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Responses of American black bears to spring resources

NATHANIEL R. BOWERSOCK,[1,†] ANDREA R. LITT,[1] JEROD A. MERKLE,[2] KERRY A. GUNTHER,[3]
AND FRANK T. VAN MANEN[4]

[1]Department of Ecology, Montana State University, P.O. Box 173460, Bozeman, Montana 59717-3460 USA
[2]Department of Zoology and Physiology, University of Wyoming, Department 3166, 1000 East University Avenue, Laramie, Wyoming 82071 USA
[3]Bear Management Office, Yellowstone Center for Resources, Yellowstone National Park, P.O. Box 168, Yellowstone National Park, Wyoming 82190 USA
[4]Interagency Grizzly Bear Study Team, U.S. Geological Survey, Northern Rocky Mountain Science Center, 2327 University Way, Suite 2, Bozeman, Montana 59715 USA

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Abstract. In temperate regions of the world, food resources are seasonally limited, which causes some wildlife species to seek out nutrient-rich resources to better meet their caloric needs. Animals that utilize high-quality resources may reap fitness benefits as they prepare for mating, migration, or hibernation. American black bears (*Ursus americanus*) are omnivores that consume both plant and animal food resources to meet macronutrient needs. Black bears capitalize on high-quality food resources, such as soft mast in summer and hard mast during autumn, but we know less about the importance of resource quality during spring. Therefore, we sought to understand the relationship between the spatiotemporal variation in the availability of food and resource selection of black bears during spring. We also aimed to infer potential changes in foraging tactics, from opportunistic foraging to more active selection. Although black bears are described as opportunistic omnivores, we hypothesized they select areas with high-quality forage when available. We instrumented 7 black bears with GPS collars in 2017 and 2018 and estimated fine-scale resource selection with integrated step-selection functions. We found evidence that black bear movements were influenced by forage quality of vegetative food resources. However, we failed to find evidence that black bears actively alter their movements to take advantage of seasonal neonate elk. Although black bears represent a substantial cause of mortality for neonate elk, we found that black bears likely feed on neonates encountered opportunistically while traveling between patches of high-quality forage. Few studies have shown evidence of an omnivorous species capitalizing on spatiotemporal variation in forage quality, yet our data suggest this may be an important strategy for species with diverse diets, particularly where resources are seasonally limited.

Key words: American black bear; *Cervus canadensis;* elk; forage quality; green-up; neonates; phenology; resource selection; step-selection functions; *Ursus americanus;* Yellowstone National Park.

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† **E-mail:** nathaniel.bowersock@gmail.com

INTRODUCTION

The quality and timing of food availability is increasingly being recognized as important to wildlife (Yang et al. 2008, Deacy et al. 2016, Abrahms et al. 2020). In temperate regions of the world, food resources are seasonally limited in space and time and the quality of these food resources can vary from year to year, directly impacting the fitness of wildlife populations

(Cook et al. 2004, Ryan et al. 2004, Proffitt et al. 2016, Birnie-Gauvin et al. 2017). In response to this seasonal variation, some wildlife species move across the landscape according to the temporary availability of nutrient-rich resources, known as resource pulses (Welch et al. 1997, Davis et al. 2006, Bojarska and Selva 2012, Denny et al. 2018, Dou et al. 2019). Resource pulses may come from plant- or animal-based foods, and individuals that follow different resource pulses can maximize their energy gains (Abrahms et al. 2020).

During summer and autumn, food resources often are readily available in temperate regions, making resource pulses less important to most wildlife populations. In comparison, during spring, foods may be more limited, making it more important for some wildlife species to find and track resource pulses. For example, some herbivore species track phenological changes of herbaceous vegetation as it greens up in early spring, referred to as the green wave or forage maturation hypothesis (Fryxell 1991, Frank and McNaughton 1992, van der Graaf et al. 2006, Bischof et al. 2012, Merkle et al. 2016). Plants at early- to mid-phenological stages are lower in biomass, but less fibrous and easier to digest, thus more nutritious (Hebblewhite et al. 2008). Therefore, animals that track the pulsed availability of vegetation during green-up are able to optimize energy intake, which can positively influence fitness (Hebblewhite et al. 2008, Bischof et al. 2012, Armstrong et al. 2016, Merkle et al. 2016, Aikens et al. 2017).

The timing and availability of food resources is particularly important for wildlife species that hibernate, as they are only active during a limited portion of the year (Fishman and Lyman 1961, Geiser 1998, Humphries et al. 2003). In North America, the American black bear (*Ursus americanus*) is a large-bodied omnivore that hibernates up to 6 months of the year and relies on multiple resource pulses to meet their energetic needs (Welch et al. 1997, Pelton 2003, Klinka and Reimchen 2009, Costello et al. 2016). During summer and autumn, a wide range of food resources are available, but black bears closely track the availability of pulsed food resources, such as hard and soft mast and spawning salmonid species (*Salmonidae* spp.), where available. These resources provide sources of fat and protein that help bears prepare for hibernation (Inman and Pelton 2002, Belant et al. 2010, McLellan 2011).

During spring, resources for black bears are less abundant and lower in carbohydrates and fats, but higher in protein, which can make it difficult for bears to regain energy stores after hibernation (Noyce and Garshelis 1998, Coogan et al. 2014, Erlenbach et al. 2014, Costello et al. 2016). After emerging from hibernation, black bears consume substantial amounts of vegetation, but are unable to fully digest plant matter due to their simple digestive systems, making it difficult to meet their energetic needs on plant matter alone (Pritchard and Robbins 1990, Costello et al. 2016, Herrero 2018). Later in spring, some black bears will take advantage of the availability of neonate ungulates, which are easier to digest than plant matter, but low in fat, which also makes regaining energy difficult (Pritchard and Robbins 1990, Barber-Meyer et al. 2008, Bastille-Rousseau et al. 2011, Schwartz et al. 2014, Rayl et al. 2018, Svoboda et al. 2019).

Although some black bears struggle to regain energy stores after hibernation in spring, there are signs that other individuals are optimizing the intake of spring resources to maintain or regain energy stores (Noyce and Garshelis 1998, Schwartz et al. 2014, Herrero 2018). For example, some black bears mainly forage on earlier phenological stages of plants that are easier to digest, suggesting they might be following the so-called green wave (Pritchard and Robbins 1990, Fryxell 1991, Costello et al. 2016, Merkle et al. 2016, Herrero 2018). This phenomenon could explain how black bears in northern and western portions of North America sustain their body mass during spring (Noyce and Garshelis 1998, Schwartz et al. 2014, Costello et al. 2016). In addition, if black bears are seeking out vegetation that is of higher quality, they may only prey on neonate ungulates opportunistically, as they encounter them on the landscape (Bastille-Rousseau et al. 2011, Svoboda et al. 2019). In comparison, where vegetative forage is lower quality, black bears may instead actively prey on neonate ungulates (Rayl et al. 2018), because neonates would provide a high-quality food resource. However, few studies have explored the importance of forage quality to black bears in spring.

Vegetative food resources comprise the highest proportion of spring diets for black bears in the

Greater Yellowstone Ecosystem (GYE; Fortin et al. 2013, Costello et al. 2016), but black bears also kill and consume neonate elk (*Cervus canadensis*) during this time (Barber-Meyer et al. 2008). Therefore, we sought to determine the relationship between the spatiotemporal variation in the availability of food resources and resource selection by black bears during spring. We also aimed to infer potential changes in foraging tactics, from opportunistic foraging to more active selection. Black bears are described as opportunistic omnivores, but we hypothesized that black bears actively select areas with high-quality forage, when available. Given that the availability of high-quality vegetation varies over space and time, movements to these quality food patches would suggest that bears are more actively selecting vegetative resources. We also hypothesized that black bears would continue to select areas with high-quality forage, even when neonate elk become available. Although black bears kill and consume elk neonates, calving grounds are more spatially restricted on the landscape compared with high-quality vegetation. Therefore, we hypothesized that bears mostly consume neonates opportunistically, while they are actively seeking out high-quality vegetation. Relationships between spatiotemporal availability of food resources and animal movement can be key to better understand how wildlife species deal with seasonal limitations.

METHODS AND MATERIALS

Study area

Yellowstone National Park (YNP) is in northwestern Wyoming, with additional portions in Montana and Idaho. Our study area was within the Northern Range, a 1530-km^2 area along the northern third of the national park that extends into southern Montana (Figure 1), with sampling restricted to areas within YNP. Elevations vary from 1590 to 3360 m with treeline around 2900 m. A mix of sagebrush (*Artemisia* spp.), grasses and sedges (*Carex* spp.), and forbs are found in the open meadows. Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and aspen (*Populus tremuloides*) comprise most of the lower elevation forest areas (1900–2200 m), whereas subalpine fir (*Abies lasiocarpa*) and whitebark pine (*Pinus albicaulis*) stands are found at higher elevations (2200–2900 m; Frank and McNaughton 1992, Singer et al. 1994).

Several ungulate species are abundant throughout the Northern Range, including elk, mule deer (*Odocoileus hemionus*), and bison (*Bison bison*) (White and Garrott 2005). Moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), pronghorn (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos americanus*) also inhabit the Northern Range, but are less abundant. The area is home to several large carnivores besides black bears, including grizzly bears (*Ursus arctos*), gray wolves (*Canis lupus*), coyotes (*Canis latrans*), and pumas (*Puma concolor*) (Barber-Meyer et al. 2008).

Live capture and collaring

We captured black bears using culvert traps from May to October 2017 and May to June 2018 with the assistance of U.S. Geological Survey (USGS) and National Park Service (NPS) personnel. Bears were chemically immobilized using syringe poles and handled following approved methods (MSU IACUC protocol 2017–24). We equipped captured black bears with Iridium GPS collars (Telonics, Mesa, AZ). During April 1–November 30, collars were programmed to record 1 location/h in 2017 and 1 location/30 min in 2018. Locations were uploaded to the Iridium satellite system every 8 h. During hibernation (December 1–March 31), we recorded 1 location/month. Collars were fitted with a CR-5 collar release system (Telonics) and programmed to release on October 15, 2018, for field retrieval. We used cotton spacers as a secondary drop-off mechanism (Hellgren et al. 1988).

Vegetation quantity and quality

To test how the spatiotemporal variation in forage quality and quantity influences black bear movements, we used two covariates (instantaneous rate of green-up [IRG] and integrated normalized difference vegetation index [INDVI]) generated from normalized difference vegetation index (NDVI) data (Geremia et al. 2019, Notaro et al. 2019). We used NDVI data collected by the MOD09Q1 MODIS terra satellite at a 250-m (pixel) spatial resolution and an 8-d temporal resolution, which we converted to daily NDVI values by fitting a double-logistic curve to the data to create a smoothed

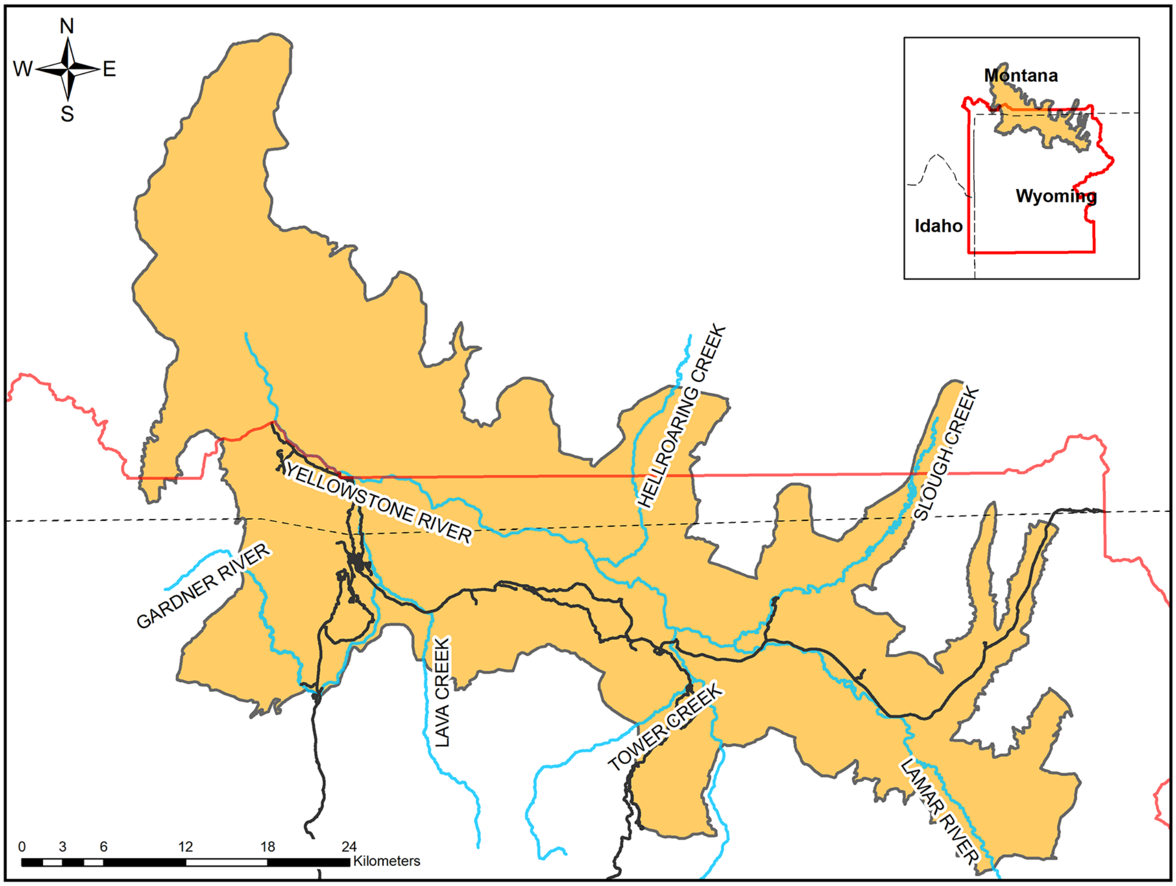

Fig. 1. Northern Range (yellow) of Montana and Wyoming, 2017–2018. Our study focused on the portion of the Northern Range within Yellowstone National Park (below the solid red line).

time-series (Bischof et al. 2012, Merkle et al. 2016). Prior to fitting these curves, we accounted for influences of spatiotemporal changes in snow cover. We used snow cover data from the MODIS satellite to develop a baseline NDVI value for each pixel by calculating the 0.025 quantile of all NDVI values that were identified as snow-free (Bischof et al. 2012, Merkle et al. 2016). We assigned this baseline NDVI value to all pixels that were snow-covered in winter, prior to green-up, and then fit a double logistic curve to each year of data (Bischof et al. 2012, Merkle et al. 2016). Because we focused on increases above the NDVI baseline in each pixel, we were able to track changes in green-up across different vegetation communities, even in areas that might already be reflecting green values in the satellite imagery, such as the overstory of coniferous forests (O'Leary et al. 2018).

To assess changes in forage quality in spring, we used IRG, which tracks how quickly vegetation reaches peak spring green-up (Merkle et al. 2016, Aikens et al. 2017). We estimated IRG by computing the first derivative of the fitted daily NDVI data curve, which we scaled between 0 and 1 (Bischof et al. 2012, Merkle et al. 2016). Scaled IRG values of 0 represent prior to green-up or after complete senescence and values of 1 represent the peak rate of green-up or optimal forage quality (Merkle et al. 2016, Aikens et al. 2017, Geremia et al. 2019). In addition, to constrain our analysis to the timing of spring green-up each year, we computed the first and second derivatives of the fitted IRG curve to index the dates when spring green-up began and ended each year (Merkle et al. 2016).

To evaluate overall changes in the quantity of green vegetation separately from the phenological state, we used INDVI (Pettorelli et al. 2005).

We calculated INDVI for each pixel by summing daily, unscaled NDVI values above the winter baseline over time, representing the accumulation of biomass (Pettorelli et al. 2005). By computing INDVI for each pixel, we were able to explore how bears responded to spatiotemporal changes in quantity and quality of vegetation resources.

Elk calving grounds

To assess whether the birth pulse of neonate elk influenced resource selection by black bears, we mapped the calving grounds of the Northern Range. Elk and other ungulates show strong site fidelity for calving areas (Vore and Schmidt 2001, Nicholson et al. 2019), so we first created a base map of calving grounds using capture locations of neonate elk from a previous study on the Northern Range (Barber-Meyer et al. 2008). We then added a 900-m buffer around each capture location to account for the average distance a female elk could travel 10 d after giving birth, when newborn calves are most vulnerable to predation (Vore and Schmidt 2001, Barber-Meyer et al. 2008).

To further identify calving ground locations and evaluate the accuracy of our base calving grounds map, we used the locational data of collared female elk to identify locations of elk parturition (D. MacNulty, Utah State University, *unpublished data*). Pregnant ungulates greatly increase their daily movements (the maximum distance traveled in a day) before giving birth and reduce their movement after giving birth (Vore and Schmidt 2001, D'Angelo et al. 2004, DeMars et al. 2013, McGraw et al. 2014, Nicholson et al. 2019). Researchers have used these changes in movement to identify parturition events (Clutton-Brock and Guinness 1975, D'Angelo et al. 2004, DeMars et al. 2013, McGraw et al. 2014). We used the *adhabitatLT* package in program R to calculate the trajectory (the distance traveled between successive GPS locations) (R Development Core Team 2013, Calenge 2015) of collared elk to look for daily average changes in movement to identify parturition events (DeMars et al. 2013), corresponding to likely calving sites. Additionally, we used the *bcpa* (behavioral change point analysis or BCPA) function (Gurarie 2014) to identify patterns of changes in behavior that might indicate parturition events (Gurarie et al. 2009, Nicholson et al. 2019). We overlaid the locations of predicted parturition events, identified by both trajectory analysis and BCPA, on the base calving grounds map to determine how well locations of captured neonates and predicted calving sites matched spatially.

Based on the trajectory analysis and BCPA, we identified 49 calving sites for 27 of the 29 elk, and 15 of the 29 elk had >2 calving sites identified over multiple years. Twelve of those elk had calving sites within 5 km of the previous year's calving location, supporting the idea that elk show strong site fidelity when calving (Vore and Schmidt 2001, Barber-Meyer et al. 2008, Nicholson et al. 2019). Of the 49 calving sites, 22 were within the Northern Range. We added 900-m buffers to these locations to create our final calving grounds map, which we converted into a binary raster map depicting areas within and outside the calving grounds. Detailed methods for generating and evaluating the calving grounds layer are available in Appendix S1.

Landscape features

While testing the influence of the forage quality and abundance on bear movement, we also wanted to account for the potential influence of landscape variables that act as proxies for food resources. We modified an existing vegetation community layer based on climatic overstory and understory plants (habitat type layer, 50-m pixel resolution; Despain 1990, Yellowstone Spatial Analysis Center 2010). We also examined slope and aspect (10-m digital elevation model; U.S. Geological Survey 2009) because these variables can influence the quality and availability of different vegetative resources and have helped explain resource selection in other studies of black bears (Bastille-Rousseau et al. 2011, Johnson et al. 2015, Rayl et al. 2018, Ahrestani and Fish 2020). We converted aspect to one of four categorical cardinal directions (E: 45°–135°, S: 135°–225°, W: 225°–320°, N: 320°–45°).

Integrated step-selection functions

We used integrated step-selection functions to test how the availability of resources influences black bear movements (Thurfjell et al. 2014, Signer et al. 2019). Step-selection functions compare characteristics of a used location to ≥ 1 paired available locations (Thomas and Taylor

2006, Thurfjell et al. 2014, Signer et al. 2019). We generated available locations to pair with each used (bear) location based on the parametric distribution of turn angles and distances traveled between successive locations, known as steps, of each collared bear using the *amt* package in R (Forester et al. 2009, Thurfjell et al. 2014, Merkle et al. 2016, Signer et al. 2019). Although collars were scheduled to record a location every ½ or 1 h, not every GPS fix was successful. Based on the mean distribution of time between successive locations, we set step length as a 2-h interval (Signer et al. 2019). We incorporated a covariate for distance between successive used locations and distance between used and available locations as a resource-independent movement kernel, to account for the potential that animal movement is conditional on resource selection (Forester et al. 2009, Signer et al. 2019). To determine an appropriate ratio of paired used to available locations, we ran a series of models that paired each used location with 5, 10, 20, or 30 available locations, respectively (Northrup et al. 2013, Thurfjell et al. 2014). We then compared estimated coefficients among models to determine where estimates stabilized and selected the model with the lowest ratio of used to available locations (Forester et al. 2009, Thurfjell et al. 2014, Peck et al. 2017). Estimates were consistent once we reached a 1:10 ratio.

We used conditional logistic regression to assess whether bears selected resources disproportionately to local availability (Fortin et al. 2005, Thurfjell et al. 2014, Signer et al. 2019). We centered and scaled all continuous covariates before fitting models. For categorical covariates, we used one of the categories as the reference level (east for the aspect covariate and big sagebrush for vegetation community type). Before fitting any models, we checked for collinearity among covariates using the *cor* function in R; the largest correlation was 0.36. To test how forage quality and the availability of neonate elk influenced black bear movements, we first created a base or null model (base) that included INDVI, vegetation community, slope, aspect, and distance between successive locations (the resource-independent movement kernel). We created three additional models that included all possible additive combinations of IRG and elk calving grounds (base + IRG, base + ElkCalf, base + IRG + ElkCalf) to test our research hypotheses how forage quality and the availability of elk neonates influenced resource selection by black bears. We compared support for these four models using small-sample corrected Akaike's information criterion (AIC_c) (Burnham and Anderson 2004). Finally, we compared dates when pixels reached peak IRG with dates of bear use to determine if bears used vegetation before or after peak green-up (Merkle et al. 2016, Aikens et al. 2017).

RESULTS

We used location data from seven of eight GPS-collared black bears (one adult male, one subadult male, two subadult females, and four adult females) in our resource selection models. We excluded one adult female bear because recorded locations did not meet our time frame requirements for the spring green-up or calving periods (April 27–June 8). For these seven bears, we analyzed a total of 3,287 used locations paired with 32,870 available locations.

The top model included both IRG and elk calving grounds covariates (base + IRG + ElkCalf) (Table 1). As we predicted, bears selected locations with higher forage quality (IRG: $\beta = 0.12$,

Table 1. Model selection results to assess the importance of forage quality (IRG) and pulsed availability of elk neonates (ElkCalf) for resource selection by black bears (n = 3,287 locations from 7 radio-collared bears), Northern Range, Yellowstone National Park, 2017–2018.

Model	K§	AIC_c¶	ΔAIC_c#	w_i‖
base† + IRG† + ElkCalf‡	13	13,704.18	0.00	0.887
base + IRG	12	13,708.48	4.30	0.103
base + ElkCalf	12	13,713.42	9.24	0.009
base	11	13,717.96	13.78	0.001

† base, base model included integrated NDVI, aspect, slope, vegetation community, and distance to successive locations (resource-independent movement kernel). IRG, covariate measuring instantaneous rate of green-up to assess selection of forage quality.

‡ ElkCalf, covariate to assess selection of elk calving grounds.

§ K, number of parameters in a model.

¶ AIC_c, Akaike's information criterion corrected for small sample sizes.

ΔAIC_c, difference between ranked models using Akaike's information criterion corrected for small sample sizes.

‖ w_i, Akaike (AIC_c) weight.

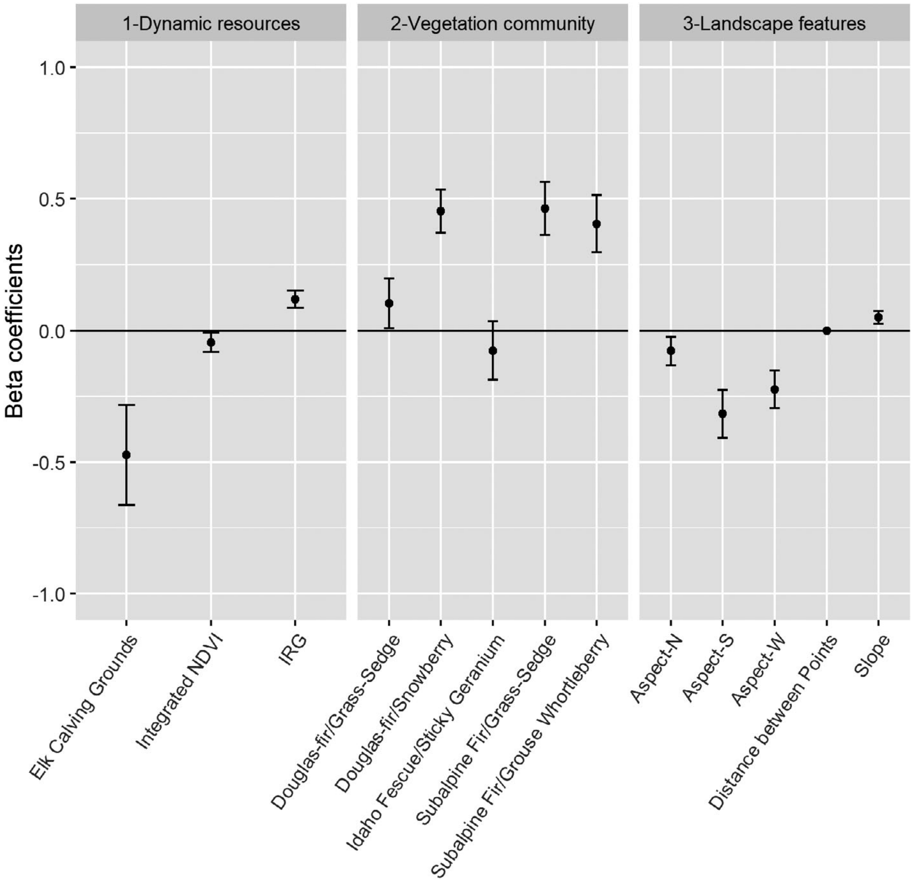

Fig. 2. Beta coefficients and standard errors for covariates for the top model (base + IRG + Elk Calving Grounds), based on locations from 7 black bears tracked April 27–June 8, Northern Range, Yellowstone National Park, 2017–2018. All continuous covariates were centered and scaled (Integrated NDVI, IRG, distance between successive points [GPS locations], slope). The elk calving grounds covariate was binary and aspect and vegetation community were categorical. The reference category for aspect was east and the reference category for vegetation community was big sagebrush. Estimates above the reference line at zero indicate positive selection for a covariate.

SE = 0.035), but lower forage biomass (INDVI: β = −0.045, SE = 0.036, Figure 2). On average, bears used locations 10.5 d after vegetation reached peak quality (SE = 0.24, range = 35 d before to 73 d after; Figure 3). However, we did observe some variation in how closely bears tracked peak forage quality in different vegetation communities (Appendix S2). Black bears tracked forage quality more closely in subalpine fir forest and non-forested areas, compared with forests dominated by Douglas fir. We also found evidence that black bears selected areas outside of the elk calving grounds (β = −0.47, SE = 0.19, Figure 2), supporting our prediction that bears consume neonates opportunistically. Additionally, black bears showed the strongest selection for forested vegetation communities over non-forested communities, particularly communities dominated by subalpine fir and Douglas fir (Figure 2). Black bears also selected steeper slopes and areas with easterly aspects (Figure 2).

DISCUSSION

We found evidence that black bear movements were influenced more by forage quality than the availability of neonate elk during spring. By focusing foraging efforts on higher quality

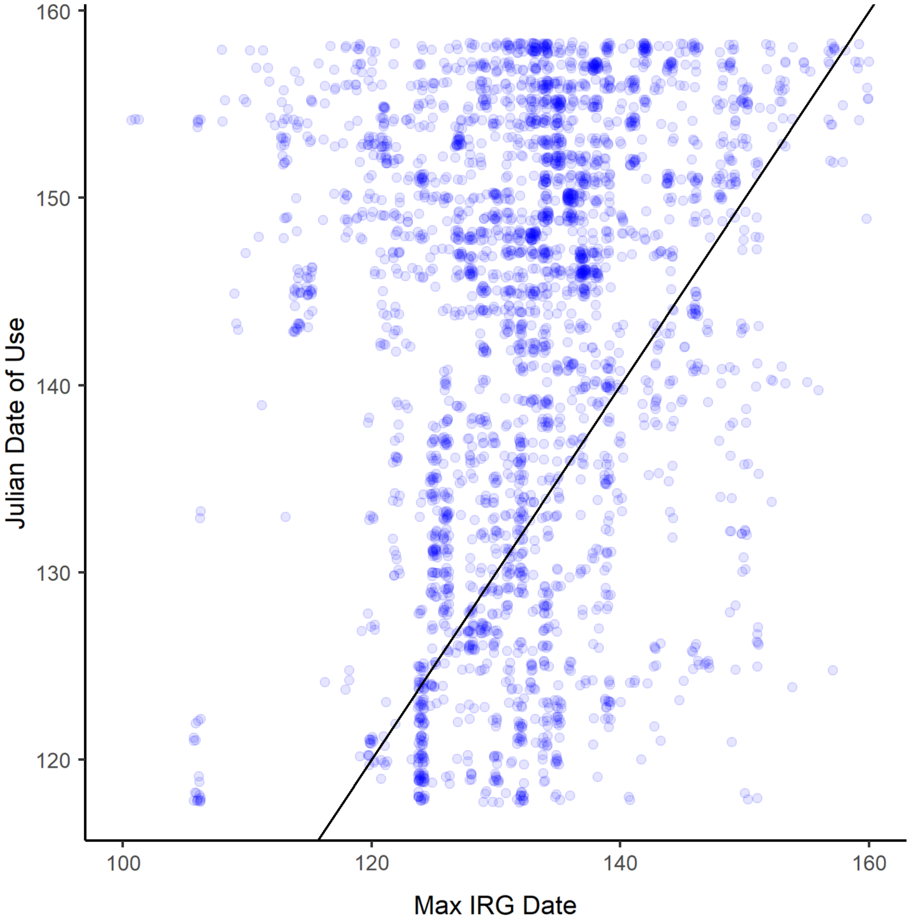

Fig. 3. Julian dates when a location on the landscape reached maximum IRG (instantaneous rate of green-up) versus when that same location was used by a collared bear during the spring green-up period (R^2 = 0.25), Northern Range, Yellowstone National Park, 2017–2018. The black diagonal line represents use of locations at maximum IRG. Observations above the line indicate locations used by black bears after maximum IRG occurred (75% of bear locations), whereas observations below the line indicate locations used by black bears before vegetation reached maximum IRG (25%). On average, bears used locations 10.5 d (SE = 0.24) after maximum IRG.

forage, black bears can obtain more digestible energy, allowing them to better maintain body mass after emerging from hibernation (Noyce and Garshelis 1998). Our findings therefore may help explain how black bears in the GYE are able to maintain fat stores throughout the spring, by capitalizing on seasonal resources (Schwartz et al. 2014). Previous studies have noted that black bears focused their spring foraging efforts on freshly emerged plant matter thought to provide better nutrition (Robbins et al. 2004, Schwartz et al. 2014, Costello et al. 2016, Herrero 2018). Our study provides empirical support that black bears indeed select vegetation based on forage quality.

Although we were able to document that the quality of vegetative forage influences black bear movements, we failed to find evidence that black bears actively alter their movements to take advantage of neonate elk when they become available, based on the negative coefficient for calving grounds. Black bears on the Northern Range are a common predator on neonate elk in spring (Barber-Meyer et al. 2008), but we found that black bears continued to focus their foraging efforts on higher quality vegetative forage during the calving period. Therefore, black bears are likely killing and feeding on elk neonates opportunistically while moving between patches of vegetative forage, a pattern found in several previous studies (Bastille-Rousseau et al. 2011, Svoboda et al. 2019).

Landscape features such as vegetation communities also influenced black bear movements. Similar to other studies, black bears selected forested vegetation communities, particularly spruce–fir forests, over non-forested vegetation communities (Johnson et al. 2015, Bastille-Rousseau et al. 2016, Svoboda et al. 2019). Forested areas provide black bears with preferred food resources such as graminoids and invertebrates (Holm et al. 1999, Mattson 2001, Rayl et al. 2018). Forested areas also provide cover for thermoregulation and allow black bears to reduce interactions with grizzly bears (Aune 1994, Mattson et al. 2005, Belant et al. 2010, Sawaya et al. 2016, Herrero 2018).

Black bears in our study selected easterly aspects, which tend to green-up earlier than other areas (Gregory et al. 2009), a pattern that also is consistent with our finding that bears selected for areas with higher quality forage. In comparison, south-facing slopes are drier and produce less vegetative biomass (Albon and Langvatn 1992, Ahrestani and Fish 2020), which may explain why bears in this and other studies selected against these areas (Mack 1988). Bears also selected areas with steeper slopes. This pattern may be a function of bears selecting areas with clover (*Trifolium* spp.), a highly nutritious food that grows on steeper slopes (Pritchard and Robbins 1990, Romain et al. 2013).

Our findings provide new insights about the influence of forage quality on resource selection by black bears, but we acknowledge that our inferences are based on a relatively small sample size, dominated by females (5 of 7 bears). Although female and male bears select different food resources to meet their varying metabolic needs during the year (Gunther et al. 2002, 2018, Apps et al. 2006, Gantchoff et al. 2019), early snowpack limits spring resources to lower elevation areas of the Northern Range (Notaro et al. 2019). Therefore, male and female bears likely were restricted to the same areas and resources during spring (Beckmann and Berger 2003, Johnson et al. 2015). Additionally, our parameter estimates had relatively small standard errors, which suggest our findings could apply to other bears on the Northern Range.

Black bears are active for as little as 6 months of the year (Pelton 2003). By tracking spatiotemporal variation in food quality, black bears are able to optimize nutrient intake to maintain and increase body mass throughout the year. Because anthropogenic activities such as climate change may not only affect availability of food resources but also the quality of those resources, such changes may have potential implications for bear fitness (Robbins et al. 2004, Gunther et al. 2014, Sawaya et al. 2016). Therefore, it is vital that resource quality be considered when assessing the importance of food resources to black bears and other wildlife species to inform future conservation and management decisions.

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LITERATURE CITED

Abrahms, B., E. O. Aikens, J. B. Armstrong, W. W. Deacy, M. J. Kauffman, and J. A. Merkle. 2020. Emerging perspectives on resource tracking and animal movement ecology. Trends in Ecology and Evolution 36:308–320.

Ahrestani, F. S., and P. C. Fish. 2020. Resource use by American black bears in suburbia: a landholder step selection approach. Human-Wildlife Interactions 14:1–12.

Aikens, E. O., M. J. Kauffman, J. A. Merkle, S. P. H. Dwinnell, G. L. Fralick, and K. L. Monteith. 2017. The greenscape shapes surfing of resource waves in a large migratory herbivore. Ecology Letters 20:741–750.

Albon, S. D., and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos 65:502–513.

Apps, C. D., B. N. McLellan, and J. G. Woods. 2006. Landscape partitioning and spatial inferences of competition between black and grizzly bears. Ecography 29:561–572.

Armstrong, J. B., G. Takimoto, D. E. Schindler, M. M. Hayes, and M. J. Kauffman. 2016. Resource waves: Phenological diversity enhances foraging opportunities for mobile consumers. Ecology 97:1099–1112.

Aune, K. E. 1994. Comparative ecology of black and grizzly bears on the Rocky Mountain Front, Montana. International Conference of Bear Research and Management 9:365–374. Retrieved from https://www.jstor.org/stable/3872723

Barber-Meyer, S. M., L. D. Mech, and P. J. White. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. Wildlife Monographs 169:1–30.

Bastille-Rousseau, G., D. Fortin, C. Dussault, R. Courtois, and J. P. Ouellet. 2011. Foraging strategies by omnivores: Are black bears actively searching for ungulate neonates or are they simply opportunistic predators? Ecography 34:588–596.

Bastille-Rousseau, G., N. D. Rayl, E. H. Ellington, J. A. Schaefer, M. J. L. Peers, M. A. Mumma, S. P. Mahoney, and D. L. Murray. 2016. Temporal variation in habitat use, co-occurrence, and risk among generalist predators and a shared prey. Canadian Journal of Zoology 94:191–198.

Beckmann, J. P., and J. Berger. 2003. Rapid ecological and behavioral changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. Journal of Zoology 261:207–212.

Belant, J. L., B. Griffith, Y. Zhang, E. H. Follmann, and L. G. Adams. 2010. Population-level resource selection by sympatric brown and American black bears in Alaska. Polar Biology 33:31–40.

Birnie-Gauvin, K., K. S. Peiman, D. Raubenheimer, and S. J. Cooke. 2017. Nutritional physiology and ecology of wildlife in a changing world. Conservation Physiology 5:cox030.

Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmermann, B. Van Moorter, and A. Mysterud. 2012. A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? The American Naturalist 180:407–424.

Bojarska, K., and N. Selva. 2012. Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. Mammal Review 42:120–143.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods & Research 33:261–304.

Calenge, C. 2015. Analysis of animal movements in R: the adehabitatLT package.

Clutton-Brock, T. H., and F. E. Guinness. 1975. Behavior of red deer (*Cervus elaphus* L.) at calving time. Behavior 55:287–300.

Coogan, S. C. P., D. Raubenheimer, G. B. Stenhouse, and S. E. Nielsen. 2014. Macronutrient optimization and seasonal diet mixing in a large omnivore, the grizzly bear: a geometric analysis. PLOS ONE 9:e97968.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. I. M. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155:1–61.

Costello, C. M., S. L. Cain, S. Pils, L. Frattaroli, M. A. Haroldson, and F. T. van Manen. 2016. Diet and macronutrient optimization in wild ursids: a comparison of grizzly bears with sympatric and allopatric black bears. PLOS ONE 11:e0153702.

D'Angelo, G. J., C. E. Comer, J. C. Kilgo, C. D. Drennan, D. A. Osborn, and K. V. Miller. 2004. Daily movements of female white-tailed deer relative to parturition and breeding. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 58:292–301.

Davis, H., R. D. Weir, A. N. Hamilton, and J. A. Deal. 2006. Influence of phenology on site selection by female American black bears in coastal British Columbia. Ursus 17:41–51.

Deacy, W., W. Leacock, J. B. Armstrong, and J. A. Stanford. 2016. Kodiak brown bears surf the salmon red wave: direct evidence from GPS collared individuals. Ecology 97:1091–1098.

DeMars, C. A., M. Auger-Méthé, U. E. Schlägel, and S. Boutin. 2013. Inferring parturition and neonate survival from movement patterns of female ungulates: a case study using woodland caribou. Ecology and Evolution 3:4149–4160.

Denny, C. K., G. B. Stenhouse, and S. E. Nielsen. 2018. Scales of selection and perception: landscape heterogeneity of an important food resource influences habitat use by a large omnivore. Wildlife Biology 2018:1–10.

Despain, D. G. 1990. Yellowstone vegetation: consequences of environment and history in a natural setting. Roberts Rinehart Publishers, Boulder, Colorado, USA.

Dou, H., H. Yang, J. L. D. Smith, L. Feng, T. Wang, and J. Ge. 2019. Prey selection of Amur tigers in relation to the spatiotemporal overlap with prey across the Sino-Russian border. Wildlife Biology 1:1–11.

Erlenbach, J. A., K. D. Rode, D. Raubenheimer, and C. T. Robbins. 2014. Macronutrient optimization and energy maximization determine diets of brown bears. Journal of Mammalogy 95:160–168.

Fishman, A. P., and C. P. Lyman. 1961. Hibernation in mammals. Circulation 17:9–13.

Forester, J. D., H. K. Im, and P. J. Rathouz. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. Ecology 90:3554–3565.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Fortin, J. K., C. C. Schwartz, K. A. Gunther, J. E. Teisberg, M. A. Haroldson, M. A. Evans, and C. T. Robbins. 2013. Dietary adjustability of grizzly bears and American black bears in Yellowstone National Park. Journal of Wildlife Management 77:270–281.

Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology 73:2043–2058.

Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. American Naturalist 138:478–498.

Gantchoff, M. G., D. Beyer, and J. L. Belant. 2019. Reproductive class influences risk tolerance during denning and spring for American black bears (*Ursus americanus*). Ecosphere 10:e02705.

Geiser, F. 1998. Evolution of daily torpor and hibernation in birds and mammals: importance of body size. Clinical and Experimental Pharmacology and Physiology 25:736–740.

Geremia, C., J. A. Merkle, D. R. Eacker, R. L. Wallen, P. J. White, M. Hebblewhite, and M. J. Kauffman. 2019. Migrating bison engineer the green wave. Proceedings of the National Academy of Sciences of the United States of America 116:25707–25713.

Gregory, A. J., M. A. Lung, T. M. Gehring, and B. J. Swanson. 2009. The importance of sex and spatial scale when evaluating sexual segregation by ELK in Yellowstone. Journal of Mammalogy 90:971–979.

Gunther, K. A., M. J. Biel, N. Anderson, and L. P. Waits. 2002. Probable grizzly bear predation on an American black bear in Yellowstone National Park. Ursus 13:372–374.

Gunther, K. A., R. R. Shoemaker, K. L. Frey, M. A. Haroldson, S. L. Cain, F. T. van Manen, and J. K. Fortin. 2014. Dietary breadth of grizzly bears in the Greater Yellowstone Ecosystem. Ursus 25:60–72.

Gunther, K. A., K. R. Wilmot, S. L. Cain, T. C. Wyman, E. G. Reinertson, and A. M. Bramblett. 2018. Managing human-habituated bears to enhance survival, habitat effectiveness, and public viewing. Human–Wildlife Interactions 12:373–386.

Gurarie, E. 2014. Behavioral change point analysis of animal movement. R CRAN Package Bcpa Version 1:1.

Gurarie, E., R. D. Andrews, and K. L. Laidre. 2009. A novel method for identifying behavioral changes in animal movement data. Ecology Letters 12:395–408.

Hebblewhite, M., E. Merrill, and G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological Monographs 78:141–166.

Hellgren, E. C., D. W. Carney, N. P. Garner, and M. R. Vaughan. 1988. Use of breakaway cotton spacers on radio collars. Wildlife Society Bulletin 16:216–218.

Herrero, S. 2018. Bear attacks: their causes and avoidance. Third edition. Rowman and Littlefield, Lanham, Maryland, USA.

Holm, G. W., F. G. Lindzey, and D. S. Moody. 1999. Interactions of sympatric black and grizzly bears in northwest Wyoming. Ursus 11:99–108.

Humphries, M. M., D. W. Thomas, and D. L. Kramer. 2003. The role of energy availability in mammalian hibernation: a cost-benefit approach. Physiological and Biochemical Zoology 76:165–179.

Inman, R. M., and M. R. Pelton. 2002. Energetic production by soft and hard mast foods of American black bears in the Smoky Mountains. Ursus 13:57–68.

Johnson, H. E., S. W. Breck, S. Baruch-mordo, D. L. Lewis, C. W. Lackey, K. R. Wilson, J. Broderick, J. S. Mao, and J. P. Beckmann. 2015. Shifting perceptions of risk and reward: dynamic selection for human development by black bears in the western United States. Biological Conservation 187:164–172.

Klinka, D. R., and T. E. Reimchen. 2009. Darkness, twilight, and daylight foraging success of bears (*Ursus americanus*) on salmon in coastal British Columbia. Journal of Mammalogy 90:144–149.

Mack, J. A. 1988. Ecology of black bears on the Beartooth Face, south-central Montana. Montana State University, Bozeman Montana, USA.

Mattson, D. J. 2001. Myrmecophagy by Yellowstone grizzly bears. Canadian Journal of Zoology 79:779–793.

Mattson, D. J., S. Herrero, and T. Merrill. 2005. Are black bears a factor in the restoration of North American grizzly bear populations? Ursus 16:11–30.

McGraw, A. M., J. Terry, and R. Moen. 2014. Preparturition movement patterns and birth site characteristics of moose in northeast Minnesota. Alces 50:93–103.

McLellan, B. N. 2011. Implications of a high-energy and low-protein diet on the body composition, fitness, and competitive abilities of black (*Ursus americanus*) and grizzly (*Ursus arctos*) bears. Canadian Journal of Zoology 89:546–558.

Merkle, J. A., K. L. Monteith, E. O. Aikens, M. M. Hayes, K. R. Hersey, A. D. Middleton, B. A. Oates, H. Sawyer, B. M. Scurlock, and M. J. Kauffman. 2016. Large herbivores surf waves of green-up in spring. Proceedings of the Royal Society B: Biological Sciences 283:20160456.

Nicholson, K. L., M. J. Warren, C. Rostan, J. Månsson, T. F. Paragi, and H. Sand. 2019. Using fine-scale movement patterns to infer ungulate parturition. Ecological Indicators 101:22–30.

Northrup, J. M., M. B. Hooten, C. R. J. Anderson, and G. Wittemyer. 2013. Practical guidance on characterizing availability in resource selection functions under a use–availability design. Ecological Society of America 94:1456–1463.

Notaro, M., K. Emmett, and D. O'Leary. 2019. Spatio-temporal variability in remotely sensed vegetation greenness across Yellowstone National Park. Remote Sensing 11:798–828.

Noyce, K. V., and D. L. Garshelis. 1998. Spring weight changes in black bears in northcentral Minnesota: the negative foraging period revisited. Ursus 10:521–531.

O'Leary, D. S., J. L. Kellermann, and C. Wayne. 2018. Snowmelt timing, phenology, and growing season length in conifer forests of Crater Lake National Park, USA. International Journal of Biometeorology 62:273–285.

Peck, C. P., F. T. van Manen, C. M. Costello, M. A. Haroldson, L. A. Landenburger, L. L. Roberts, D. D. Bjornlie, and R. D. Mace. 2017. Potential paths for male-mediated gene flow to and from an isolated grizzly bear population. Ecosphere 8:e01969.

Pelton, M. R. 2003. Black bear. Pages 547–555 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild Mammals of North America: biology, management, and conservation. Second edition. Johns Hopkins University Press, Baltimore, Maryland, USA.

Pettorelli, N., J. O. Vik, A. Mysterud, J. Gaillard, C. J. Tucker, N. C. Stenseth, and C. B. Lyon. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Ecology and Evolution 20:503–510.

Pritchard, G. T., and C. T. Robbins. 1990. Digestive and metabolic efficiencies of grizzly and black bears. Canadian Journal of Zoology 68:1645–1651.

Proffitt, K. M., M. Hebblewhite, W. Peters, N. Hupp, and J. Shamhart. 2016. Linking landscape- scale differences in forage to ungulate nutritional ecology. Ecological Applications 26:2156–2174.

R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rayl, N. D., et al. 2018. Spatiotemporal heterogeneity in prey abundance and vulnerability shapes the foraging tactics of an omnivore. Journal of Animal Ecology 87:874–887.

Robbins, C. T., C. C. Schwartz, and L. A. Felicetti. 2004. Nutritional ecology of ursids: a review of newer methods and management implications. Ursus 15:161–171.

Romain, D. A., M. E. Obbard, and J. L. Atkinson. 2013. Temporal variation in food habits of the American black bear (*Ursus americanus*) in the boreal forest of northern Ontario. The Canadian Field-Naturalist 127:118–130.

Ryan, C. W., J. C. Pack, W. K. Igo, J. C. Rieffenberger, and A. B. Billings. 2004. Relationship of mast production to big-game harvests in West Virginia. Wildlife Society Bulletin 32:786–794.

Sawaya, M. A., A. B. Ramsey, and P. W. Ramsey. 2016. American black bear thermoregulation at natural and artificial water sources. Ursus 27:129–135.

Schwartz, C. C., J. K. Fortin, J. E. Teisberg, M. A. Haroldson, C. Servheen, C. T. Robbins, and F. T. van Manen. 2014. Body and diet composition of sympatric black and grizzly bears in the Greater Yellowstone Ecosystem. The Journal of Wildlife Management 78:68–78.

Signer, J., J. Fieberg, and T. Avgar. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecology and Evolution 9:880–890.

Singer, F. J., L. C. Mark, and R. C. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. Journal of Range Management 47:435–443.

Svoboda, N. J., J. L. Belant, D. E. Beyer, J. F. Duquette, and P. E. Lederle. 2019. Carnivore space use shifts in response to seasonal resource availability. Ecosphere 10:e02817.

Thomas, D. L., and E. J. Taylor. 2006. Study designs and tests for comparing resource use and availability. The Journal of Wildlife Management 54:324–336.

Thurfjell, H., S. Ciuti, and M. S. Boyce. 2014. Applications of step-selection functions in ecology and conservation. Movement Ecology 2:1–12.

U.S. Geological Survey. 2009. National elevation dataset. U.S. Geological Survey, EROS Data Center, Sioux Falls, South Dakota, USA.

van der Graaf, S., J. Stahl, R. H. Drent, A. Klimkowska, and J. P. Bakker. 2006. Surfing on a green wave - how plant growth drives spring migration in the Barnacle Goose *Branta leucopsis*. Ardea 94:567–577.

Vore, J. M., and E. M. Schmidt. 2001. Movements of female elk during calving season in northwest Montana. Wildlife Society Bulletin 29:720–725.

Welch, C. A., J. Keay, K. C. Kendall, and C. T. Robbins. 1997. Constraints on frugivory by bears. Ecology 78:1105–1119.

White, P. J., and R. A. Garrott. 2005. Yellowstone's ungulates after wolves - expectations, realizations, and predictions. Biological Conservation 125:141–152.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from resource pulses? Ecology 89:621–634.

Yellowstone Spatial Analysis Center. 2010. Yellowstone Spatial Analysis Center. Yellowstone National Park, Mammoth, Wyoming, USA.

DATA AVAILABILITY

Data are sensitive and cannot be provided publicly (black bear location data are protected under the National Parks Omnibus Act of 1998: section 207 and require a research permit and data sharing agreement to be established before data can be shared). Inquires about data sharing can be directed to the Yellowstone Research Permit Office (307) 344-2239.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3773/full