large variation in the availability and amount of human food attractants and human activity. Our first objective was to evaluate seasonal shifts in red fox space use by comparing the size of seasonal home ranges across male and female foxes. Based on optimal foraging theory, when food patches are reduced in quality, time spent by an organism within a patch decreases, which leads to more diffuse space use (Charnov, 1976). We predicted that red fox would display smaller home ranges during summer months relative to winter months because of the increase in accessibility of natural prey items (e.g., voles, ground squirrels) due to snow melt, coupled with the influx of anthropogenic food during the summer months. Our second objective was to assess seasonal variation in habitat selection of Rocky Mountain red fox, with a particular emphasis on behavior related to forest productivity and human structures. Given the behavioral and dietary breadth observed in other subspecies of red fox, we expected substantial interindividual variation among Rocky Mountain foxes, and therefore attenuated patterns in habitat selection at the population level (Lesmerises & St-Laurent, 2017). We expected some foxes to express strong selection toward human structures, whereas others would likely avoid human structures and select for more remote and forested environments. Collectively, this work not only advances the understanding of a high-elevation subspecies of red fox but also explores general ideas in ecology such as behavioral flexibility and optimal foraging theory.

METHODS

Study area

We conducted fieldwork in northwestern Wyoming, USA, in Grand Teton National Park (Figure 1) between January 2016 and August 2021 (43.813480° N, -110.691896° W). Grand Teton contributes 1300 km^2 to the southern end of the Greater Yellowstone Ecosystem ($72,000 \text{ km}^2$) and receives extreme variation in human recreation and park visitation. For instance, in 2021 and 2022, 89% of annual human visitation occurred during the non-winter months (May–October) relative to the remaining 11% in the winter months (November–April). This variation facilitates a vast gradient in anthropogenic food availability that may influence the spatial ecology of red fox. Monthly garbage disposal weight for 2021 and 2022 in the summer months (May–October) was on average 89,780 kg, about 4.7 times greater than the winter months (November–April; 19,100 kg). Moreover, the park offers over 1000 campsites distributed between seven

designated campgrounds operational only in the summer, and four visitor centers: one operational between April and November (Craig Thomas Discovery and Visitor Center in Moose), and three open between May and September (Colter Bay Visitor Center, Jenny Lake Visitor Center, and the Laurance S. Rockefeller Preserve Center). Visitors can access 152 miles of paved roads, 65 miles of unpaved roads, and 242 miles of trails during the summer months (National Park Service, 2021a).

Grand Teton received around 490 cm of annual precipitation in the valley from 2016 to 2022, most of which came from snowfall (Moose, WY; National Oceanic and Atmospheric Administration, 2022). Temperatures within the park averaged around $2.8^{\circ}\text{C}/-11.4^{\circ}\text{C}$ during the winter to $21.6^{\circ}\text{C}/2.4^{\circ}\text{C}$ in the summer from 2016 to 2022 (Moose, WY; National Oceanic and Atmospheric Administration, 2022). The Snake River runs through the middle of the park in the valley, creating low elevation (1855 m) riparian areas and wetlands comprised of narrowleaf cottonwood stands (*Populus angustifolia*) which give way to grasslands and shrublands dominated by Kentucky bluegrass (*Poa pratensis*), and big sagebrush (*Artemisia tridentata*). Along the mountainsides at intermediate elevations (2400 m), forests of lodgepole pine (*Pinus contorta*) and Douglas fir (*Pseudotsuga menziesii*) predominate, and as elevations increase, whitebark pine (*Pinus albicaulis*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and subalpine meadows can be found ending in tundra conditions between 3000 and 4193 m (Knight et al., 1994; LANDFIRE, 2016). Wolves (*Canis lupus*), grizzly bears (*Ursus arctos horribilis*), mountain lions (*Puma concolor*), and black bears (*Ursus americanus*) make up some of the largest predators in Grand Teton. Common ungulate species include elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), moose (*Alces alces*), and bison (*Bison bison*).

Red foxes' primary prey items include birds (Aves), snowshoe hare (*L. americanus*), northern pocket gopher (*Thomomys talpoides*), and multiple species of voles (*Arvicolinea* sp.) and squirrels (*Spermophilus* sp.; *Tamiasciurus hudsonicus*; Cross & Crabtree, 2021). Seasonal shifts in weather (i.e., snowfall and snowmelt) within Grand Teton influence wildlife activity patterns and particularly prey availability for red foxes (Halpin & Bissonette, 1988). For instance, during the spring and summer months, most mammals produce their young, ground squirrels come out of hibernation, and voles exploiting the subnivean zone during winter become more accessible to foxes with the melting of snow. Snowmelt and resulting growth of new vegetation during early summer months (e.g., end of May–August) generates a natural increase in prey

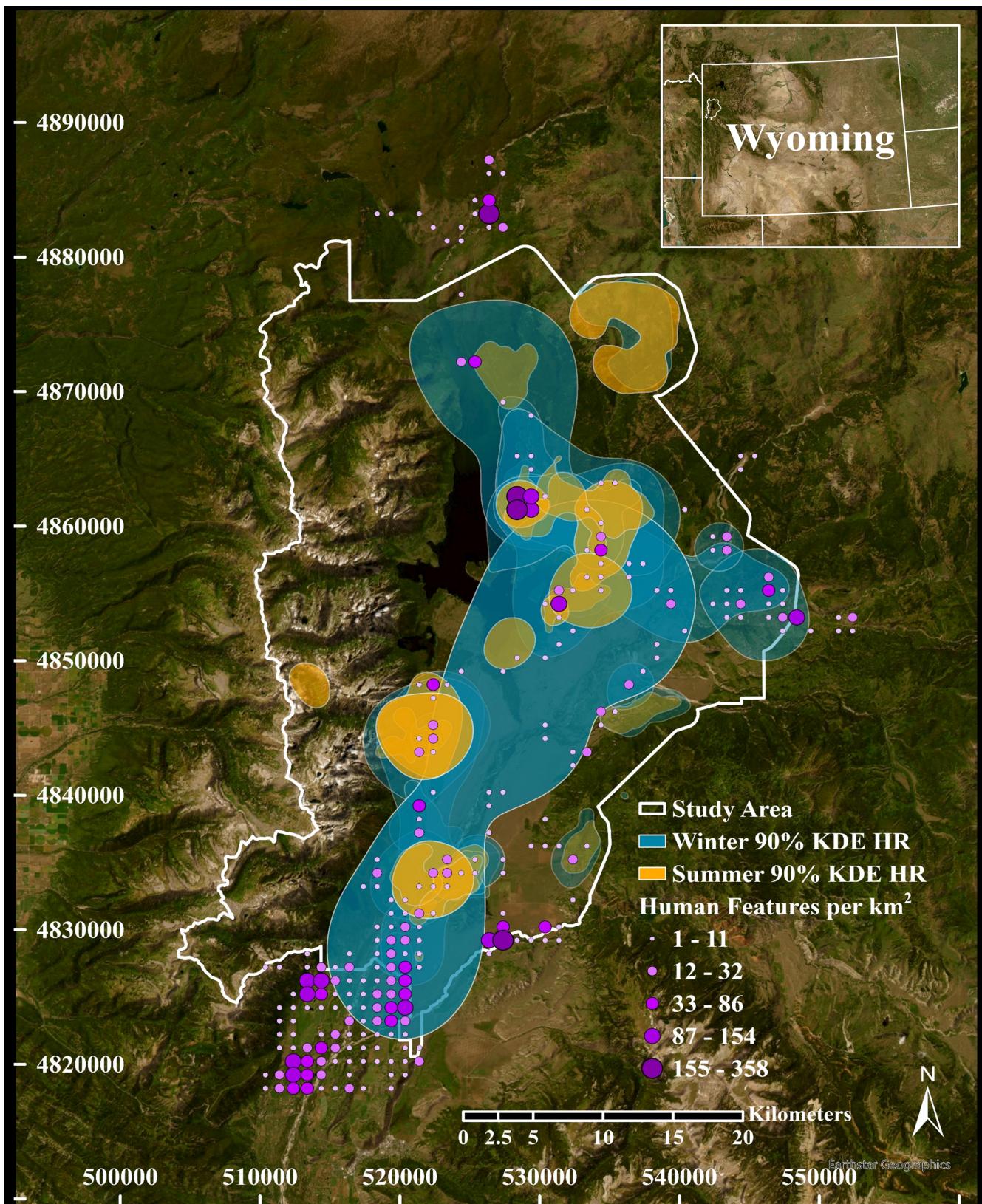


FIGURE 1 Map of study area in Grand Teton National Park, Wyoming, with Rocky Mountain red fox (*Vulpes vulpes macroura*) 90% home ranges using kernel density estimates (KDE HR) for winter and summer during 2016–2021. The map also shows the number of human features per square kilometer using increasingly larger circles to illustrate different levels of concentration of human features within the study area.

biomass, coinciding with the peak in human visitation to Grand Teton.

Capture methods and sample collection

We captured red foxes using cage traps (Models BC100, BC200, and BC300; Tomahawk Live Trap Company, Tomahawk, Wisconsin, USA) from January 2017 to March 2021 primarily within areas accessible by vehicles during the winter months (Figure 1). This sampling included developed areas of the park as well as more remote locations of the park. We anesthetized captured foxes using Telazol (10 mg/kg tiletamine-zolazepam; Kreeger & Arnemo, 2018) and then transported them to an indoor processing facility to ease thermoregulatory strain, where we then recorded biometrics, collected demographic information and aged individuals (using tooth wear and weight), and equipped the individuals with Global Positioning System (GPS) or Very High Frequency (VHF) radio collars and colored-metal ear tags. Foxes were fit with collars when collar weight (105–150 g) was less than 3.0% of the total body mass of the fox (WY_GRTE_Stephenson_RedFox_2020.A3). Capture and handling protocols followed American Society of Mammalogists' guidelines (Sikes, 2016) and were approved by the National Park Service Institutional Animal Care and Use Committee (WY_GRTE_Stephenson_RedFox_2020.A3).

Home range estimation

We constructed seasonal (i.e., summer and winter) home ranges at the 90% and 50% contours for all red foxes equipped with a GPS collar (Börger et al., 2006). We first screened GPS data for erroneous locations by removing locations with ≤ 3 satellites. Additionally, we removed locations if a fox was in a trap and had inconsistent fix rate success or if a fox was less than 1 year old (based on tooth wear and size of animal at capture). We removed 6700 of 36,507 locations, retaining 82% of original data. GPS fix rate success on our finalized dataset was 77%. We then determined range residency of individuals prior to estimating home ranges (Calabrese et al., 2016); all individuals included in analyses demonstrated range residency by 1 month. We estimated home ranges using three different estimators to ensure our results were comparable with previous studies: (1) adaptive-local convex hull technique ($a = 75$ km; Getz et al., 2007), (2) minimum convex polygons, (3) and bivariate normal kernel density estimates using a reference bandwidth (Worton, 1989). The adaptive-local convex hull technique was chosen because it performs well when hard

boundaries (e.g., Jackson Lake in our study area) are present in the study area (Getz et al., 2007). We used the R package adehabitatHR to estimate home range sizes (Calenge, 2006). Season was determined based on the inverse relationship between increasing visitation rate and decreasing snow pack (summer: May–October; winter: November–April). We included individuals that were older than 1 year, and we grouped data together for those five individuals that were recaptured and received an additional GPS collar (summer $n = 16$, winter $n = 18$). We calculated the size for each seasonal home range and compared average home range size between sex and seasons using 90% CIs. If the CIs did not overlap, we considered the difference statistically supported.

To assess how food accessibility influenced territorial behavior within foxes, we calculated home range overlap for seasonal home ranges at the 90% and 50% contour using the utilization distribution overlap index (UDOI; as described in Fieberg & Kochanny, 2005). This index assumes each animal uses space independently of one another, corrects for relative size of each independent home range, and considers high-use areas such that values greater than 1 indicate both animals are sharing a relatively small space. Values greater than 0 and less than 1 indicate overlap for animals using a larger area uniformly (Fieberg & Kochanny, 2005). Because of sample size and temporal fluctuations in territories, we only calculated overlap for males collared in 2021 ($n = 7$).

To examine finer resolution fluctuations in home range expression, we estimated monthly home ranges at the 90% kernel density estimates for all red foxes. We assessed whether there was a qualitative relationship between fluctuating resources and space use (home range size), with the expectation of smaller home ranges during the summer months due to an increase in the abundance of both natural and anthropogenic food. We compared the average monthly home range size between sexes and only included individuals, which were over 1 year old, with more than 20 locations in a month (Schoener, 1981).

Habitat use and selection

To assess habitat use and selection, we first defined availability at the study area extent (i.e., between second and third order of selection; Johnson, 1980) and characterized environmental resources presumably important to red fox. We defined the western and northern boundaries of the study area using the park's boundary and the eastern and southern boundaries based on 95% minimum convex polygons (buffered by 1 km) of each fox. Bodies of water (e.g., Jackson Lake) were excluded from the study area for consistency between summer and winter. We characterized

abiotic metrics using topographic variables including topographic position index (indicates topographic position such as valley bottoms [near 0] or ridges [high positive values]), heat load index (describes incident radiation ranging from 0 [coldest; northeast facing slope] to 1 [warmest; southeast facing slope]; McCune & Keon, 2002), and vector ruggedness measure (measures terrain ruggedness using variation in slope and aspect simultaneously ranging from 0 [no terrain variation] to 1 [complete terrain variation]; Google Earth Engine Landsat 8). We developed indices of habitat structure using LANDFIRE existing vegetation type (EVT) and calculated the proportion of lodgepole pine, Douglas fir, and meadows within our study area (LANDFIRE, 2016; ArcGIS Pro v.2.7.0 ESRI, 2020). We also incorporated normalized burn ratio (NBR = Near-infrared–Short-wave infrared/Near-infrared + Short-wave infrared) from Google Earth Engine Landsat 8 imagery to index wet, productive forests. We used NBR because it generally has increased resolution to discern differences in vegetation biomass compared with Normalized Difference Vegetation Index (NDVI = Near-infrared–Red/Near-infrared + Red; Escuin et al., 2008; Harris et al., 2011). Recently, NBR has been used to understand habitat selection of Canada lynx (Holbrook et al., 2018; Olson et al., 2023) as well as moose (Mumma et al., 2021). Finally, we identified human structures (i.e., buildings, campgrounds, and picnic tables) within the study area and constructed a point features layer. We then created a distance to human feature raster (in meters). Each covariate had a base resolution of 30×30 m that we then summarized at a 250×250 m window using the mean value. We applied the moving window for all covariates except distance to human features. We sampled availability across our study area using a systematic sample with each point spaced 500 m apart.

We summarized habitat use and availability across foxes and used resource selection functions to model selection of environmental and anthropogenic resources (Manly et al., 2007). We used individual models to allow each individual fox to express its own selection or avoidance for all variables examined (DeCesare et al., 2012; Muff et al., 2020). We compared GPS locations of each fox with our sample of availability for both summer and winter seasons. This resulted in a use to availability ratio ranging from 1:2 to 1:42 with an average ratio of 1:11, and the sample of availability remained constant across seasons for every fox. The implication of keeping our sample of availability similar across foxes was that observed differences in selection or avoidance across individuals could be attributed to differences in habitat use, rather than unknown alterations to either habitat use or the sample of availability (Beyer et al., 2010). Logistic regression software was used in R to estimate β coefficients within

the resource selection function (Johnson et al., 2006; Manly et al., 2007), where fox locations (1 = used) were compared with available locations (0 = available). We standardized all numeric covariates [(value – mean)/SD] and used the car package in R to calculate variance inflation factors (VIFs) to assess collinearity (Zuur et al., 2009). We only included predictor variables with VIF < 3 (Zuur et al., 2007). We summarized selection, avoidance, or no response among male and female foxes across winter and summer. We then calculated a weighted average of model coefficients by sex for each season following Murtaugh (2007).

Finally, we developed predictive maps characterizing the relative probability of use for red fox in the summer and winter within our study area, which we then reclassified into equal-area bins (Boyce et al., 2002). To evaluate whether our population-level maps characterized red fox habitat use, we assessed predictive performance using cross-validation. We randomly sampled 75% of foxes for training (withholding 25% for validation), refit our model and generated predictions, and assessed the correlation between the equal-area bins and percentage of the withheld foxes' GPS locations. We repeated this process five times for both summer and winter and computed Spearman's rank correlation coefficient (r_s ; Boyce et al., 2002) for each iteration. We then calculated the average r_s . If our model predicted red fox use at the population level, we would observe a strong correlation between withheld fox locations and the binned probability of use (e.g., Holbrook et al., 2017). To visualize among-individual variation across our study area, however, we developed maps for each individual in the summer and winter and calculated the SD per pixel across the suite of individuals. All statistical analyses were completed in program R (v.4.2.2; R Core Team, 2021).

RESULTS

We deployed 23 GPS-enabled radio collars on 18 individual red foxes (11 males; 7 females) from 2017 to 2021. We deployed 2 collars in 2017, 2018, and 2020, 5 collars in 2019, and 12 collars in 2021 (Lotek, Havelock North, New Zealand; Telonics, Mesa, Arizona, USA). Over the sampling period, three males and two females were recaptured and fitted with new radio collars (two in 2019 and 2021, and one in 2020). Collars typically lasted between 6 months and over 20 months and varied in programming over the years from 2-h fix rates (the amount of time between GPS location collection) to 7-h fix rates. We recorded nearly 30,000 locations of Rocky Mountain red fox (18,224 locations in summer, 11,583 locations in winter). The number of GPS locations per fox ranged

from 263 locations to 2237 locations in summer and 131 locations to 1196 locations in winter. Our GPS collars sampled males 11,367 times in summer and 8186 times in winter. Females were sampled 6857 times in summer and 3397 times in winter.

Home range estimates

Home range estimates for foxes were variable across estimators. Estimates derived from local convex hulls were significantly smaller than minimum convex polygons (paired *t*-test, 90% $t_{51} = -2.19$, $p = 0.035$; 50% $t_{51} = -2.28$, $p = 0.029$) and kernel density estimates (paired *t*-test, 90% $t_{51} = -2.32$, $p = 0.026$; 50% $t_{51} = -2.43$, $p = 0.020$). Minimum convex polygons and kernel density estimates captured exploratory movements, which resulted in outlying positions that increased home range sizes. Even at more conservative 90% home range estimates, minimum convex polygons and kernel density estimates were almost 2.5 times larger than local convex hulls (mean 90% local convex hull = 19.63 km²; mean 90% minimum convex polygons = 49.06 km²; mean 90% kernel density estimates = 55.13 km²). Minimum convex polygons, however, were not statistically different from kernel density estimates (paired *t*-test, 90% $t_{51} = -0.31$, $p = 0.76$; 50% $t_{51} = -0.18$, $p = 0.85$).

Consistent with our expectations, home ranges were statistically smaller in the summer than in the winter, but only for males (Table 1). The average 90% home range for males during the summer for all home range estimators ranged from 9.7 to 18.7 km², while in winter they ranged from 33.7 to 109.48 km² (Table 1). Females, however, demonstrated more consistent space use patterns (Figure 2a). In summer, females had average 90%

home ranges from 13.4 to 30.3 km² for all home range estimators, and in the winter, they ranged from 17 to 43 km² (Table 1). Male home ranges were generally larger than females during the winter, yet the opposite was suggested (although not statistically different) during the summer (Figure 2a). We observed low amounts of overlap using 50% and 90% kernels between pairs of our 2021 sample of male foxes. In the summer, overlap ranged between 0.02 and 0.29 ($\bar{x} = 0.165$), while in the winter, all seven males showed some degree of overlap ranging between 0.005 and 0.37 ($\bar{x} = 0.10$). Core home ranges (50%) had a very minor overlap between our male foxes in summer (between one pair UDOI = 0.04) and winter (between two pairs UDOI = 0.06 and 0.06).

Monthly 90% kernel density estimates provided additional insight regarding seasonal fluctuations in home range size for males and females and highlighted that male red fox generally expressed more variation than females (Figure 2b). The reduction in home range sizes coincided with human activity during summer (May–November) compared with winter, which was consistent with our expectations (Figure 2b).

Habitat selection

We observed substantial variation with respect to habitat use and selection across our sample of individual foxes. The habitat types most used by red foxes were lodgepole pine, followed by Douglas fir and meadows (Figure 3). Additionally, foxes exhibited substantial use and selection for the NBR (metric of forest productivity) in both winter and summer (Figure 3). Most foxes were indifferent regarding selection for more ridge-like areas (positive topographic position index) or valley bottoms (negative

TABLE 1 Estimates of seasonal home ranges for >1-year-old male and female Rocky Mountain red foxes (*Vulpes vulpes macroura*) sampled from Grand Teton National Park, Wyoming, during 2016–2021, using three home range estimators (means with 90% CIs in parentheses).

Home range contour	LCH	MCP	KDE
Female 90% winter	17.04 (10.25–23.83)	36.92 (13.83–60.01)	43.05 (20.40–65.71)
Female 90% summer	13.44 (5.82–21.06)	29.62 (11.58–47.65)	30.29 (12.40–48.18)
Female 50% winter	6.09 (3.25–8.93)	8.32 (4.25–12.39)	10.56 (5.86–15.26)
Female 50% summer	2.89 (0.67–5.10)	13.51 (2.03–24.99)	8.27 (2.94–13.60)
Male 90% winter	33.66 (16.88–50.44)	95.83 (30.94–160.71)	109.48 (34.30–184.66)
Male 90% summer	9.71 (7.12–12.30)	17.80 (8.68–26.92)	18.69 (11.55–25.83)
Male 50% winter	6.73 (3.35–10.11)	26.24 (4.94–47.54)	24.74 (7.09–42.38)
Male 50% summer	2.28 (1.28–3.29)	4.88 (2.77–7.00)	4.74 (3.06–6.41)

Abbreviations: KDE, kernel density estimate; LCH, local convex hull; MCP, minimum convex polygon.

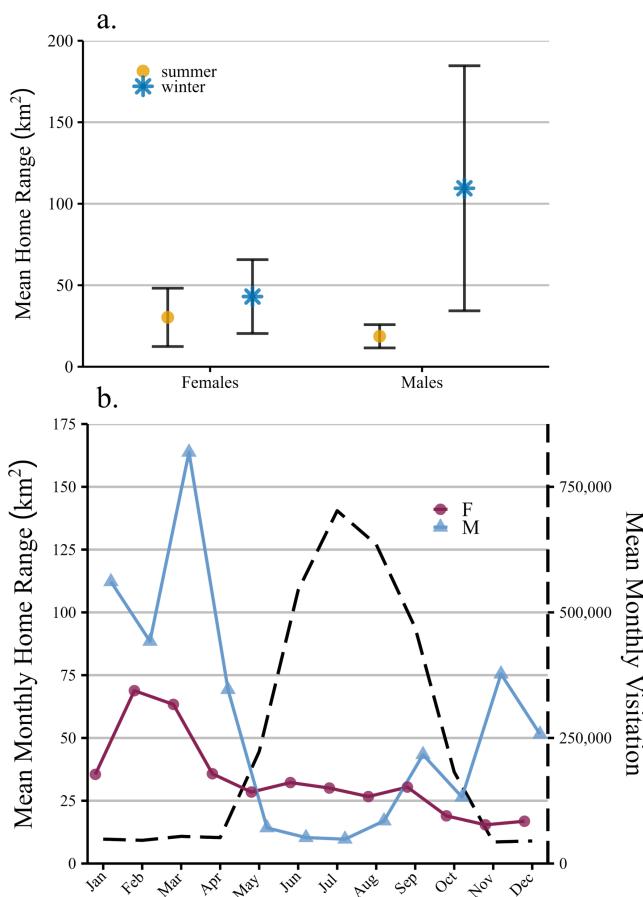


FIGURE 2 (a) Home range size (mean \pm 90% CI) and (b) monthly estimates of home range size using 90% kernel density estimates (KDE, in square kilometers) for female and male Rocky Mountain red foxes (*Vulpes vulpes macroura*) within Grand Teton National Park, Wyoming, 2016–2021. The black dashed line in (b) indexes monthly human visitation rate.

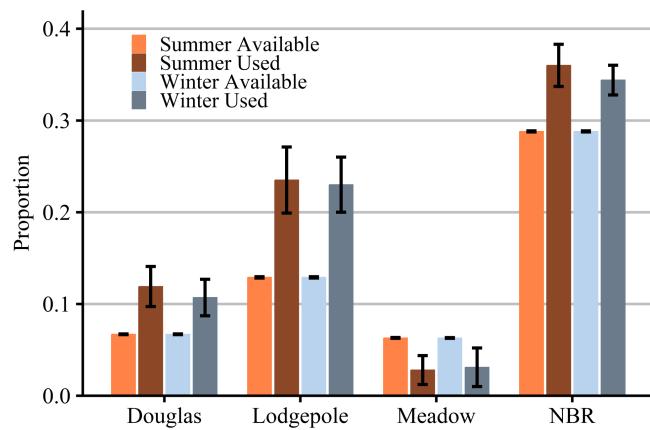


FIGURE 3 Proportion of different habitat types (Douglas fir, lodgepole pine, meadow) and an index for normalized burn ratio (NBR = Near-infrared–Short-wave infrared/Near-infrared + Short-wave infrared) at used and available locations for Rocky Mountain red fox (*Vulpes vulpes macroura*) within Grand Teton National Park, Wyoming, 2016–2021.

TABLE 2 Resource selection patterns (as indicated by the number of foxes exhibiting selection, avoidance, or indifference relative to each environmental covariate) from our winter and summer models characterizing habitat relationships of Rocky Mountain red fox (*Vulpes vulpes macroura*) within Grand Teton National Park, Wyoming, 2016–2021.

Covariates	Selected	Avoided	Significant
Winter model covariates			
Topographic position index	3	2	13
Heat load index	8	4	6
Vector ruggedness measure	4	7	7
Douglas fir	10	6	2
Lodgepole pine	12	3	3
Meadow	3	12	3
Normalized burn ratio	10	5	3
Distance to human features	17	1	0
Summer model covariates			
Topographic position index	4	4	8
Heat load index	8	6	2
Vector ruggedness measure	8	5	3
Douglas fir	8	6	2
Lodgepole pine	11	4	1
Meadow	5	10	1
Normalized burn ratio	10	5	1
Distance to human features	15	1	0

Note: Statistical significance was determined by $p \leq 0.05$.

topographic position index) in both summer and winter (Table 2; Appendix S1: Table S2). Approximately 45% of foxes in winter and about 50% of foxes in summer were selected for warmer, southwest-facing slopes, whereas about 22% in the winter and about 38% in the summer selected for cooler southeast-facing slopes (Table 2; Appendix S1: Table S2). More foxes avoided rugged terrain in the winter (39%) compared with the summer (31%) where more foxes selected for rugged terrain (50% in summer vs. 22% in the winter; Table 2; Appendix S1: Table S2). Regarding vegetation covariates, selection for forests was high in both summer and winter. Half of the foxes selected for Douglas fir in both summer and winter, with 33% in the winter and 38% in the summer avoiding Douglas fir (Table 2; Appendix S1: Table S3). Half of the foxes in the winter (55%) also selected for higher values of NBR indicating selection for wet, productive forest such as spruce-fir habitat types (Figure 4a, Table 2; Appendix S1: Table S4). Selection for more productive forests increased to 62% in the summer, and avoidance increased from 28% in the winter to 32% in the summer.

(Figure 4a, Table 2; Appendix S1: Table S4). The majority of foxes selected for lodgepole pine and avoided meadows in both summer (69% and 63%, respectively) and winter (67% and 67%, respectively; Table 2; Appendix S1: Table S3). Finally, 94% of monitored foxes in both the summer and winter selected for closer distances to human features (Table 2, Figure 4b). Seven males and five females had higher selection for human features in the summer than in the winter, and there was high

individual variation in the degree of selection for human features.

We used the regression coefficients from our resource selection models to develop predictive maps characterizing probability of habitat use. We developed a map for summer and winter at the population level (Figure 5a,b), summarized spatial variation in predictions for summer and winter (i.e., SD in predictions across individual foxes; Figure 5c,d), and illustrated the range in predictions

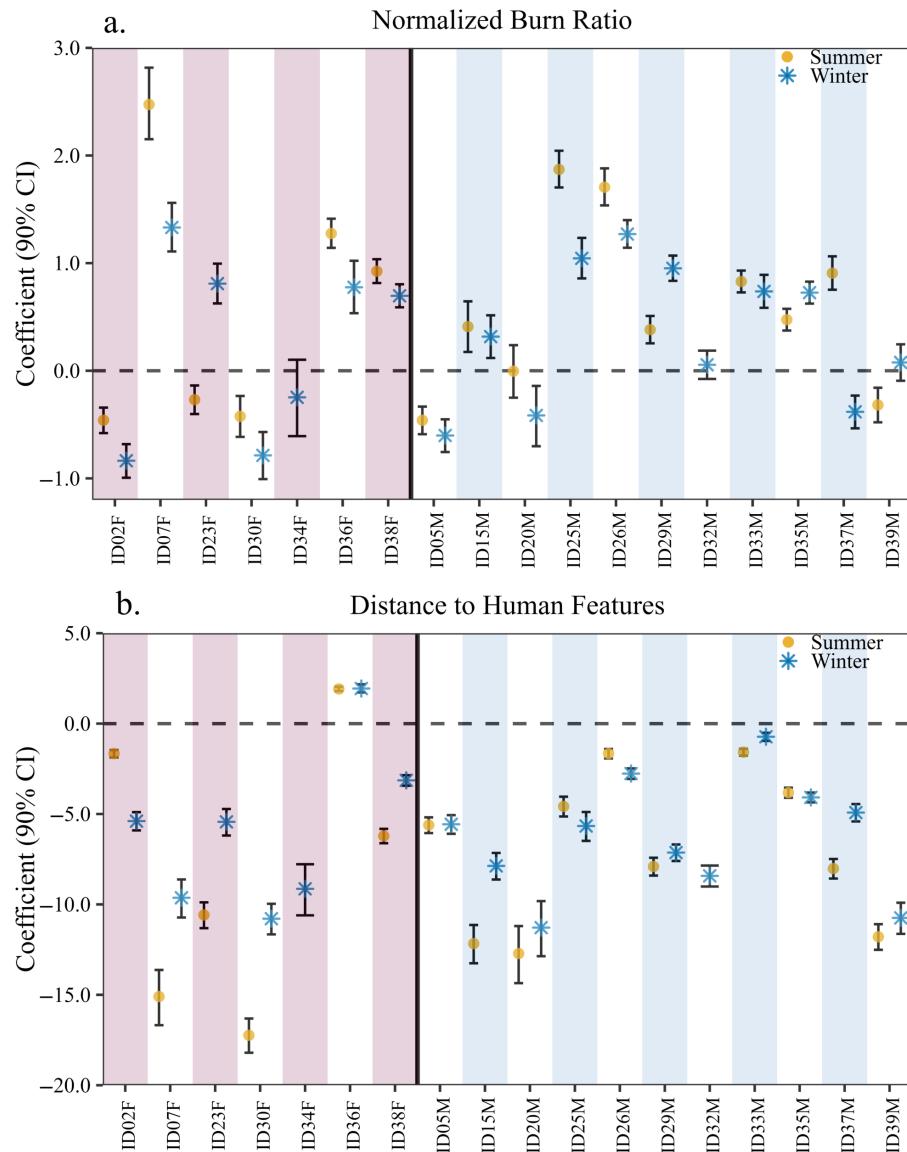


FIGURE 4 Interindividual selection coefficients ($\pm 90\%$ CI) for (a) the normalized burn ratio (NBR = Near-infrared–Short-wave infrared/Near-infrared + Short-wave infrared) from Google Earth Engine Landsat 8 imagery and for (b) distance to human features for summer and winter for female (left of solid black line) and male (right of solid black line) Rocky Mountain red fox (*Vulpes vulpes macroura*) within Grand Teton National Park, Wyoming, 2016–2021. The horizontal dashed black line indicates proportional use. Because the covariate in (b) is distance to human features, more negative selection coefficients correspond to stronger selection for closer distances to human features, whereas positive coefficients indicate avoidance.

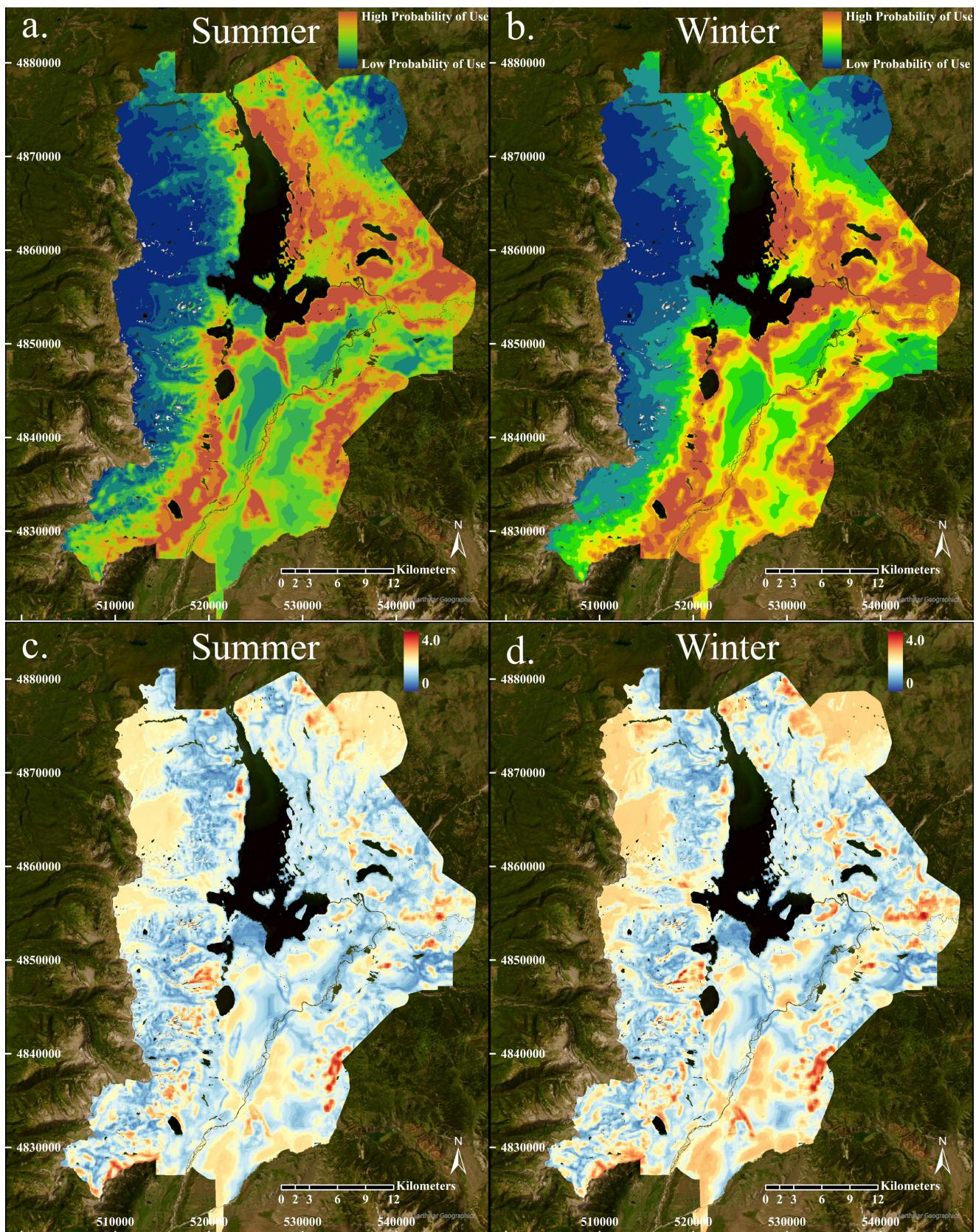


FIGURE 5 Predicted probability of use for Rocky Mountain red fox (*Vulpes vulpes macroura*) within Grand Teton National Park, Wyoming, for (a) summer and (b) winter. These maps were generated from our top resource selection functions. We then created maps for each individual and calculated the SD across individuals for both (c) summer and (d) winter to illustrate among-individual variation in probability of use.

using two example individuals within the population (Figure 6a,b). Our population-level predictions were strongly correlated with the frequency of red fox use as measured by withheld fox locations in summer ($r_s = 0.95$) and in winter ($r_s = 0.85$; Figure 7) with p -values consistently less than 0.05.

DISCUSSION

Movement, habitat selection, and space use are fundamental processes in population and behavioral ecology and are essential to understand for animal conservation and management. Understanding interindividual variation in behavior can be especially important when studying species that exhibit complex and flexible tactics, or when opposing behaviors are expected within a population. We evaluated interindividual variation in space use and habitat selection relative to fluctuating seasonal resources for an understudied and behaviorally diverse carnivore, the Rocky Mountain red fox. Consistent with our expectations, we observed high individual variation in home range size with generally larger home ranges in the

winter months. We also observed substantial individual variation in habitat selection across environmental gradients. Some foxes exhibited plasticity in their selection for habitat types between summer and winter, indicating foxes might be modifying their behavior to exploit different seasonal resources. Distance to human features was the primary driver for habitat selection for both seasons and across foxes, and on average, foxes had stronger selection for human features in the summer. These findings indicate that most foxes within our study are attracted to developed areas of the park either to exploit anthropogenic food or to fill other resource needs (i.e., protection from predators, safe den sites to raise young). Our work advances the spatial ecology of the Rocky Mountain red fox within wilderness areas that allow human recreation (Fuhrmann, 1998; O’Malley et al., 2018; Van Etten et al., 2007) and demonstrates how human activity can influence their spatial behavior, which provides the much-needed context complementing previous work on their trophic patterns (Burkholder, Stephenson, Hegg, Gustine, Robinson, et al., 2024).

Rocky Mountain red fox exhibited similar behavioral flexibility as the European red fox, which allowed them to

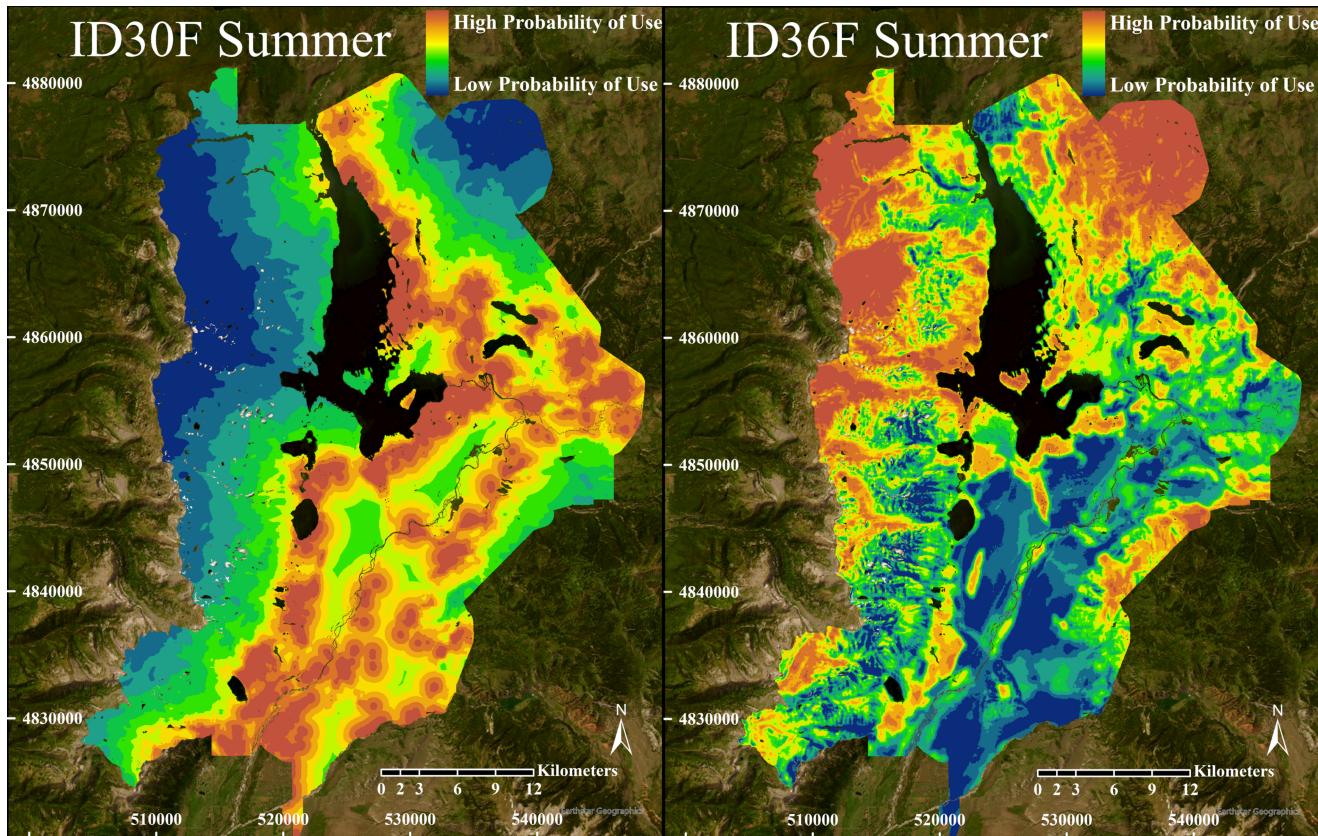


FIGURE 6 The breadth of variation in predicted probability of use among Rocky Mountain red fox (*Vulpes vulpes macroura*) within Grand Teton National Park, Wyoming. This figure illustrates mapped probability of use for two female foxes during summer.

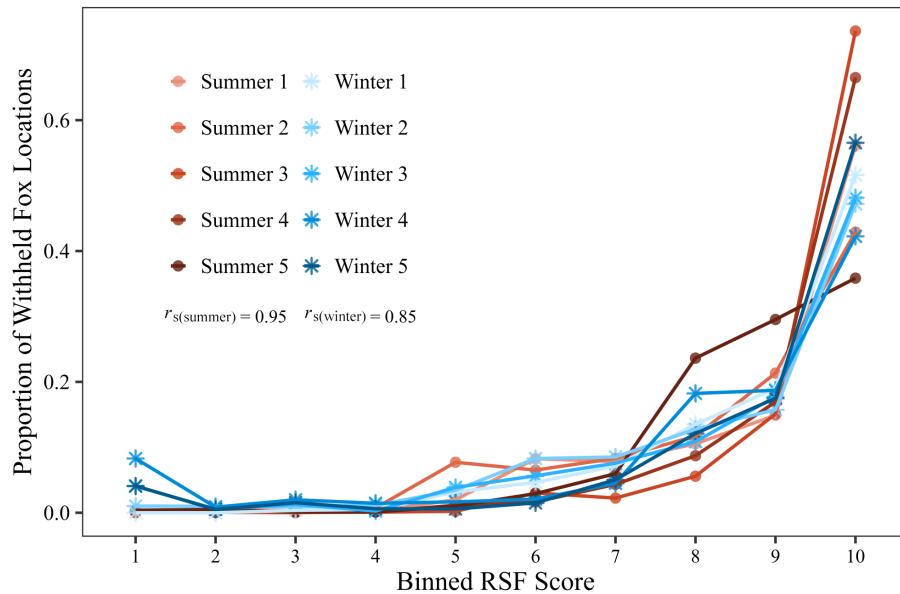


FIGURE 7 Proportion of withheld GPS locations from Rocky Mountain red foxes (*Vulpes vulpes macroura*) across our predicted probabilities of fox use in Grand Teton National Park, Wyoming, 2016–2021. The x-axis represents 10 equal-area bins ranging from low to high probability of use as generated by resource selection functions (RSF), while the y-axis indicates the proportion of the withheld GPS locations within each bin during summer or winter. The 10 lines indicate the five different iterations we ran for summer and winter. The proportion of withheld locations was strongly correlated with bin number, indicating our predictions generally characterized fox use.

exploit various food sources and habitat types in response to changing environmental conditions. In the summer months in Grand Teton, human visitation increased to almost eight times the number of visitors in the winter months, creating approximately a fourfold increase in anthropogenic food abundance that wildlife can also exploit (Burkholder, Stephenson, Hegg, Gustine, Robinson, et al., 2024; National Park Service, 2021b). We observed selection for closer distances to human features regardless of season, though approximately 75% of foxes had a greater selection for human features in summer. There were varying degrees of selection across our sample of foxes, however, and combined with diet information (e.g., Burkholder, Stephenson, Hegg, Gustine, Robinson, et al., 2024) suggests that some foxes are using human structures for other purposes such as den sites, foraging for natural prey, and/or protection from predators (i.e., human-shield hypothesis; Berger, 2007). Burkholder, Stephenson, Hegg, Gustine, Robinson, et al. (2024) demonstrated that red foxes consume more anthropogenic food in the winter relative to summer, emphasizing that the spatial affinity we observed toward human features in the summer may be for reasons beyond food. Indeed, coyotes were the cause of mortality for 40% of foxes in agricultural areas compared with 0% in urban areas in Illinois, indicating that red foxes in urban areas might be exploiting human features to avoid risk of predation from

coyotes (Gosselink et al., 2007). Moreover, when examining foxes with the lowest selection for human features, we observed some of the strongest selection for the NBR (Figure 4a,b). We used NBR to index wet, productive forests that may translate to herbivorous prey habitat for species such as snowshoe hare (Holbrook et al., 2018) or other small mammals. Foxes that selected for high vegetation biomass, away from human features, are likely exploiting natural habitat structures and associated prey instead of anthropogenic-associated species. Mesic meadows provide habitat for some prey species like pocket gophers, voles, and other rodents, but the majority of our foxes seemingly avoided these areas, which is consistent with the only other habitat selection studies for this subspecies (Fuhrmann, 1998; Van Etten et al., 2007). We did observe greater uncertainty in selection for meadows within some foxes, which could indicate that these foxes are likely using meadows to forage, but either not regularly or in small stints along edges (Fuhrmann, 1998). Importantly, the strong affinity toward human features across our sample of foxes could be associated with sampling bias such that we may have missed more elusive individuals given our trapping tactics. Thus, inference associated with our work should be tempered with this context.

Variation in resource selection for key habitat types was small between summer and winter, relative to the

interindividual variation we observed in selection behavior (Figure 4a,b) along with variation in home range expression. Indeed, our work supported the contention that Rocky Mountain red fox exhibit a suite of differing spatial tactics to exploit resources, which is consistent with work on their trophic ecology. Under optimal foraging theory, we expected red foxes to exploit a higher number of patches when the quality per patch was reduced leading to more diffuse space use (i.e., larger home ranges; Charnov, 1976). This was generally supported with males in that we observed larger home ranges in winter than in summer, but even more compelling was the vast interindividual differences in home range sizes (Table 1, Figure 2a). Many factors can play a role in the formation and maintenance of a home range, including forage acquisition, risk avoidance, and mating. Male home range size increased between January and April, peaking in March. Mating season in Grand Teton typically occurs between January and March (unpublished data from Grand Teton). Thus, the patterns we observed in home range size likely reflected elements of optimal foraging theory as well as increased male movement in searching for mates (Soulsbury et al., 2011). Compared with previous estimates of home range size in Rocky Mountain red fox within the Greater Yellowstone Ecosystem (Van Etten et al., 2007), our estimates were larger in both summer and winter, which we attributed to the use of GPS collar data (rather than VHF) and the increased capacity to detect excursions and multiple highly used areas. We also observed larger home ranges compared to some red fox studies (Castañeda et al., 2018; Roshier & Carter, 2021; Šálek et al., 2014; Walton et al., 2017; Table 1), but not the largest that have been observed (358 km²; Walton et al., 2017). Larger home ranges could implicate more patchily distributed resources in our sampled population of red fox.

Red foxes are typically considered a territorial species, with complex and highly flexible social systems (Cavallini, 1996). Red foxes can live solitary lives, in pairs, or family groups, and a population can encompass all types of individuals. Family groups are typically more common in urban environments where resources are abundant and can sustain larger densities (Baker et al., 2000; Cavallini, 1996; Newsome, 1995). Degree of territoriality for red fox has been shown to fluctuate with home range size (Goszczyński, 2002), concentration of food resources (Bino et al., 2010; Tsukada, 1997), and distribution of food in mountainous terrain (Boitani et al., 1984). We observed low home range overlap of male foxes in 2021 during summer and winter, but overlap was greater in the winter when home ranges were larger. Home range overlap was not concentrated in

space and suggested that individuals were trespassing or perhaps exploiting neutral zones that were not defended by any fox (Boitani et al., 1984), which should increase as home range size increases. Foxes at higher elevations may need to travel farther distances in the winter to gain sufficient resources when food is scarce. Additionally, anthropogenic food could be providing a concentration of resources in a “neutral” space influencing the degree of territoriality in both seasons. Research into the seasonal variation in diet using tools such as DNA metabarcoding (e.g., Roffler et al., 2021) and exploring the sociality of this subspecies would provide further information into the mechanisms driving intraspecific variation in space use behavior and formation of home ranges.

Rocky Mountain red foxes occupy broad trophic (Burkholder, Stephenson, Hegg, Gustine, Robinson, et al., 2024) and environmental niches within the Greater Yellowstone Ecosystem and illustrate a similar flexibility in distribution and movement behavior as other red fox populations. By considering interindividual variation in habitat use and selection, we were able to provide a more comprehensive understanding of this generalist carnivore, especially in reference to fluctuating human activity and anthropogenic food resources. Coupled with trophic patterns (Burkholder, Stephenson, Hegg, Gustine, Robinson, et al., 2024), some foxes are primarily exploiting anthropogenic food resources; however, some are likely attracted to human features for other reasons. Other foxes, however, seem to employ natural tactics and are either indifferent to or avoid humans. These insights can provide managers with a more complete understanding of the complexity associated with red fox behavior, while also understanding what factors might attract red foxes to human features. Collectively, our discoveries will aid communication strategies targeted at reducing human–fox conflicts. In conclusion, our work advances the understanding of human–wildlife interactions in one of the most recreated places in North America and provides foundational information on an understudied forest carnivore, the Rocky Mountain red fox.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Burkholder, Stephenson, Hegg, Gustine, Robinson, et al., 2024) are available from Dryad: <https://doi.org/10.5061/dryad.dv41ns27v>.

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SUPPORTING INFORMATION

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

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