SPATIOTEMPORAL PATTERNS OF RESOURCE USE AND DENSITY OF AMERICAN BLACK BEARS ON YELLOWSTONE'S NORTHERN RANGE

by

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ABSTRACT

The availability of resources, such as food and cover, can directly influence the movement and distribution of wildlife populations. The abundance and seasonal timing of many resources have changed in Yellowstone National Park (YNP), which has influenced populations of American black bears (*Ursus americanus*), an opportunistic omnivore. Previous studies have focused on how changes in resources have influenced black bears in the central and southern regions of YNP, however little work has focused on black bears in the northern part of the park. In 2017-2018, we used GPS collars and non-invasive genetic sampling to understand resource selection and variation in densities of black bears on the Northern Range. We sought to 1) assess whether black bears were following seasonal pulses of resources (resource waves) in the spring, such as the green wave and elk (*Cervus canadensis*) calving wave and 2) evaluate how densities of black bears varied based on landscape features, generating a baseline abundance estimate to help track changes in the population over time. We found evidence that black bears followed the green wave, prioritizing forage quality over quantity when selecting patches of green vegetation in early spring. However, black bears were less likely to select areas near historical elk calving grounds, suggesting that consumption of neonates is more opportunistic. Densities of black bears varied among vegetation communities, with the highest densities in forested communities dominated by Douglas fir. Our study provides the first baseline density estimates for black bears on the Northern Range, with an average density of 12.8 bears/100km^2 (95% CI = 9.4 – 17.5), which is higher than other regions in YNP. Availability of high-quality resources may allow for higher densities of black bears, with potential ramifications for other wildlife populations on the Northern Range. Information about resource selection and variation in estimated densities could be used to guide management decisions to continue to reduce human-bear conflicts and provide safe wildlife viewing experiences for the growing number of visitors to YNP.

CHAPTER ONE

INTRODUCTION TO THESIS

Variation in the availability of resources can impact the distribution and abundance of wildlife populations (Brown et al. 1995, Pettorelli et al. 2001, Beckmann and Berger 2003, Armstrong et al. 2016, Rayl et al. 2018, Welfelt et al. 2019). For example, some animals alter their movement to follow seasonal pulses in food resources, such as masting vegetation or spawning salmonid species (*Oncorhynchus* spp.) (McCarty et al. 2002, Armstrong et al. 2016, Deacy et al. 2016, 2017, Service et al. 2019). Inter- and intra-specific competition may increase as the availability of food resources declines (Pettorelli et al. 2001, Belant et al. 2010, Service et al. 2019). In some cases, competition for resources can lead to niche partitioning, altering how species are distributed (Toft 1985, Voeten and Prins 1999). Human activity also can influence the distribution of animal populations by altering access to resources (Beckmann and Berger 2003, Pelletier 2006, Goad et al. 2014, Gingery et al. 2018). Therefore, studying the relationships between wildlife populations and resources can help develop conservation and management strategies (Pettorelli et al. 2001, McCarty et al. 2002, Manly et al. 2007, Loosen et al. 2019, Welfelt et al. 2019).

The American black bear (*Ursus americanus*) is a large-bodied omnivore and the most widely distributed species of bear in North America (Pelton 2003). Black bears select contiguous forested areas and consume large quantities of plant matter, but also will consume animal matter when available (Bastille-Rousseau et al. 2011, Costello et al.

2016, Rayl et al. 2018, Svoboda et al. 2019). The quality and availability of resources can influence the distribution of black bears (Drewry et al. 2013, Humm et al. 2017, Loosen et al. 2019, Welfelt et al. 2019). For example, when food resources are limited, larger male bears can outcompete and displace smaller female bears (Beckmann and Berger 2003, Johnson et al. 2015, Duquette et al. 2017). In addition, the abundance of food resources also can affect the degree of competition with grizzly bears (*Ursus arctos*) in areas where they are sympatric (Aune 1994, Mattson et al. 2005, Fortin et al. 2013, Costello et al. 2016).

In Yellowstone National Park (YNP), USA, black bears are sympatric with grizzly bears (Barnes and Bray 1967, Cole 1976, Schwartz et al. 2014, Teisberg et al. 2014). Since the 1960s, black bears in YNP have experienced substantial ecological changes (Barnes and Bray 1967, Cole 1976, Fortin et al. 2013, Teisberg et al. 2014, Gunther et al. 2015). For example, the population of grizzly bears in YNP has increased in abundance since being listed as a threatened species in 1975, resulting in higher levels of interspecific competition and niche partitioning between the two bear species (Schwartz et al. 2014, Costello et al. 2016). In addition, abundance and availability of high-calorie food resources, such as whitebark pine (*Pinus albicaulis*), elk (*Cervus canadensis*), and cutthroat trout (*Oncorhynchus clarkii*), have changed, causing some bears to seek out alternative food sources (Fortin et al. 2013, Teisberg et al. 2014, Gunther et al. 2015, Costello et al. 2016). However, black bears might be better adapted to capitalize on lower-calorie foods such as vegetative food resources, due their smaller body size and lesser metabolic needs, compared to grizzly bears that require higher-nutritious foods such as neonate elk (Noyce and Garshelis 1998; Robbins et al. 2004, 2007; McLellan 2011).

The Northern Range of YNP occurs at lower elevations and undergoes longer green-up periods compared to other regions of the park, resulting in increased availability of vegetative food resources (Singer et al. 1994, Frank et al. 2016, Notaro et al. 2019). This abundance of vegetation allows diverse and abundant ungulate populations to occur on the Northern Range (Frank and McNaughton 1992, Barber-Meyer et al. 2008, Metz et al. 2012, Mosley and Mundinger 2018). The current abundant food resources on the Northern Range could support higher densities of black bears compared to the rest of YNP, with concomitant implications for other species (Murphy et al. 1998, Mattson et al. 2005, Barber-Meyer et al. 2008, Rayl et al. 2018).

Therefore, we sought to better understand how availability of resources on the Northern Range influenced resource use and population density of black bears. In Chapter 2, we assessed whether black bears alter their movements to follow pulses of resources (resource waves) in the spring. We were specifically interested if black bears tracked the green wave, choosing patches of highly-digestible plant resources at intermediate biomass (Merkle et al. 2016, Aikens et al. 2017, Middleton et al. 2018). In addition, we assessed whether black bears tracked the elk calving wave, selecting areas where neonate elk could be found (Bastille-Rousseau et al. 2011, Rayl et al. 2018, Svoboda et al. 2019). In Chapter 3, we estimated the abundance of black bears on the Northern Range, making use of non-invasive genetic sampling techniques. Specifically, we investigated how the density of black bears might vary with landscape features

(Loosen et al. 2019, Stetz et al. 2019, Welfelt et al. 2019). In our final chapter, we describe how these findings contribute to our understanding of the influence of resources on the spatiotemporal distribution of black bears.

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CHAPTER TWO

INFLUENCE OF RESOURCE WAVES ON AMERICAN BLACK BEARS DURING SPRING IN THE NORTHERN RANGE OF YELLOWSTONE NATIONAL PARK

Contribution of Authors and Co-Authors

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Author: Nathaniel R. Bowersock

Contributions: Implemented the study, collected and analyzed the data, wrote the manuscript

Co-Author: Andrea R. Litt

Contributions: Guided study design, helped secure funding, assisted with data analysis, extensive review of manuscript

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Manuscript Information

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Influence of resource waves on American black bears during spring in the Northern Range of Yellowstone National Park

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ABSTRACT Seasonal pulses in resources, also known as resource waves, can drive movement and behavior of consumers. American black bears (*Ursus americanus*) are opportunistic omnivores that consume diverse foods to meet macronutrient needs. During the fall, black bears capitalize on resource waves such as hard mast, but we know less about the importance of resource waves during other seasons. We sought to understand whether the green wave, when green vegetation reaches optimal foraging quality, and the elk (*Cervus canadensis*) calving wave, when neonate elk are born, influence black bear resource selection in the spring. We hypothesized that black bears would follow the green wave, but would be less likely to track the calving wave. We instrumented 8 black bears with GPS collars in 2017 and 2018 in the Northern Range of Yellowstone National Park, USA and estimated fine-scale resource selection with integrated step-selection functions based on used and available locations. During spring, black bears selected areas based on forage quality over quantity, suggesting they were following the green wave. Specifically, we found that black bears followed the trailing edge of the green wave, reflecting consumption of vegetation shortly after it reached optimal foraging quality. During the calving wave, black bears were more likely to select areas outside of the calving grounds, suggesting that if they consumed elk calves, they did so opportunistically. Because of their smaller body size and different metabolic needs, black bears might be able to capitalize on the phenological state of plant resources, a potential benefit if grizzly bears (*Ursus arctos*) are better competitors for energy-rich foods, such as neonate elk. Few studies have shown evidence of an omnivorous species following the green wave, suggesting there is need to further understand how temporal and spatial variation in available resources influence selection by species with diverse diets such as black bears.

KEY WORDS American black bear, forage quality, green wave, Northern Range, phenology, resource selection, step-selection functions, *Ursus americanus*, Yellowstone National Park

The distribution and abundance of food resources are vital for wildlife species, but the timing of when foods are available may be even more influential on energy gains of consumers (Armstrong et al. 2016). Seasonal pulses in resources, also known as resource waves, can drive the movement and behavior of consumers (Welch et al. 1997, Davis et al. 2006, Bojarska and Selva 2012, Merkle et al. 2016, Denny et al. 2018, Dou et al. 2019). For example, masting plants create an important resource pulse in the summer and fall, supplying energy-rich foods to many wildlife species for migration, mating, or hibernation in late summer and fall (Inman and Pelton 2002, McCarty et al. 2002, Ryan et al. 2004). Resource pulses may come from plant or animal-based foods and in some cases, consumers will transition from one resource pulse to another (Armstrong et al. 2016, Deacy et al. 2017, 2019). In Alaska, brown bears (*Ursus arctos*) shift their movements to take advantage of seasonally abundant spawning salmon (*Oncorhynchus* spp.), but later shift their diets to take advantage of seasonally-limited red elderberry (*Sambucus racemosa*) berries, allowing bears to build fat reserves for hibernation (Armstrong et al. 2016, Deacy et al. 2017).

During spring, some wildlife species alter their movements to track the phenological changes in green vegetation, a pattern referred to as the green wave (van der Graaf et al. 2006, Hebblewhite et al. 2008, Bischof et al. 2012, Merkle et al. 2016). Plants at early to mid-phenological states are lower in fibrous material, making them easier to digest and therefore more nutritious. Animals that follow the green wave select patches of vegetation at optimal forage quality, which is a balance between nutritional quality and abundance on the landscape (Bischof et al. 2012, Armstrong et al. 2016, Merkle et al. 2016, Aikens et al. 2017). By consuming vegetation at optimal forage quality, animals can maximize energy intake, which can have important fitness consequences (Hebblewhite et al. 2008, Merkle et al. 2016). For example, migratory elk (*Cervus canadensis*) that tracked the green wave could consume more digestible vegetation, resulting in higher body fat composition, compared to non-migratory elk (Hebblewhite et al. 2008, Middleton et al. 2018). In addition, migrating Barnacle Geese (*Branta leucopsis*) that followed the green wave had higher fledgling survival, potentially due to consuming more nutritious vegetation (van der Graaf et al. 2006).

In North America, the American black bear is an opportunistic omnivore that balances the intake of fat and protein for efficient mass gains while meeting macronutrient needs (Coogan et al. 2014, Erlenbach et al. 2014, Costello et al. 2016). Maintaining this balance can be challenging due to seasonality of energy-rich food resources but the mobility of bears allows them to shift movements in late summer and fall to track the pulsed availability of masting vegetation (Welch et al. 1997, Klinka and Reimchen 2009, Belant et al. 2010, Fortin et al. 2013, Coogan et al. 2014, Erlenbach et al. 2014, Costello et al. 2016). Soft mast, such as *Vaccinium* species, are easily digestible foods that bears can convert and store as fat as they prepare for hibernation (Belant et al. 2010, Armstrong et al. 2016, Deacy et al. 2017). Hard mast, such as oak acorns (*Quercus* spp.) and pine nuts (*Pinus* spp.), provide good sources of fat and protein that also allow bears to quickly build lean mass and fat (Diamond et al. 2000, Inman and Pelton 2002, Ryan et al. 2004, Moyer et al. 2007, Mazur et al. 2013, Schwartz et al. 2014, Costello et al. 2016). In addition, some black bears shift their foraging activities to feed on spawning salmon and trout species (*Oncorhynchus* spp.) that supply a rich source of fat and protein (Klinka and Reimchen 2009, Belant et al. 2010, Fortin et al. 2013).

Compared with fall, food resources are more limited in spring when bears are more likely to seek high-protein foods (Coogan et al. 2014, Erlenbach et al. 2014, Costello et al. 2016). Many species of ungulates give birth during a narrow time window in the spring, providing predators with a pulse of abundant protein (Testa 2005, Hodge et al. 2010). Some black bears shift their foraging strategies to actively prey on neonate ungulates when they are available (Rayl et al. 2018), whereas other black bears capitalize on these resources opportunistically (Bastille-Rousseau et al. 2011, Svoboda et al. 2019). Even when black bears prey on neonate ungulates (Ballard et al. 1999, Jacoby et al. 1999, Griffin et al. 2011, Rayl et al. 2018), they also consume substantial amounts of green vegetation in the spring (Lariviere 2001, Pelton 2003, Duquette et al. 2017). Although plants can be high in protein, body mass gains may be lower for black bears due to their limited ability to digest green vegetation (Erlenbach et al. 2014, Schwartz et al. 2014, Costello et al. 2016, Herrero 2018).

Many ecological changes have occurred recently in the Greater Yellowstone Ecosystem (GYE) that may affect food resources for black bears, such as changes in the abundance and distribution of whitebark pine (*Pinus albicaulis*), elk, and cutthroat trout (*Oncorhynchus clarkii*) (Fortin et al. 2013, Middleton et al. 2013). In addition, the recovery of grizzly bears and the reintroduction of gray wolves (*Canis lupus*) may have increased competition (Smith et al. 2003, Fortin et al. 2013, Costello et al. 2014). Despite these changes, black bears in the GYE seem to meet their macronutrient needs in the late summer and fall (Fortin et al. 2013, Costello et al. 2016), but maintaining this balance is more challenging during spring (Schwartz et al. 2014, Costello et al. 2016). Therefore, we sought to determine the importance of resource waves for black bears during spring. First, we investigated whether black bears follow the green wave, consuming vegetation at its optimal forage quality, which might allow black bears to gain body mass (Noyce and Garshelis 1998). Second, we examined how the birth pulse of neonate elk (calving wave) influences movements of black bears and whether bears actively or opportunistically seek this food resource (Bastille-Rousseau et al. 2011, Rayl et al. 2018). Given that green vegetation comprises the largest proportion of black bears' diets in the spring (Costello et al. 2016), we predicted that black bears would follow the green wave, tracking the optimal forage quality of vegetation as it transitions across the landscape. However, we predicted that black bears would be less likely to alter their movements to track calving locations, because black bears tend to consume fewer elk calves compared to grizzly bears (Barber-Meyer et al. 2008).

STUDY AREA

Yellowstone National Park (YNP; 8,991 km^2) is in northwestern Wyoming, with additional portions in Montana and Idaho (Barber-Meyer et al. 2008). We focused our study on the Northern Range of YNP, a 1,530-km^2 area along the northern third of the national park extending into portions of southern Montana (Figure 2.1; Metz et al. 2012). We focused on about 1,000 km^2 of the Northern Range within YNP. Although the diversity and abundance of plants, ungulates, and predators on the Northern Range have been studied extensively, little is known about black bears in this region (Frank and McNaughton 1992, Singer et al. 1994, Barber-Meyer et al. 2008, Metz et al. 2012, MacNulty et al. 2016). Elevation in the Northern Range ranges from 1,590 to 3,360 m and treeline occurs around 2,900 m. Whitebark pine stands dominate high-elevation areas at 2,600–2,900 m, with subalpine fir (*Abies lasiocarpa*) occurring below this elevation zone (Frank and McNaughton 1992, Singer et al. 1994). Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and aspen (*Populus tremuloides*) comprise most of the lower-elevation forest around 1,900–2,200 m. A mix of sagebrush (*Artemisia* spp.), grasses and sedges (*Carex* spp.), and forbs are found in the open meadows of the park.

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 in lower abundance. The area is home to all native large carnivores, including black bears, grizzly bears, gray wolves, coyotes (*Canis latrans*), and puma (*Puma concolor*).

METHODS

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 jab poles, and handled following approved methods (MSU IACUC protocol 2017-24). We equipped captured black bears with Iridium GPS collars (Telonics, Inc., Mesa, AZ). During April 1–November 30, the GPS collars were programmed to record 1 location/hour in 2017 and 1 location/30 min in 2018. Locations were uploaded to the Iridium satellite system every 8 hours. During hibernation (December 1–March 31), we saved battery life by recording only 1 GPS location/month. Collars were fitted with a CR-5 collar release system (Telonics, Inc., Mesa, AZ) programmed to release on 15 October 2018 and retrieved from the field. We used cotton spacers as a secondary drop-off mechanism (Hellgren et al. 1988).

Vegetation Quantity and Quality

We developed two covariates to characterize the quality and quantity of green vegetation based on the normalized difference vegetation index (NDVI), a type of Landsat data that can be used to measure plant productivity (Notaro et al. 2019). We used NDVI data collected by the MOD09Q1 MODIS terra satellite at a 250-m spatial resolution and an 8-day temporal resolution. We converted the 8-day window to daily NDVI values following methods of Bischof et al. (2012) and Merkle et al. (2016) by fitting a smoothed and scaled time-series analysis to these data, which was then scaled between 0 and 1 (Merkle et al. 2016, Aikens et al. 2017). Scaled NDVI values of 0 are associated with no vegetation and values of 1 are associated with peak vegetation biomass (Bischof et al. 2012, Aikens et al. 2017).

To assess changes in forage quality in the early spring, we used Instantaneous Rate of Green-Up (IRG), which tracks the growth rate of green vegetation (Merkle et al.

2016, Aikens et al. 2017). We estimated IRG by fitting a double-logistic curve to the daily NDVI for each individual patch of vegetation (pixel) and computing the first derivative of the fitted curve to estimate the rate of green up, which was scaled between 0 and 1, following the methods of Bischof et al. (2012) and Merkle et al. (2016). Scaled values of 0 represent no green-up and values of 1 represent the peak rate of green up or optimal forage quality (Merkle et al. 2016, Aikens et al. 2017). We also identified when vegetation green-up began and ended for each pixel, by finding the date the first positive IRG values occurred and the date IRG values returned to zero.

To evaluate overall changes in the quantity of green vegetation separately from the phenological state, we used integrated NDVI (INDVI) (Pettorelli et al. 2005). We calculated INDVI by summing positive daily NDVI values over time, representing the accumulation of biomass (Pettorelli et al. 2005). By computing daily values for INDVI and IRG for each pixel, we explored how bears responded to vegetation resources that varied over both time and space.

Elk Calving Grounds

We generated spatial predictions of calving grounds based on locations of captured elk calves from a study conducted on the Northern Range in the early 2000s (Barber-Meyer et al. 2008). We validated these predictions and identified additional calving grounds using trajectory data and behavioral point change analysis (BPCA) (see Appendix A; Vore et al. 2001, Nicholson et al. 2019) based on locations of GPS-collared elk from 2016–2018, collected as part of a long-term study by Utah State University (D. MacNulty, unpublished data). To create our final calving grounds layer, we added a 900-

m buffer around all predicted calving locations to account for the average distance a cow elk could travel within 10 days after giving birth, when newborn calves are most vulnerable to predation (Vore and Schmidt 2001, Barber-Meyer et al. 2008). We scaled this layer to a resolution of 10-m pixels.

Landscape Features

To create a proxy for food resources for bears, we modified an existing vegetation classification layer based on dominant overstory and understory plants (50-m pixel resolution, Table 2.1; Despain 1990, Yellowstone Spatial Analysis Center 2010). We also used elevation, slope, and aspect (10-m Digital Elevation Model; U. S. Geological Survey 2009) as covariates because these variables helped explain resource selection in other studies of black bears (Bastille-Rousseau et al. 2011, Duquette et al. 2017, Rayl et al. 2018). We converted numeric degrees for aspect to one of 4 categorical cardinal directions (E: 45°-135°, S: 135°-225°, W: 225°-320°, N: 320°-45°). Finally, we quantified proximity of roads and streams (Roever et al. 2010, Bastille-Rousseau et al. 2011, Northrup et al. 2012, Duquette et al. 2017) based on GIS layers (Yellowstone Spatial Analysis Center 2010) and used the *st_distance* function in the *sf* package in program R to generate nearest distances (R Development Core Team 2013, Pebesma 2018).

Integrated Step-Selection Functions

Given that we were interested in modeling fine-scale movement and resource selection of bears, we used integrated step-selection functions (iSSF; Thurfjell et al. 2014, Signer et al. 2019). Step-selection functions compare characteristics of a used (bear) location to ≥1 paired available locations (Thomas and Taylor 2006, Thurfjell et al. 2014, Signer et al. 2019). We used the *amt* package in R (R Development Core Team 2013, Signer et al. 2019) to generate random available locations for each used location based on the distribution of turn angles and distances traveled between successive locations, known as steps, of our collared bears (Fortin et al. 2005, Thurfjell et al. 2014, Merkle et al. 2016). Although collars recorded a location every 1/2 or 1 hour, not every GPS fix was successful. Based on the distribution of successful fixes, we set the step length to 2 hours, which allowed us to generate consistent steps for each bear. We incorporated a covariate for the distance between successive used locations and the distance between used to 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 the appropriate ratio of paired available to used locations, we built models with ratios of 1 used location paired with 5, 10, 20, or 30 available locations and compared coefficient estimates (Northrup et al. 2013, Thurfjell et al. 2014). We found that estimates were consistent for models with a 1:10 ratio of used to available locations (Forester et al. 2009, Thurfjell et al. 2014, Peck et al. 2017).

We used conditional logistic regression to assess whether bears are selecting locations with particular resources disproportionately to what is available on the landscape, conditional on the individual bear's movements (*fit_issf* function in the *amt* package, Signer et al. 2019). All continuous covariates were centered and scaled before fitting models. Categorical covariates were compared to a baseline level.

To explore the importance of the green wave for resource selection by black bears, we restricted our analysis to data associated with spring green up. We selected bear locations between April 27 to June 8, which were the 2nd and 3rd quartile dates for spring green-up for all collared bears (Merkle et al. 2016). We created a base model (base) that included: INDVI, distance to nearest road, distance to nearest stream, vegetation community, elevation, slope, categorical aspect, and distance between successive locations. We compared this to a second model that incorporated IRG (base + IRG) using small-sample corrected Akaike's Information Criterion (AIC_c) (Burnham and Anderson 2004, Merkle et al. 2016). We also compared the dates when a patch of vegetation reached peak IRG to the date a bear used that patch of vegetation, as a way to assess how well bears followed the green wave (Merkle et al. 2016, Aikens et al. 2017).

To understand whether black bears were more likely to select locations near calving grounds (and track the calving wave), we computed the Euclidean distance between each used or random location and the nearest calving ground using the *st_distance* function in the *sf* package in program R (R Development Core Team 2013, Pebesma 2018). We used this approach to assess the selection of the calving grounds because distances to fixed or linear features can better assess selection than categorical covariates with iSSF models (Thurfjell et al. 2014, Peck et al. 2017). Locations within the buffered calving grounds were represented by negative distance values and locations outside of the calving grounds were represented by positive distances. We restricted data to May 15–June 30, the elk calving season for the Northern Range (Barber-Meyer et al. 2008) and again fit a base model (base) that included: INDVI, distance to nearest road, distance to nearest stream, vegetation community, elevation, slope, categorical aspect, and distance between successive locations. We compared this model to a second model that included the covariate identifying the distance to elk calving grounds (base + ElkCalf) using AIC_c (Bastille-Rousseau et al. 2011, Rayl et al. 2018).

RESULTS

We used location data from 7 of 8 GPS-collared black bears (1 adult male, 1 sub-adult male, 2 sub-adult females, 4 adult females) in our resource selection models. We excluded 1 adult female bear because recorded locations did not meet our requirements for the time frame of these analyses. Based on these 7 bears, we analyzed 3,287 used locations paired with 32,870 available locations for our green wave model and 6,268 used locations paired with 62,680 available locations for the calving wave model.

Green wave

The model that included the IRG covariate (base + IRG) better described the data than the base model ($\Delta AIC_c = 9.59$; Table 2.2), suggesting that black bears follow the green wave on the Northern Range. Bears selected locations with higher values of IRG (forage quality), but lower INDVI (vegetation quantity) compared with available resources (Figure 2.2). Bears tended to use the trailing edge of the green wave, as 75% of the locations were used after peak IRG (Figure 2.3); these patterns varied but overall were fairly consistent for different vegetation communities and with varying distances from landscape features (Appendix B; Figs. B1–B3). On average, bears used locations 10.5 days (SE = 0.24, range = 35 days before to 73 days after) after vegetation reached peak quality (Figure 2.3).

Of the static landscape features, black bears showed the strongest selection for areas closer to roads (mean = 907.6 m, range = 0 – 9971) and for forested vegetation communities over non-forested communities, especially communities dominated by subalpine fir and Douglas fir (Table 2.1, Figure 2.2). Black bears showed some selection for areas farther from streams (mean = 376.2 m, range = 0 – 1527; Figure 2.2), with steeper slopes (mean = 13.3°, range = 0 – 71.8), and preferring eastern aspects (Figure 2.2).

Elk calving wave

Although the model that included the calving grounds covariate (base + ElkCalf) better helped to explain resource selection by black bears compared to the base model (ΔAIC_c = 10.74, Table 2.2), bears selected areas farther from the elk calving grounds with higher INDVI (Figure 2.4). Bears showed the strongest selection for forested communities, especially those dominated by whitebark pine, over non-forested communities, and also strongly selected for areas closer to roads (mean = 1462.6 m, range = 0 – 15,557 m; Figure 2.4). Bears also showed some selection for locations with lower elevations (mean = 2193 m, range = 1699 – 3084 m), easterly aspects, and that were closer to streams (mean = 166.6 m, range = 0 – 1,075 m) (Figure 2.4).

Based on our spatial predictions, calving grounds generally were in non-forested communities with lower average INDVI values, whereas the collared black bears generally used locations in forested communities with higher average INDVI (Table 2.3). The average slope, aspect, and elevation of calving grounds were similar to locations used by black bears (Table 2.3).

DISCUSSION

Our study provides evidence that black bears followed the green wave during spring. Specifically, they followed the trailing edge of the green wave, suggesting they used spring forage shortly after it reached optimal forage quality (Merkle et al. 2016, Aikens et al. 2017). Consuming green vegetation at or near optimal forage quality supplies animals with higher digestible energy, compared with later phenological states that are less digestible and less nutritious (Merkle et al. 2016, Aikens et al. 2017, Mysterud et al. 2017). Our findings are consistent with previous studies indicating that black bears consume more vegetation in the spring when plants are more digestible (Robbins et al. 2004, Schwartz et al. 2014, Costello et al. 2016, Herrero 2018).

Protein helps bears to gain muscle mass and compete for resources (Pritchard and Robbins 1990, Robbins et al. 2007, McLellan 2011, Costello et al. 2016), but such gains can be inhibited when protein-rich foods, such as animal matter, are less abundant (Welch et al. 1997, McLellan 2011). In the GYE, competition with grizzly bears may reduce black bears' ability to access protein-rich foods (Fortin et al. 2013, Schwartz et al. 2014, Costello et al. 2016). However, with smaller bodies and lower metabolic needs compared with grizzly bears, black bears can feed primarily on green vegetation and still maintain or even gain muscle mass by capitalizing on the nutrients available in plants during spring green-up (Noyce and Garshelis 1998; Robbins et al. 2004, 2007; McLellan 2011). Our findings support the notion that black bears may mitigate limitations in resources by spatially and temporally tracking the nutritional quality of vegetation resources during spring.

In our study, black bears capitalized on the abundance of green vegetation, but were less likely to select areas closer to elk calving grounds. During the calving season, black bears selected forested communities with higher INDVI values, consistent with other studies of black bears in the GYE (Holm et al. 1999, Fortin 2011, Frattaroli 2011, Schwartz et al. 2014); the elk calving grounds were mostly in non-forested communities with lower INDVI values. Although black bears are known to prey on elk calves in the Northern Range (Howell 1921, Rush 1932, Houston 1982, Singer et al. 1997, Barber-Meyer et al. 2008), our data suggest they do not actively target calving areas. Given the lower rate of predation on elk neonates on the Northern Range compared with grizzly bears (Barber-Meyer et al. 2008), we speculate black bears consume elk calves opportunistically. Black bears in Canada and northern Michigan USA also preyed on ungulate neonates opportunistically and selected forested areas with higher NDVI values instead of the more open, less green areas where calving occurred (Bastille-Rousseau et al. 2011, Duquette et al. 2014).

Our results provide evidence that the phenological state of green vegetation can affect how bears use the landscape. Although black bears in some areas avoid roads due to the increased risk of human-caused mortality, black bears in our study showed selection for locations closer to roads (Laske et al. 2010, van Manen et al. 2012, Gantchoff et al. 2019). Green vegetation first becomes available at lower elevations and near roads, due to the earlier timing of snow melt (Frank et al. 2016, Notaro et al. 2019). Bears that live in national parks or other areas with lower human-caused mortality are more likely to use food resources along roads (Kasworm and Manley 1990, Apps et al.

2006, Gunther and Wyman 2008, Graham et al. 2010, Schwartz et al. 2010, Gantchoff et al. 2019), which may facilitate their ability to follow resource waves.

During the green wave in early spring, black bears selected areas with high values of IRG (vegetation quality) and lower INDVI that were closer to roads, but farther from streams. Grasses and sedges are some of the first plants to green up and are also more digestible at this time (Frank and McNaughton 1992, Frank et al. 2016), suggesting these plants may be important to black bears after emerging from hibernation. However, by mid to late spring, during the elk calving season, black bears showed some selection for areas closer to streams with higher INDVI. During this later period, more riparian plants are available, such as cow parsnip (*Heracleum maximum*), which are more digestible than grasses (Rode et al. 2001, Fortin et al. 2013, Costello et al. 2016, Duquette et al. 2017, Herrero 2018, Svoboda et al. 2019).

All trapping efforts for our study occurred within 1,000 m of roads, which could lead to increased use of locations in proximity of roads. In addition, 6 of the 7 bears in our study were subadults or females. Subadult or female bears with young may spend more time near roads to avoid competition with and predation by grizzly bears (Gunther et al. 2002, Mattson et al. 2005, Schwartz et al. 2013), and interactions with aggressive male black bears that tend to avoid roads (Mattson et al. 1987, Apps et al. 2006, Gunther et al. 2018, Gantchoff et al. 2019). Male bears typically consume more vertebrate protein than females (Lafferty et al. 2015, Costello et al. 2016), such that female bears also may be less likely to use areas near the calving grounds.

Although black bears have the ability to consume a wide array of foods, we found bears on the Northern Range capitalized on nutritional quality of green vegetation, which may be an effective strategy to compete for resources in time and space. Additionally, we found that vegetative resources drove black bear movements more than the availability of protein-rich elk calves. Furthermore, tolerance of human activity (e.g., in a national park) may facilitate the ability of bears to follow resource waves. This increased understanding of how the availability of resources influenced bears activity, will allow managers to better predict how bears may shift their diets and movements in response to future changes in availability and distribution of food resources.

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Table 2.1. Vegetation communities used in resource selection models and proportion of locations of black bears in each vegetation community for the green wave and calving wave datasets, Northern Range, Yellowstone National Park, Wyoming and Montana 2017–2018. Big sagebrush/sticky geranium and Idaho fescue/sticky geranium are non-forested communities, whereas all other communities are forested.

Vegetation community	**Proportion of data - green wave model**	**Proportion of data - calving wave model**
Big sagebrush/sticky geranium	0.20	0.21
Idaho fescue/sticky geranium	0.07	0.09
Douglas-fir/grass-sedge	0.14	0.10
Douglas-fir/snowberry	0.25	0.25
Subalpine fir/grass-sedge	0.22	0.22
Subalpine fir/grouse whortleberry	0.12	0.08
Whitebark pine/subalpine fir/ grouse whortleberry	0.00	0.05
TOTAL	1.00	1.00

Table 2.2. Model selection results to assess the importance of the green wave and calving wave in resource selection of black bears (*n* = 7 individuals), Northern Range, Yellowstone National Park, 2017–2018.

Model	***K*** §	**AIC$_c$** ¶	**ΔAIC$_c$** #
base + IRG †	16	13,678.61	0
base	15	13,688.36	9.75

Model	***K***	**AIC$_c$**	**ΔAIC$_c$**
base + ElkCalf ‡	17	26,150.79	0
base	16	26,157.45	6.66

Notes: Base model included integrated NDVI, distance to roads, distance to streams, aspect, elevation, slope, vegetation community, and distance to successive points (integrated step selection function).† IRG, Instantaneous rate of green up covariate used to assess if bears were tracking the green wave.

‡ ElkCalf, Elk calving ground covariate used to assess if bears were selecting for area closer to or farther from 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

Table 2.3. Landscape characteristics for elk calving grounds (*n* = 182; 151 capture locations of elk calves and 31 locations of parturition behavior) and locations used by black bears (*n* = 6,268 locations from 7 collared bears) during the elk calving season, Northern Range, Yellowstone National Park, 2017–2018.

	Elk calving grounds	**Black bear locations**
Non-forested vegetation community	93.5% (170)	25.0% (1,573)
Forested vegetation community	6.5% (12)	75.0% (4,695)
INDVI min	8.44	13.42
INDVI mean	32.12 (SE = 0.84)	37.31 (SE = 0.11)
INDVI max	63.24	65.11
Slope (°)	10.8 (SE = 0.6)	13.2 (SE = 0.1)
Elevation (m)	2,132 (SE = 18.4)	2,190 (SE = 2.6)

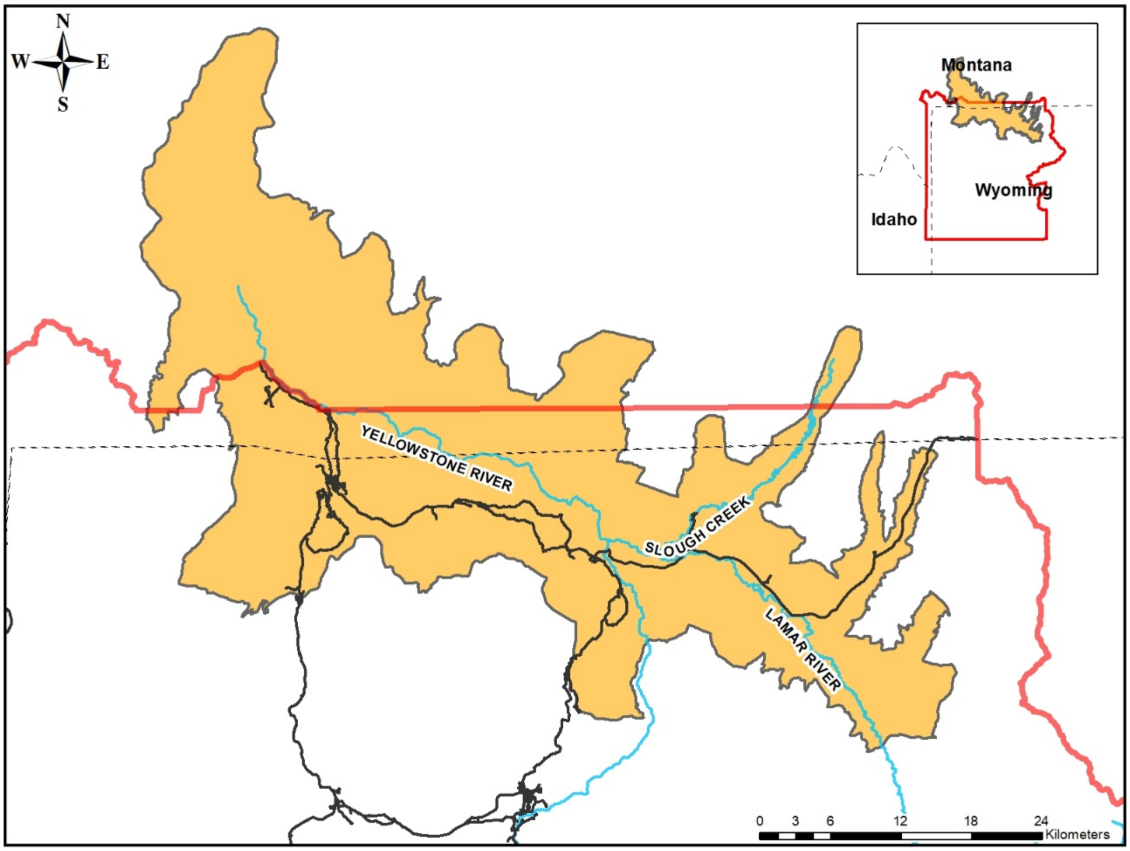

Figure 2.1. Map of the Northern Range (yellow) of Yellowstone National Park, Montana and Wyoming, 2017–2018. Our study of resource selection by black bears during spring focused on the portion of the Northern Range within the national park boundary (below the solid red line).

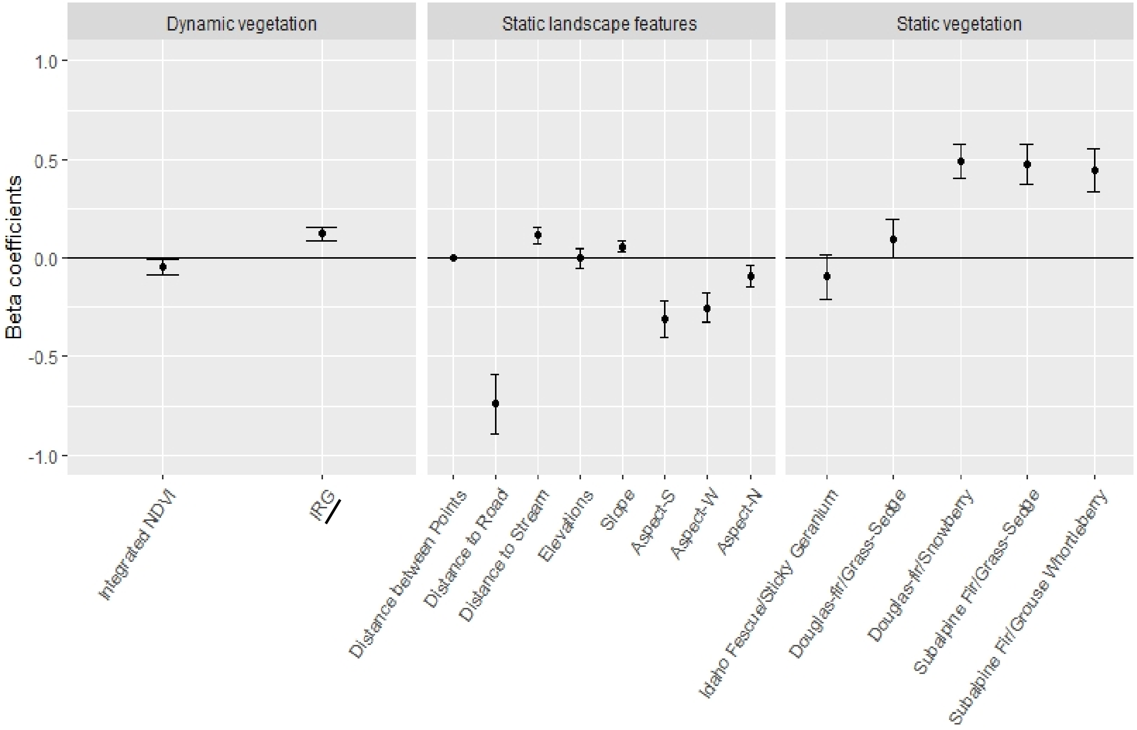

Figure 2.2. Beta coefficients and standard errors for covariates in the green wave model (base + IRG), based on locations from 7 black bears tracked April 27–June 8 2017–2018, Northern Range, Yellowstone National Park, Montana and Wyoming. All covariates were centered and scaled, except for categorical covariates (aspect and vegetation community). The reference category for aspect was East and the reference category for vegetation community was big sagebrush. Estimates above the zero line indicate positive selection for a covariate. Dynamic covariates vary over both space and time, whereas static covariates only vary over space.

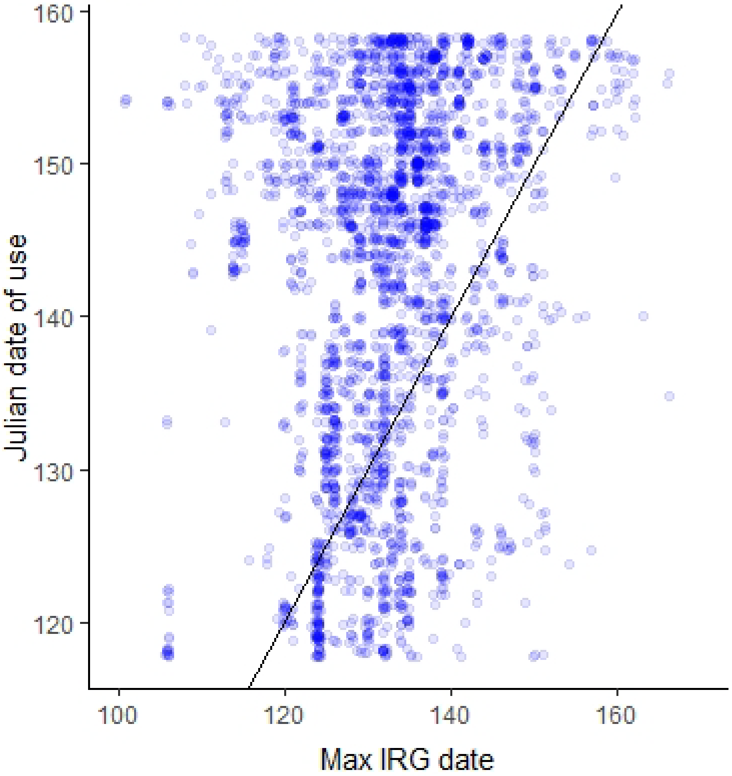

Figure 2.3. Julian dates when a location on the landscape reached maximum IRG versus when that same location was used by a collared bear during the spring green-up period Northern Range, Yellowstone National Park, Montana and Wyoming, 2017–2018. The black diagonal line represents perfect green wave surfing, if a collared black bear uses a location at maximum IRG. Observations above the line indicate locations that black bears used after maximum IRG occurred (75% of used locations), whereas observations below the line indicate locations that black bears used before the vegetation reached maximum IRG (25%). On average, bears used locations 10.5 days (SE = 0.24) after maximum IRG.

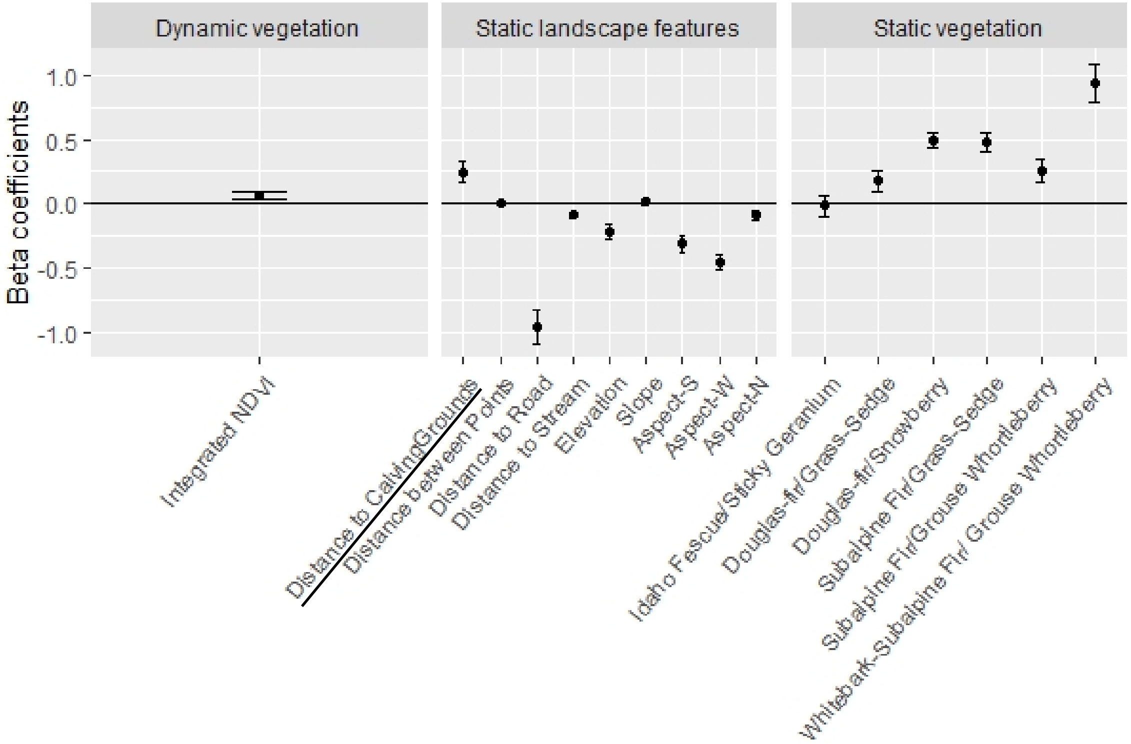

Figure 2.4. Beta coefficients and standard errors for covariates in the calving wave model (base + Elk Calf), based on locations from 7 collared black bears during May 15-June 30, 2017-2018, Northern Range, Yellowstone National Park, Montana and Wyoming. Estimates above the zero line indicate positive selection for a covariate. All covariates were centered and scaled, except for categorical covariates (aspect and vegetation community). The reference category for aspect was East and the reference category for vegetation community was big sagebrush. Estimates above the zero line indicate positive selection for a covariate. Dynamic covariates vary over both space and time, whereas static covariates only vary over space.

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CHAPTER THREE

FACTORS ASSOCIATED WITH VARYING DENSITY OF BLACK BEARS ON YELLOWSTONE NATIONAL PARK'S NORTHERN RANGE

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Factors associated with varying density of black bears on Yellowstone National Park's Northern Range

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ABSTRACT Variation in the availability of resources can influence how wildlife populations are distributed. In Yellowstone National Park (YNP), American black bears (*Ursus americanus*) have experienced many changes to available resources, which has changed their distribution in the park. The Northern Range of YNP is known for its abundant vegetative resources that could support a larger number of black bears compared to the rest of the park, but little is known about black bears in this region. We used non-invasive genetic sampling and spatially explicit capture-recapture models to quantify variation in black bear density as a function of landscape features. During 2017 and 2018, we obtained 3,673 hair samples from 26 hair corrals and 270 rub objects, which we genotyped to identify 138 unique individual black bears (66 males, 72 females). Densities were highest in Douglas fir communities (23.2 bears/100 km^2, 95% CI = 15.2–35.6) and lowest in big sagebrush (1.8 bears, 0.19–16.7). We estimated an average density of 12.8 bears/100km^2 (95% CI = 9.4 – 17.5), which is higher than other portions of the Greater Yellowstone Ecosystem, suggesting that food resources and other conditions on the Northern Range can support more black bears. Our study provides the first baseline density estimates of black bears on the Northern Range, which can guide management decisions in the face of continued changes in available resources and increased visitation to the park. This information could help prioritize the placement of additional food storage boxes in backcountry settings, especially in forested areas, to reduce access to human foods and subsequent human-wildlife interactions.

KEY WORDS abundance, American black bear, density, non-invasive genetic sampling, Northern Range, resource, spatially explicit capture-recapture models, Yellowstone National Park, *Ursus americanus*

Variation in the abundance and availability of resources, such as food and cover, can influence the density and distribution of wildlife populations (Brown et al. 1995, Ives and Klopper 1997, Delibes et al. 2001, Greene and Stamps 2001, Pettorelli et al. 2001, Manly et al. 2007, Gaillard et al. 2010). Access to resources can change due to inter- and intraspecific competition (Toft 1985, Gaston et al. 1997, Voeten and Prins 1999), which may lead to resource partitioning among individuals (Toft 1985, Voeten and Prins 1999, Pettorelli et al. 2001, Belant et al. 2010). Human activities, such as habitat alteration and human-wildlife interactions, also can affect resource availability and the distribution and density of animal species (Delibes et al. 2001, Beckmann and Lackey 2008, Mazur et al. 2013, Goad et al. 2014, Johnson et al. 2015, Newsome et al. 2015, Baker and Leberg 2018). Therefore, understanding the relationship between wildlife population density and environmental conditions is important to inform management decisions (Brown et al. 1995, Stetz et al. 2019, Welfelt et al. 2019).

The American black bear (*Ursus americanus*) is an omnivorous mammal that can occur in a wide range of environmental conditions (Costello and Sage 1994, Pelton 2003, Robbins et al. 2004, Teunissen van Manen et al. 2014). Black bears generally occur in contiguous forests that provide under- and overstory cover and food resources (Pelton 2003, Bastille-Rousseau et al. 2011, Costello et al. 2016, Duquette et al. 2017). Plant matter comprises most of a black bear’s diet, but bears will consume animal matter, such as neonate ungulates, when available (Barber-Meyer et al. 2008, Bastille-Rousseau et al. 2011, Rayl et al. 2018, Svoboda et al. 2019). Black bears generally avoid areas with high levels of anthropogenic activity, such as residential developments and areas with major highways or roads (Laske et al. 2010, van Manen et al. 2012, Duquette et al. 2017, Gantchoff et al. 2019). However, black bears can develop a tolerance for humans when human activity is low, when natural foods are less abundant and anthropogenic foods provide an attractant, or when human activity is high but very predictable (Kasworm and

Manley 1990, Aune 1994, Apps et al. 2006, Gunther and Wyman 2008, Graham et al. 2010, Gunther et al. 2018, Gantchoff et al. 2019).

Intraspecific interactions between black bears are driven by local population densities and availability of resources (Beckmann and Berger 2003, Duquette et al. 2014, Johnson et al. 2015). When densities of black bears are low and natural foods are abundant, male and female bears select similar resources (Beckmann and Berger 2003, Duquette et al. 2014, Johnson et al. 2015). However, when bear densities increase and food becomes limited, larger males become more active around resources and reduce females' access to food (Pelton 2003, Johnson et al. 2015, Duquette et al. 2017, Gantchoff et al. 2019). In response, female black bears may select areas with lower-quality resources or tolerate greater human activity (e.g., areas closer to roads and developments) to access high quality resources. By shifting their selection, females also may reduce the risk of cub mortality from male-caused infanticide (Beckmann and Berger 2003, Garrison et al. 2007, Duquette et al. 2017, Gantchoff et al. 2019).

Some black bear populations are sympatric with grizzly bears (*Ursus arctos*) in western North America (Aune 1994, Mowat et al. 2005, Apps et al. 2006). In areas that have abundant, high-quality foods, such as salmon and fruiting plants, black bears typically change their movements and resource selection to reduce competition and limit direct encounters with grizzly bears (Welch et al. 1997, Apps et al. 2006, Frattaroli 2011, Fortin et al. 2013). However, when foods are less abundant or are of lower quality, both species select similar resources (Aune 1994, McLellan 2011, Stetz et al. 2019). In such areas, black bears can have a competitive advantage and may occur at higher densities because of the lower energy requirements associated with their smaller body mass (Aune 1994, McLellan 2011, Schwartz et al. 2014, Stetz et al. 2019).

Both species of bears occur in Yellowstone National Park (YNP) (Schwartz et al. 2014), where resources typically are heterogeneously distributed along an elevational gradient (Holm et al. 1999, Fortin et al. 2013, Notaro et al. 2019). Black bears in YNP typically select forested areas at lower elevations and consume more vegetative resources compared to grizzly bears (Chapter 2, Barnes and Bray 1967, Fortin et al. 2013). Biologists used mark-recapture studies to estimate abundance of black bears in YNP during the late 1960s and early 1970s, but loss of markings on individuals affected the consistency of estimates (Barnes and Bray 1967, Cole 1976). More recently, non-invasive genetic sampling (NGS) techniques were used to estimate abundance of black and grizzly bears, but estimates were limited to bears visiting streams around Yellowstone Lake before and after the decline of cutthroat trout (*Oncorhynchus clarkii*) (Haroldson et al. 2005, Teisberg et al. 2014).

The Northern Range of YNP is located at lower elevations and experiences longer green-up periods that can provide black bears with more abundant vegetative resources, compared to other regions of the park (Singer et al. 1994, Costello et al. 2016, Frank et al. 2016, Notaro et al. 2019). Additionally, the Northern Range has diverse and abundant ungulate populations, which can provide black bears with protein-rich foods (Singer et al. 1994, Mech and Barber-Meyer 2015, Frank et al. 2016, Boyce 2018). These resources could support higher densities of black bears on the Northern Range compared with other regions of the park. Knowing how black bears are distributed across the Northern Range may help managers prioritize where to focus limited resources to decrease human-bear interactions (Coleman et al. 2013, Stetz et al. 2014, Gunther et al. 2018). A baseline density estimate of black bears on the Northern Range can be used to track changes in the population, particularly against a backdrop of changing resources and climate conditions (Mattson et al. 2005, Stetz et al. 2014, 2019, Rayl et al. 2018, Svoboda et al. 2019). In addition, reliable density estimates would provide a foundation for future research exploring the influence of black bears on ungulate and other wildlife populations (Barber-Meyer et al. 2008). To fill this information gap, we sought to investigate variation in black bear densities as a function of landscape features and estimate overall abundance on the Northern Range. We tested hypotheses related to how landscape features and demographic factors may be associated with variation in black bear densities.

STUDY AREA

The Northern Range consists of a 1,530-km^2 area in southern Montana and northern portions of YNP (Figure 3.1; Metz et al. 2012). Elevations range from 1,590 to 3,360 m, with whitebark pine (*Pinus albicaulis*) and subalpine fir (*Abies lasiocarpa*) at elevations between 2,600 and 2,900 m (Frank and McNaughton 1992, Singer et al. 1994). Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and trembling aspen (*Populus tremuloides*) comprise most of the lower elevation forest around 1,900–2,200 m, and a mix of sagebrush (*Artemisia* spp.), grasses and sedges (*Carex* spp.), and forbs occur in the open meadows of the park.

The most abundant ungulate species include elk (*Cervus canadensis*), 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 occur, but are less abundant. The Northern Range is home to several large carnivores including: grizzly bears, gray wolves (*Canis lupus*), coyotes (*Canis latrans*), and pumas (*Puma concolor*) (Barber-Meyer et al. 2008).

METHODS

Non-invasive genetic sampling and analysis

We collected hair based on two different non-invasive methods: hair snare corrals (hair snares) (Woods et al. 1999) and rub objects (Kendall et al. 2008). To establish a network of hair snares, we followed established protocols (e.g., Mowat and Strobeck 2000, Kendall et al. 2009, 2016, Sawaya et al. 2012, Lamb et al. 2016) and overlaid a 5 × 5 km grid across the study area (Figure 3.1). We chose a 5 × 5 km grid based on average home-range sizes of female black bears within the mountain west (Grogan and Lindzey 1999, Holm et al. 1999, Nilsen et al. 2005, Frattaroli 2011), optimizing the probability of detecting an individual bear multiple times and minimizing the probability that an individual female goes undetected (Boulanger et al. 2006). A single hair snare was established in each grid cell and remained in the same location for the entire study. For human safety, snare sites were placed out of sight, >500 m from developed areas, and >200 m from trails, campsites, or roads (Kendall et al. 2008, 2009). We visited each hair snare once per week from mid-May through mid-July in 2017 and 2018, resulting in 8 sampling occasions per year.

Hair snares consisted of a single strand of 4-point barbed wire stretched around three or more trees to create an enclosure at a height of ~50 cm, so we could target collection of hair from subadult and adult bears. We poured a scent lure on a brush pile constructed in the middle of each enclosure to encourage bears to investigate each site, thus increasing the probability of obtaining a hair sample as the bear crossed over or under the wire. We used 1 of 4 scent lures during each sampling occasion: 2 commercial hunting scent lures (smoky bacon or raspberry doughnuts; Moultrie Feeders, AL, USA) and 2 natural scent lures (rotten cattle blood or a mixture of rotten cow blood and fish oil). We obtained the cattle blood from a local slaughterhouse, and the fish oil was created from ground lake trout (*Salvelinus namaycush*) carcasses supplied by the Yellowstone Lake fish removal program. We allowed the blood and ground fish to decompose in plastic buckets for at least 4 weeks before applying to snare sites.

We used rub objects, such as trees and power poles, as our second hair collection method (Kendall et al. 2008, 2009). We searched for and established rub objects throughout the 2017 sampling season. Rub objects were identified by their smooth, dirty surfaces typically associated with frequent bear use (Burst and Pelton 1983). We attached 3 to 5 short pieces of 4-point barbed wire to rub trees to increase the probability that hair would be deposited for sample collection; we did not modify other rub objects. In 2017, we collected samples from rub objects as we traveled to hair snares during weekly checks from mid-May through mid-July, resulting in 8 sampling occasions. From August 21 through September 29, we collected samples from all rub objects as part of a ninth sampling occasion. In 2018, we increased our sampling frequency because we no longer were searching for rub objects. We checked >80% of the rub objects every two weeks from mid-May until the end of August, resulting in 8 sampling occasions. Each rub object was checked an average of 6.6 times (range = 2–8) during the 2018 season.

Hair samples were collected from the field using sterilized hemostats, to prevent DNA contamination, and placed in coin envelopes. We sterilized all surfaces of hair snares or rub objects with butane torches after collecting hair, to prevent DNA contamination between sampling occasions. We stored hair samples in plastic containers with desiccant for drying and storage until they were sent to Wildlife Genetics International (WGI, Nelson, British Columbia) for microsatellite genotyping analysis. Following standard protocols for non-invasive genetic samples, QIAGEN DNeasy kits were used to extract DNA (Paetkau 2003). Individual bears were identified based on an established regional set of 10 microsatellite markers (G1D, G10H, G10J, G10P, G10L, MU59, MU51, MU23), including ZFX/ZFY for sex. The G10J microsatellite marker was used to differentiate between black and grizzly bears. To minimize genotyping errors, weak or difficult to read samples were rerun multiple times in an attempt to increase the confidence in the genotyping of samples (Paetkau 2003, Kendall et al. 2009). If weak samples failed to amplify further, they were removed from analysis. All genotyped samples were referenced to existing genotype records from the Greater Yellowstone Ecosystem, Northern Continental Divide Ecosystem, and Cabinet-Yaak Ecosystem, to look for additional genotyping errors.

Hair samples were sub-sampled each year based on recommendations from WGI, to maximize individual identifications with available funds. In 2017, we analyzed a maximum of 10 samples/hair snare/sampling occasion. If we collected multiple samples along consecutive barbs at a hair snare, we analyzed only 1 of every 3 samples (Tredick et al. 2007). For rub objects, we analyzed a maximum of 5 samples/rub object/sampling occasion. This sub-sampling was random and did not depend on where the sample was collected on the rub object. With greater sampling effort in 2018, we altered the sub-sampling rules due to the greater number of samples collected and budget constraints, reducing the number of samples analyzed to a maximum of 8 samples/hair snare/sampling occasion and a maximum of 2 samples/rub object/occasion.

Estimating variation in density and overall abundance

We used spatially explicit capture-recapture (SECR) models to understand variation in black bear density and generated an overall estimate of abundance using the *secr* package (v. 3.2.1-2019, Efford 2019) in program R (R Development Core Team 2013). These models estimate 3 spatially dependent parameters: 1) detection probability at an individual animal's activity center (*g0*), 2) a spatially-scaled detection parameter based on the distance from an animal's activity center (σ), and 3) density (D) (Efford et al. 2009, Roffler et al. 2016).

We created encounter histories for each individual bear based on the location, timing, and method of detection. To assess associations between resources and black bear density, we first built a habitat mask consisting of a buffered grid of points around each trap location to extract spatial information from landscape descriptors. We used the *suggest.buffer* and *make.mask* functions within the *secr* package, applied a 9-km buffer around each trap site (Efford 2019), and spaced grid points 1,000 m apart, based on recommendations ($\sigma < 0.5$) in Royle et al. (2014), which resulted in a habitat mask encompassing 1,592 km^2. We used a Poisson distribution, half-normal detection function, and the full likelihood to examine factors that could influence detection and density parameters (Efford et al. 2009).

Modelling Detection **-** We used a 2-step approach to evaluate covariates in our SECR models (Gould et al. 2018, Loosen et al. 2019, Stetz et al. 2019). In our first step, we compared models focused on factors that might influence the detection parameters (*g0* and σ), while keeping density spatially uniform. Home ranges of black bears typically differ between males and females, and space use can be influenced by the opposite sex, so we used sex as a covariate on both *g0* and σ (Sawaya et al. 2012, Kendall et al. 2015, Tattoni et al. 2015, Loosen et al. 2019, Stetz et al. 2019, Welfelt et al. 2019). Because we were using a maximum-likelihood approach and not partitioning the data between males and females, we set sex as a group covariate in our models (Efford 2019). The ability to detect individual bears could differ between hair snares and rub objects (Sawaya et al. 2012, Kendall et al. 2015, Tattoni et al. 2015, Loosen et al. 2019, Stetz et al. 2019), so we considered collection method (hair snare or rub object) as a covariate on *g0* and σ. Additionally, previous experiences at trap sites might influence detection probability for some individuals, so we considered a behavioral covariate (bk) on *g0* (Harris et al. 2011, Loosen et al. 2019). We further assumed there was spatial heterogeneity in detection of individuals, and we considered 2-class finite mixtures (*h2*) for σ (Pledger 2000, Drewry et al. 2013, Hooker et al. 2015). Finally, we included sampling occasion (*t*) and year (session) as additional covariates on *g0*. We considered combinations of covariates (*g0*:

sex, sampling method, behavior, time of sampling occasion, and year; σ: sex, method, spatial heterogeneity) to create 132 additive models (Appendix C), and used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to compare model fit (Burnham and Anderson 2004).

***Modelling Density* -** In our second step, we used the top model for the detection parameters from step 1 and focused on covariates that might influence bear density. Black bears typically select forested areas and areas with abundant green vegetation (Chapter 2, Bastille-Rousseau et al. 2011, Fortin et al. 2013, Costello et al. 2016, Duquette et al. 2017). Therefore, we expected black bear density to increase with the productivity of vegetation and vary among vegetation communities, with higher densities in forested areas because these areas provide food and cover (Loosen et al. 2019, Stetz et al. 2019, Welfelt et al. 2019).

We classified vegetation communities based on dominant over- and understory plants (Despain 1990), which we used as a proxy for food resources. We used vegetation community layers (50-m pixel resolution, Yellowstone Center for Resources, Yellowstone Spatial Analysis Center 2010) and potential natural vegetation (PNV) data (U.S. Forest Service, PNV Classification for Western and Central Montana, and Northern Idaho) to classify vegetation for our habitat mask using the *raster* package in program R (Hijmans et al. 2015). We reclassified vegetation communities into 4 categories broadly representative of the study area (big sagebrush, Douglas fir, Idaho fescue, subalpine fir) (Figure 3.2).

To assess how green vegetation influenced black bear densities, we initially considered using yearly averaged normalized difference vegetation index (NDVI) data. However, NDVI varied little across the landscape when averaged over our sampling season. Net primary productivity (NPP), the amount of energy available on the landscape from vegetation, better described variation on the landscape compared with NDVI (Xu et al. 2012). We used NPP (kg C/m^2) data at a 250-m resolution from 2017 and 2018 (Numerical Terradynamic Simulation GroupMOD 17 MODIS; http://www.ntsg.umt.edu/data; accessed 10 Sep 2019). Values of NPP in 2017 and 2018 were highly correlated ($r = 0.999$), so we averaged the two years, then centered and scaled these values (subtracting the mean from NPP values, divided by the standard deviation), to describe vegetation for both years.

The presence of roads can influence the spatial distribution of black bears, depending on their tolerance of humans and inter- and intraspecific interactions (Kasworm and Manley 1990, Laske et al. 2010, Gunther et al. 2018, Gantchoff et al. 2019). Within YNP, black bears are observed along roads most often on the Northern Range (National Park Service, unpublished data). We considered distance to the nearest road as a potential covariate and expected black bear densities to be higher near roads. This prediction also was informed by data from collared bears that selected locations closer to roads (see Chapter 2). We used a geospatial layer of paved roads (Yellowstone Spatial Analysis Center 2010) and the *st_distance* function in the *sf* package, to compute proximity of nearest road for locations in the density mask array, which we scaled following the same procedures as the averaged NPP values (Pebesma 2018).

Finally, home-range sizes differ for male and female black bears on the Northern Range (Appendix D), which can lead to differences in density (Drewry et al. 2013, Humm et al. 2017, Azad et al. 2019, Welfelt et al. 2019). Therefore, we included sex as a potential covariate in density models. We predicted that the sex ratio would be female-biased, given that female black bears have lower resource needs and smaller home ranges compared with males (Tredick and Vaughan 2009, Frary et al. 2011, Drewry et al. 2013, Murphy et al. 2016, Gould et al. 2018).

Before creating models to explore factors that influence variation in bear density, we first examined correlations between covariates. Values of NPP were related to the vegetation community categories, so we did not include both covariates in the same models. We considered 11 additive models and used AIC_c to compare model fit (Burnham and Anderson 2004). Finally, we estimated overall abundance of black bears within our study area (the 1,592-km^2 habitat mask) with the *region.N* function in the *secr* package (Efford 2019).

RESULTS

Genetic analysis

Between 2017 and 2018, we collected a total of 3,673 hair samples from 26 hair snares, 217 from rub trees, and 53 other rub objects (see Appendix E for data on the success rates of lures at hair snares). In 2017, we collected 67% of the 1,358 samples from hair snares (Table 3.1) and 33% from rub objects (Table 3.2). When we increased our sampling effort in 2018, 27% of the 2,315 samples came from hair snares (Table 3.1) and 73% from rub objects (Table 3.2). We submitted 1,998 hair samples for genetic analysis. Of the analyzed samples, 1,226 (61%) produced genotypes for individual identification. Samples collected from hair snares had a 91% genotyping success rate, compared with 67% for samples from rub objects.

We identified a total of 138 black bears (66 males, 72 females) from the genotyped samples during our study; 76 individuals in 2017 (28 males, 48 females) and 62 in 2018 (38 males, 24 females). Fifty-five individuals were identified in both years (20 males, 35 females). Overall, a greater proportion of female black bears were identified with just hair snares (40%) than with just rub objects (27%) or both methods (33%). A greater proportion of male black bears were identified with hair samples collected from rub objects (39%) than from hair from hair snares (26%) or by both methods (35%).

Variation in detection

The top detection model from step 1 included sex, method, behavioral response (*bk*), sampling occasion (*t*), and session (year) as covariates on *g0*; and method and finite mixture (h2) on σ (Table 3.3). The probability of detecting female bears was higher than for males, and bears had a higher detection probability at hair snares compared with rub objects (Table 3.4). If a bear deposited hair at a snare or rub object, they showed a positive behavioral response (*bk*) to return on another occasion (Table 3.4). Detection probabilities were similar for sampling occasions 1 through 6, with a slight increase in detection on occasion 4 (Figure 3.3). Detection declined between sampling occasions 7 and 9 (Figure 3.3); overall detection probability was higher in 2018 than 2017 (Table 3.5). The size of activity centers (σ) varied based on the sampling method and finite mixture groups. In general, activity centers around rub objects were smaller than around hair snares. Most bears (94.5%) fell into mixture group 1, which had smaller activity centers (2,221-m radius around hair snares, 95% CI = 1,784–2,765; 1,100-m radius around rub objects, 95% CI = 940-1,286) compared to mixture group 2 (7,315-m radius around hair snares, 5,858–9,133; 3,622-m radius around rub objects, 3,106 – 4,233).

Variation in density and overall abundance

Vegetation community was included in the top model and all three competing models ($\Delta AIC_c \leq 4$) from step 2 ($\Delta AIC_c \leq 2$: Table 3.5), explaining some variation in the density of black bears. Densities were highest in Douglas fir communities (23.2 bears/100 km^2, 95% CI = 15.2–35.6) and lowest in big sagebrush (1.8 bears/100 km^2, 0.19–16.7). Although densities were intermediate in subalpine fir (15.2 bears/100 km^2, 8.38–27.4) and Idaho fescue (9.95 bears/100 km^2, 4.53–21.9), the range of plausible estimates included in confidence intervals overlapped with other vegetation communities. Based on the top model, we estimated an average of 12.8 bears/100km^2 (95% CI = 9.4 – 17.5) or a total of 204 black bears (150–278) across all vegetation communities within the 1,592 km^2 habitat mask.

The two competing models ($\Delta AIC_c \leq 4$) also included distance to road or sex (Table 3.5), but these were likely uninformative parameters (Arnold 2010), based on the changes in AIC_c and confidence intervals that overlapped zero (roads: average $\beta = 0.11$, 95% CI = -0.19–0.41; sex: average $\beta = 0.004$, -0.32–0.33). We found little evidence that NPP was associated with variation in bear density (Table 3.5).

DISCUSSION

Varying densities of black bears

Densities of black bears varied among vegetation communities and we hypothesize that differences are, at least partially, related to food resources. Densities were highest in vegetation communities dominated by Douglas fir, which provide cover and foods such as graminoids and masting vegetation (Barnes and Bray 1967, Fortin et al. 2013, Costello et al. 2016, Duquette et al. 2017). Much of the mid- to upper-elevation areas of YNP are dominated by lodgepole pine (Haroldson et al. 2005, Fortin et al. 2013); this vegetation community is less common at lower elevations such as the Northern Range. Although we were not able to estimate bear densities in lodgepole pine forests, the availability of foods for black bears is typically lower than other forested communities (Barnes and Bray 1967). We found little evidence that densities of black bears differed based on NPP (Xu et al. 2012). Because we averaged NPP values over the entire sampling period, this covariate may not have been sufficiently sensitive to explain variation in bear density.

Although we found some evidence that densities of black bears increased farther from roads, there was substantial uncertainty around the estimated change. Vegetation communities dominated by Douglas fir, where we estimated the highest densities of bears, are mostly located farther from roads in the Northern Range (Figure 3.2). Thus, associations between bear density and roads may instead reflect the distribution of forested vegetation communities on the landscape. We found limited evidence of differences in density between male and female black bears. In the Northern Range, food resources are abundant and females typically have smaller home ranges than males (Appendix D), as has been documented in many other bear studies (Drewry et al. 2013, Humm et al. 2017, Azad et al. 2019, Welfelt et al. 2019). However, when hunting pressure is low, males and females may occur at similar densities (Loosen et al. 2019).

Our work provides the first population estimate of black bears for the Northern Range, with higher estimated densities compared with other regions of the GYE, such as the Yellowstone Lake area in YNP (63 black bears, 95% CI = 30 – 96, Teisberg et al. 2014) and the Grey River region of Wyoming (6.81 bears/100 km^2, Kindermann and Bjornlie 2019). The Yellowstone Lake region within YNP has a different composition of vegetation communities (Schwartz et al. 2010, 2014), potentially resulting in lower densities of black bears. Vegetation communities in the Grey River region are similar to our study area, but human uses, such as grazing and hunting, are higher (Kindermann and Bjornlie 2019), which can contribute to lower densities of black bears (Loosen et al. 2019). Estimated densities in the Northern Range are comparable to those found in Glacier National Park (GNP) in northern Montana (11.4 bears/100 km^2, Stetz et al. 2014), where black and grizzly bears are also sympatric. In GNP, densities of black bears were highest in low-elevation, forested areas, whereas grizzly bears were more abundant in high-elevation, alpine areas (Kendall et al. 2008, Stetz et al. 2014, 2019). Findings from our work, along with other population studies, suggest that resource availability, human use, and inter-specific competition may influence densities of black bears (Drewry et al. 2013, Stetz et al. 2014, 2019, Teisberg et al. 2014, Kindermann and Bjornlie 2019, Loosen et al. 2019, Welfelt et al. 2019).

Variation in detection

Subgroups of bears differentially encounter and use hair snares and rub objects, based on previous visits by other bears, home-range size, habitat conditions, or habituation to human activity (Kendall et al. 2008, Sawaya et al. 2012). We found higher detection probabilities for females compared with males, consistent with previous work and likely a function of differences in home-range sizes (Appendix D; Gould et al. 2018, Loosen et al. 2019, Welfelt et al. 2019). Detection probabilities also were higher for hair snares compared with rub objects. In contrast, female grizzly bears in Banff National Park, Canada were detected less often at rub objects, likely due to the regular presence of male grizzly bears (Sawaya et al. 2012). Sawaya et al. (2012) detected male grizzly bears more often at rub objects; males have larger home ranges and rub objects were more abundant and widely distributed compared with hair snares. In our study, higher bear densities likely were associated with smaller home ranges, such that bears would have been more likely to encounter a hair snare due the scent attractant, compared with rub objects (Sawaya et al. 2012). However, we detected more unique individuals based on samples from rub objects, despite lower detection probabilities, particularly with the increased sampling effort in 2018 (Kendall et al. 2008, Graves et al. 2011, Sawaya et al. 2012, Stetz et al. 2014, Gould et al. 2018). Declines in detection probabilities late in the sampling period coincided with seasonal changes in food availability, possibly decreasing the effectiveness of the scent lure at hair snares (Costello et al. 2016).

Implications for other species

Grizzly bears outcompete and displace black bears throughout the interior and southern regions of the GYE, where lodgepole pine is the dominant forest type (Barnes and Bray 1967, Schwartz et al. 2010, Frattaroli 2011, Fortin et al. 2013). However, conditions on the Northern Range seem to support higher densities of black bears, potentially because of differences in vegetative communities and more abundant food resources, which could in turn influence the distribution and abundance of grizzly bears (Aune 1994, Stetz et al. 2019).

High densities of black bears also can influence recruitment of ungulate populations (Bastille-Rousseau et al. 2011, Rayl et al. 2018, Svoboda et al. 2019). Barber-Meyer et al. (2008) documented that black and grizzly bears accounted for 69% of all predator-related mortality of elk calves on the Northern Range, with grizzly bears involved in a larger proportion of predation events. Although Barber-Meyer et al. (2008) attempted to estimate the annual number of elk calves killed by bears on the Northern Range, they lacked accurate estimates of bear numbers. Based on our high estimated density, black bears could be preying on more elk calves and having a greater effect on elk recruitment than previously thought. In addition, bears (black or grizzly bear) visited at least 42% of kills made by cougars and displaced cougars from >10% of these kills (Murphy et al. 1998). Our study provides new information that can contribute to a more complete understanding of the diverse animals on the Northern Range and the influence of these black bears on other trophic levels (Ruth et al. 2011, Metz et al. 2012, MacNulty et al. 2016, Tallian et al. 2017, Kohl et al. 2019).

MANAGEMENT IMPLICATIONS

Visitation continues to increase in YNP, creating challenges for national park managers simultaneously tasked with providing safe wildlife viewing opportunities and protecting bears from people. Our estimates of black bear density were greatest in Douglas fir and subalpine fir communities and managers may consider this when evaluating where human-black bear interactions would be most likely to occur. Fine-scale information regarding the distribution of bears also can help managers prioritize where to use limited resources to reduce conflicts between bears and people. For example, road patrols could be focused along sections of roadway that overlap with Douglas fir and subalpine fir forests or more food storage boxes could be provided at backcountry campsites in forested communities.

We also expect the abundance of food resources for bears will change with altered climate conditions (Frank and McNaughton 1992, Frank et al. 2016, Notaro et al. 2019). In the central regions of YNP, abundance of some foods already have changed, such as cutthroat trout and whitebark pine cones, displacing bears from some areas and causing some bears to seek alternative foods (Middleton et al. 2013, Teisberg et al. 2014). Because of the unique conditions of the Northern Range, vegetation communities may be affected by climate change differently and at different time scales, compared with other regions of YNP. If the availability of vegetative resources decrease, bears might explore areas outside of YNP in search of alternative foods, possibly increasing vulnerability to human-caused mortality, such as hunter harvest and management removal. Based on daily movement data and home-range estimates (Appendix D), some adult male bears do not exclusively use YNP lands and several of these animals (2 of 5 collared males between 2014 – 2018) have been harvested by hunters. Future changes in the availability of resources on the Northern Range may affect vital rates of population segments differently, which can translate into population-level impacts (Bunnell and Tait 1980, Miller 1990, Hebblewhite et al. 2002, Malcolm and Van Deelen 2010, Mace and Chilton-Radandt 2011).

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Table 3.1. Summary of samples collected from hair snares to estimate density of American black bears, Northern Range, Yellowstone National Park, Wyoming and Montana, 2017–2018.

Year	**Sampling occasion**	**Dates**	**No. traps**	**No. trap days**	**New individuals detected**		**Total individuals detected**		**% of hair snares with ≥1 hair**	**Samples per trap**		**No. of samples**
					F	**M**	**F**	**M**		**mean**	**SD**	**total**
2017	**1**	28 May–3 June	26	182	5	3	5	3	30.8	2.38	4.29	62
	2	4 June–10 June	25	175	8	6	10	6	44.0	6.36	11.28	159
	3	11 June–17 June	26	182	4	2	7	5	61.5	2.69	3.32	70
	4	18 June–24 June	26	182	14	8	22	15	80.8	10.35	9.69	269
	5	25 June–1 July	25	175	6	3	11	7	52.0	4.88	7.35	127
	6	2 July–8 July	26	182	0	1	6	4	57.7	2.84	3.43	74
	7	9 July–15 July	26	182	0	0	5	3	38.5	1.63	2.99	49
	8	16 July–25 July	28	188	6	3	13	5	46.4	3.69	5.18	96
	Total			**1,448**	**43**	**26**			**51.5%**	**4.35**		**906**
2018	**1**	20 May–26 May	26	182	8	3	8	3	61.5	2.81	4.01	73
	2	May 27–2 June	26	182	7	1	11	1	46.2	3.12	4.61	78
	3	3 June–9 June	26	182	3	1	5	1	46.2	2.65	3.61	69
	4	10 June–16 June	26	182	2	3	5	3	50.0	2.65	4.15	69
	5	17 June–23 June	26	182	4	8	6	9	50.0	2.73	3.85	71
	6	24 June–30 June	26	182	7	3	13	7	65.4	3.96	5.69	111
	7	1 July–July 7	26	182	1	0	4	1	38.5	2.00	5.22	54
	8	July 8–July 17	26	182	4	2	12	3	50.0	4.00	5.88	108
	Total			**1,456**	**36**	**21**			**51.0%**	**2.99**		**633**

Table 3.2. Summary of samples collected from rub objects, by sampling occasion and year, used to estimate density of American black bears, Northern Range, Yellowstone National Park, Wyoming and Montana, 2017–2018.

Year	**Sampling occasion**	**Dates**	**No. rubs**	**No. trap days**	**New individuals detected**		**Total individuals detected**		**% of rub objects with ≥1 hair**	**Samples per rub**		**No. of samples**
					F	**M**	**F**	**M**		**mean**	**SD**	**total**
2017	**1**	28 May–3 June	27	189	1	0	1	0	22.2	1.5	1.97	9
	2	4 June–10 June	27	189	0	4	0	4	40.7	2.33	2.01	28
	3	11 June–17 June	27	189	2	0	3	0	18.5	3.4	2.61	17
	4	18 June–24 June	27	189	1	1	1	1	29.6	3.13	3.48	25
	5	25 June–1 July	27	189	0	2	2	4	44.4	2.33	2.31	28
	6	2 July–8 July	27	189	3	2	4	3	48.1	2.1	2.72	27
	7	9 July–15 July	27	189	0	0	1	1	44.4	0.75	1.86	9
	8	16 July–23 July	27	189	3	0	4	1	66.7	1.83	3.45	33
	9	14 Aug–8 Sept	270	5670	10	2	12	6	97.0	0.98	2.17	276
	Total			**7,182**	**20**	**11**			**45.8%**	**2.04**		**452**
2018	**1**	13 May–26 May	229	3206	10	15	10	15	67.7	1.54	2.11	261
	2	27 May–9 June	228	3192	4	9	6	15	78.1	1.39	1.91	250
	3	10 June–23 June	227	3178	4	9	8	23	82.4	1.34	2.12	263
	4	24 June–7 July	227	3178	6	3	10	20	74.4	1.34	2.22	239
	5	8 July–21 July	227	3178	5	3	14	17	68.7	1.35	1.93	211
	6	22 July–4 Aug	227	3178	9	7	18	15	89.9	0.95	1.62	195
	7	5 Aug–18 Aug	227	3178	8	1	23	9	88.1	1.02	1.42	203
	8	19 Aug–1 Sept	227	3178	0	0	1	6	70.9	0.36	1.01	60
	Total			**25,466**	**46**	**47**			**77.5%**	**1.16**		**1682**

Table 3.3. Model selection results (number of parameters, log likelihood values, AIC_c, and ΔAIC_c) for the top 8 of 132 models focused on variables (sex, method, behavior, time, session, finite mixture) that influence the detection parameters (*g0* and *σ*), while holding density (D) of black bears constant, derived from spatially explicit capture-recapture models, Northern Range, Yellowstone National Park, Wyoming and Montana, 2017–2018. Sex was categorized as a group variable (g). Results for all 132 models are in Appendix B.

Model	***K***	**logLik**	**AIC_c**	**ΔAIC_c**
g0~1 + sex + method + bk + t + session, σ~method + h2 pmix~h2	18	-2,770.50	5,581.09	0.00
g0~1 + sex + bk + t + session, σ~method + h2 pmix~h2	17	-2,772.50	5,582.64	1.55
g0~1 + sex + bk + t, σ~method + h2 pmix~h2	16	-2,773.83	5,582.89	1.80
g0~1 + sex + Method + bk + t, σ~method + h2 pmix~h2	17	-2,773.07	5,583.79	2.70
g0~1 + method + bk + t + session σ ~method + h2 pmix~h2	17	-2,776.01	5,589.67	8.58
g0~1 + method + bk + t, σ~method + h2 pmix~h2	16	-2,779.15	5,593.51	12.42
g0~1 + bk + t + session, σ~method + h2 pmix~h2	16	-2,779.64	5,594.50	13.40
g0~1 + bk + t, σ~method + h2 pmix~h2	15	-2,780.93	5,594.68	13.59

Table 3.4. Beta coefficients, standard errors, and 95% confidence intervals for the detection parameter (*g0*) from a spatially explicit capture-recapture study of black bears based on the top model (Table 3.2), Northern Range, Yellowstone National Park, Wyoming and Montana, 2017–2018. Values are expressed on the log-odds scale and are relative to the baseline detection probability (*g0*) for a female bear, using a hair snare in the first sampling occasion (*t*) in 2017 (*session*). Variation in detection by sampling occasion (*t*) is shown in Figure 3.3.

Detection parameter	**beta**	**SE**	**95% CI**	
g0	-3.31	0.23	-3.75	-2.87
g0.Sex	-0.39	0.12	-0.66	-0.14
g0.Method	-0.39	0.18	-0.76	-0.03
g0.Behavior	1.89	0.13	1.63	2.15
g0.Session	0.45	0.21	0.04	0.85

Table 3.5. Model selection results (number of parameters, log likelihood values, AIC_c, ΔAIC_c, and AIC_c weights) for all candidate models focused on variables influencing (D) density of black bears, based on spatially explicit capture-recapture models, Northern Range, Yellowstone National Park, Wyoming and Montana, 2017–2018. Vegetation community and sex were categorical covariates and distance to road and NPP were centered and scaled continuous covariates. Sampling locations were 4,519 m from roads, on average (range = 5–14,553 m). Detection parameters (g0 and σ) were modeled based on results from step 1 (Table 3.3).

Model	***K***	**logLik**	**AIC_c**	**ΔAIC_c**	**AIC_c wt**
D~vegetation community	21	-2,761.41	5,570.45	0.00	0.56
D~vegetation community + distance to road	22	-2,761.16	5,572.53	2.07	0.20
D~vegetation community + sex	22	-2,761.41	5,573.03	2.57	0.15
D~vegetation community + distance to road + sex	23	-2,761.16	5,575.13	4.68	0.05
D~distance to road	19	-2,767.85	5,578.27	7.82	0.01
D~NPP + distance to road	20	-2,766.59	5,578.28	7.82	0.01
D~NPP	19	-2,768.06	5,578.70	8.24	0.01
D~distance to road + sex	20	-2,767.84	5,580.77	10.32	0.00
D~NPP + distance to road + sex	21	-2,766.58	5,580.80	10.34	0.00
D~1	18	-2,770.50	5,581.09	10.64	0.00
D~ NPP + sex	20	-2,768.05	5,581.19	10.73	0.00

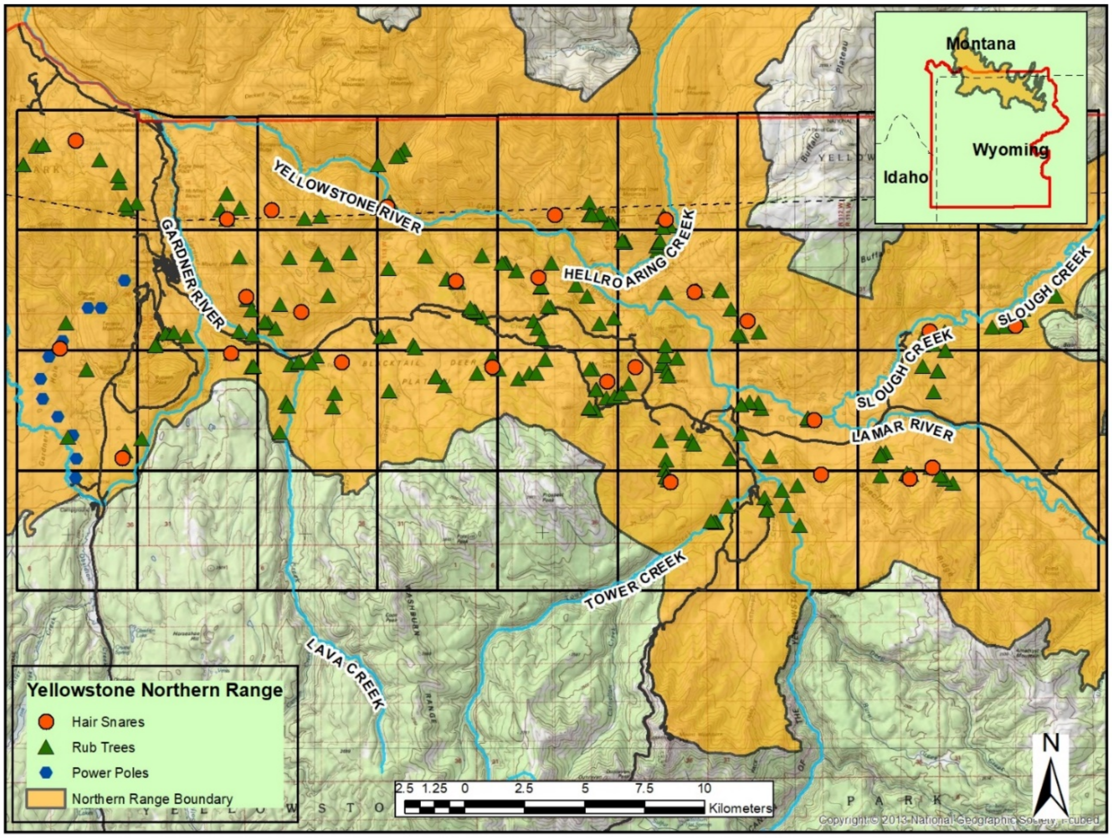

Figure 3.1. Study area within the Northern Range (in yellow) and our 5- x 5-km sampling grid, Yellowstone National Park, Wyoming and Montana, 2017–2018. We collected black bear hair samples using hair snares (red circles), rub trees (green triangles), and other rub objects (e.g., power poles; blue hexagons).

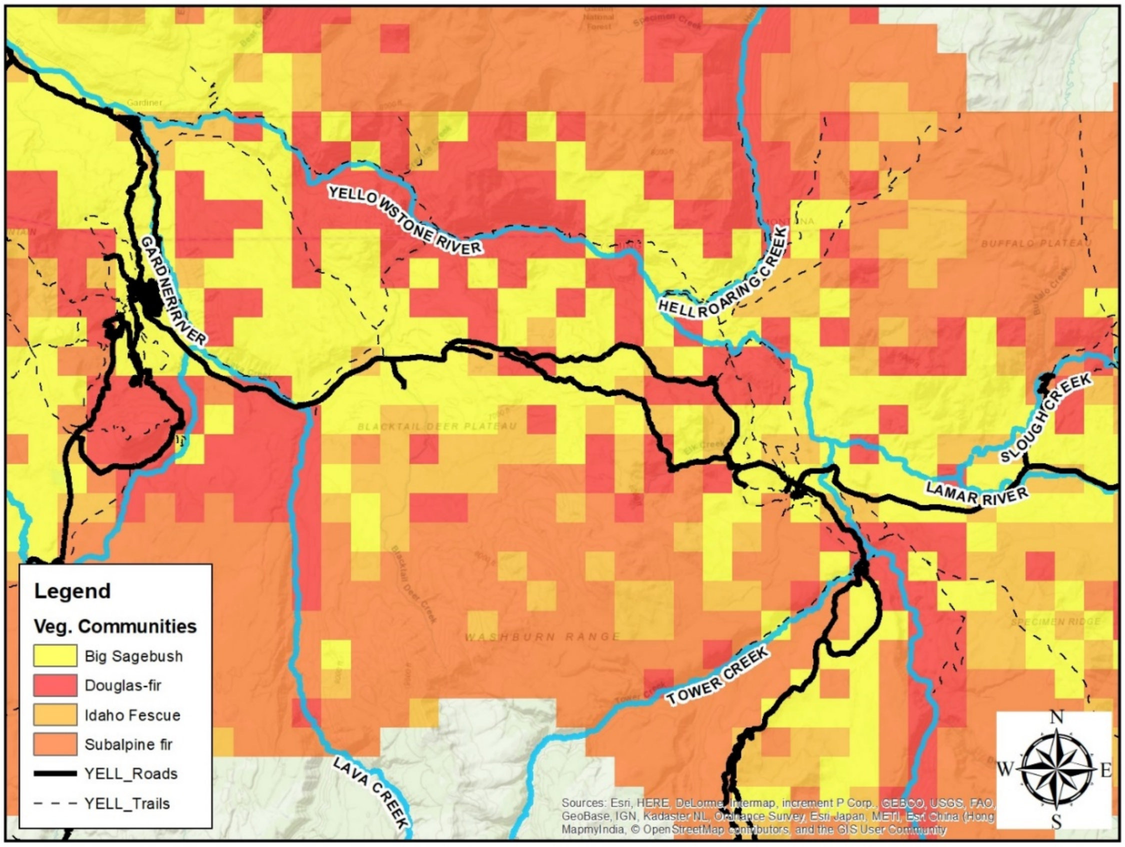

Figure 3.2. Map of vegetation communities on the Northern Range, which we used to estimate variation in the density of black bears Yellowstone National Park, Wyoming and Montana, 2017–2018. Each pixel represents a 1-km^2 area within the density surface mask, created with a 9-km buffer around hair snares and rub objects. Areas outside of our study area are not colored. Roads are represented with solid black lines, trails with dashed lines.

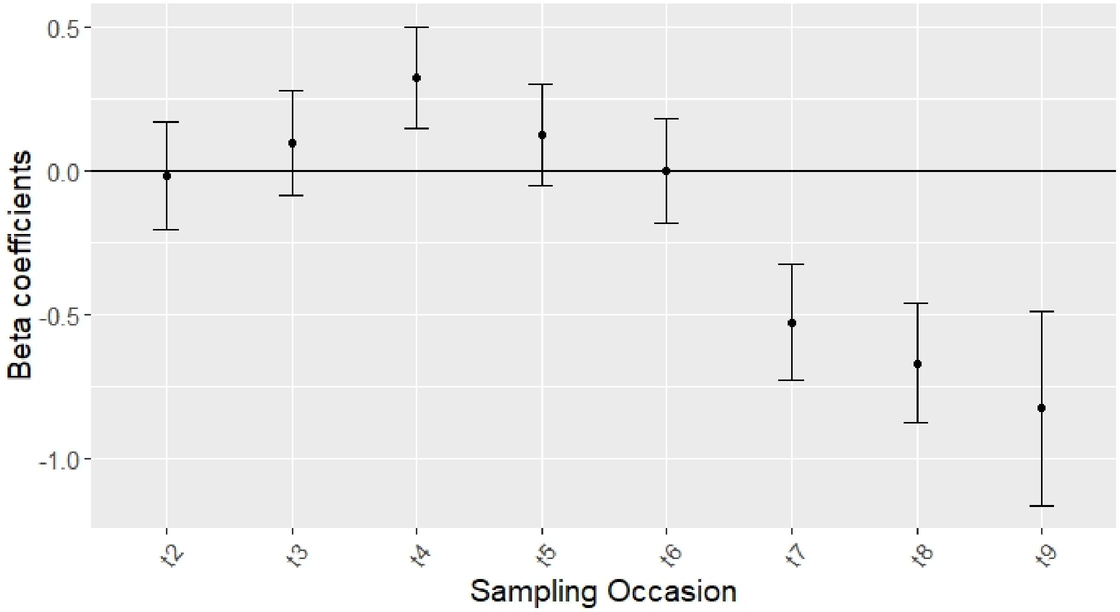

Figure 3.3. Changes in the detection parameter (*g0*) over time (beta coefficients and standard errors for sampling occasions 2 through 9) based on the top detection model (from step 1, Table 3.1) for American black bears on the Northern Range, Yellowstone National Park, Wyoming and Montana, 2017–2018. All estimates are on the log scale and expressed as the difference from the reference level (a female black bear using a hair snare on the first sampling occasion in 2017). Beta estimates and standard errors for other covariates in the detection model are in Table 3.4.

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CHAPTER FOUR

CONCLUSIONS

Animals often alter their movements and foraging strategies to account for temporal and spatial shifts in the availability of food resources across the landscape (McCarty et al. 2002, Armstrong et al. 2016, Deacy et al. 2017, Service et al. 2019). In the early spring, black bears in the Northern Range of YNP prioritized forage quality over quantity when selecting green vegetation (Chapter 2), which may allow them to maintain body mass until food resources become more abundant (Pritchard and Robbins 1990). Later in the spring, black bears shifted foraging to patches of abundant vegetation (Chapter 2), potentially in response to variation in the digestibility of plant species that grow earlier or later in the season (Pritchard and Robbins 1990, Herrero 2018). Black bears spent relatively limited time in non-forested areas where seasonally abundant and protein-rich elk calves are available (Chapter 2). Instead, bears focused on vegetative resources found in forested areas. Accordingly, estimates of black bear density reflected differences among vegetation communities, with the highest density estimates in Douglas fir and subalpine fir communities (Chapter 3).

Black bears are forest-dwelling specialists (Pelton 2003, Herrero 2018), which is reflected by our finding that forested vegetation communities, specifically those dominated by Douglas fir and subalpine fir, appeared to influence movement and densities of black bears on the Northern Range (Chapters 2 and 3). These forest communities provide good cover for black bears to avoid encounters with grizzly bears or humans (Herrero 2018). Forested vegetation communities also supply bears with abundant vegetative resources, such as grasses and sedges earlier in the spring and masting vegetation later in the year, that help bears quickly gain fat in the late summer and fall (Barnes and Bray 1967, Fortin 2011, Frattaroli 2011). Compared to other portions of the GYE, Douglas fir and subalpine fir forests are more dominant on the Northern Range (Despain 1990), which might explain the higher densities of black bears we detected.

High densities of black bears in forest communities could have concomitant effects on other wildlife populations. For example, cougars on the Northern Range also prefer forested areas (Kohl et al. 2019) and black bears may be more likely to encounter cougar kills than previously thought. Black bears may displace cougars from these food resources and affect their kill rates. We found evidence that predation on neonate elk calves by black bears was opportunistic (Chapter 2), but high densities of black bears (Chapter 3) could still influence recruitment rates of elk (Bastille-Rousseau et al. 2011, Rayl et al. 2018, Svoboda et al. 2019). Although we generated a single estimate of density for the entire summer, the availability of food resources changes during this time, which could contribution to variation in density of bears (Stetz et al. 2019). Therefore, generating separate density estimates during and after the elk calving seasons would likely provide important insights.

Our study provides evidence of foraging strategies black bears use in the spring when food resources are limited. Previous research has focused on foraging strategies of bears in response to calorie-rich foods during the late summer and fall, such as whitebark pine seeds (Schwartz et al. 2006, 2014; Gunther et al. 2014). As whitebark pine seeds become less abundant, grizzly bears are less likely to meet their caloric needs with this food source, such that they may spend less time in whitebark pine stands (Bjornlie et al. 2014, Costello et al. 2014). Therefore, black bears may capitalize on this limited food resource, as they consume fewer calories and, unlike most grizzly bears, can obtain cones while still on the tree (Kendall 1983, Robbins et al. 2004, McLellan 2011). By furthering our overall understanding of foraging strategies black bears use in each season, we can better predict how they may respond to future changes in the quantity and quality of seasonal food resources.

As park visitation increases, managers are seeking effective options that simultaneously allow for the safety of both people and bears. Our work can be used to guide management decisions to reduce human-bear conflicts within the Northern Range and other portions of YNP. For example, park personnel may prioritize patrols in areas selected by black bears during spring, such as forested sections near roads, to ensure visitors keep sufficient distance while bears are foraging. Adding more food storage options in backcountry campsites in Douglas fir and subalpine fir forests, where we predicted high densities of bears, could ensure bears are not exposed to unnatural foods.

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APPENDICES

APPENDIX A

IDENTIFYING THE ELK CALVING GROUNDS OF THE NORTHERN RANGE

Identifying the Elk Calving Grounds on the Northern Range

To understand whether black bears actively or opportunistically prey on neonate elk calves, we first needed to identify locations of elk calving grounds on the Northern Range (NR) of Yellowstone National Park (YNP). Barber-Meyer et al. (2008) captured 151 newborn elk calves (≤6 days old) from May 16 to June 20 (2003-2005) to estimate survival and focused their capture efforts in areas of previous survival studies on the Northern Range (Mattson 1997, Singer et al. 1997). We used these capture locations as a starting point for identifying calving grounds, assuming that elk give birth in similar areas each year (Vore and Schmidt 2001). We then compared alternative methods to generate spatial predictions of the calving grounds on the Northern Range.

Researchers have used several different methods to examine patterns in GPS locational data of large ungulates to identify the timing and location of parturition (the action of giving birth) (Vore and Schmidt 2001, D’Angelo et al. 2004, DeMars et al. 2013, Mcgraw et al. 2014, Nicholson et al. 2019). We explored three of these methods (changes in daily movement, track analysis, and behavioral change point analysis [BCPA]) using data from 29 GPS-collared cow elk (hourly locations collected from 2016-2018) that were part of an ongoing, long-term study within YNP by Utah State University. Unlike other parturition studies, we did not always know whether elk in this dataset gave birth to a calf. Initially, we focused on 14 individuals that had pregnancy tests completed upon capture in 2016. Initially, we sought to evaluate multiple methods based on this smaller dataset ($n = 14$ individuals) to assess whether using the calf capture locations from the early 2000s (Barber-Meyer et al. 2008) was appropriate to identify the calving grounds of the Northern Range, so we could later apply the most effective methods to our larger dataset (*n* = 29 individuals).

Changes in daily movements

Vore et al. (2001) found that pregnant elk traveled more than twice their average daily movements (the maximum distance traveled in a day) before giving birth, then reduced movement to less than half their daily average after successfully giving birth for 10 or more days. This change in daily movement distances surrounding parturition also has been observed in other ungulate species (Clutton-Brock and Guinness 1975, D'Angelo et al. 2004, DeMars et al. 2013, Mcgraw et al. 2014). Elk in YNP tend to give birth between May 15 and June 15 (Singer et al. 1997, Barber-Meyer et al. 2008), so we focused our search for changes in daily movements to a window between May 1 and June 30. We used the *adhabitatLT* package in program R to calculate the trajectory (the distance traveled between successive GPS locations) of each elk and examine their daily movements (Calenge 2006, R Development Core Team 2013). We plotted daily movements for each elk over time and looked for changes that might suggest a calving event; 11 of 12 elk with positive pregnancy tests showed changes in their daily movements (Figures A1 and A2). Specifically, these elk showed initial spikes in movement, then declining below their daily mean for ≥7 days, and returning to daily movements closer to their mean. In comparison, the two elk that had negative pregnancy tests did not show major deviations in daily movements (Figure A3). Only one elk with a positive pregnancy test lacked changes in daily movements that would suggest a potential calving event. Therefore, most of the elk in our dataset displayed similar changes in movement surrounding calving events as previously documented in other ungulates.

Track analysis

To link potential calving events to locations on the landscape, we assessed the application of the Tracking Analyst® (TA) tool in ArcGIS, previously used by Nicholson et al. (2019) in their study of moose (*Alces alces*). The TA tool identifies changes in movement on the landscape over time based on trajectory data, which includes locational points with associated changes in speed or distance traveled between successive points. These points (and distances) are categorized and colored in ArcMap according to the distribution of changing movements. Given that we already generated trajectory data using the *adhabitatLT* package, which included both the distance traveled between GPS locations and the location of each daily movement, we exported these data into ArcMap and plotted the daily movements of the elk, creating the same data as the TA tool. We categorized the daily movement data based on the quartile distribution of the trajectory data (0-477, 478-985, 986-1215, and 1216-7000 m for our data on 14 elk). The daily movement points associated with shorter distances were more clustered together, which suggested a calving event (Figure A4).

We then evaluated how well the clustered points (associated with short distances) on the Northern Range overlaid with the locations of calves captured in the early 2000s (Barber-Meyer et al. 2008). We first mapped the locations of captured calves in ArcMap and added a conservative buffer of 900 m around each point, based on the daily mean movement traveled after a birthing event for the 14 GPS-collared elk from 2016 (mean =

985 m). We then overlaid the daily movement points on the buffered capture locations. We observed five of 14 elk with short distance points clustered inside the buffered capture locations and two additional elk that had clustered points within 2 km of the buffered capture locations (Figure A5). The other elk showed clustered points at calving grounds previously identified in the interior of YNP. These observations supported the idea that elk use similar calving areas over time.

Behavioral change point analysis

The daily movement points helped to visualize potential calving grounds, but clusters of points also could result from other behaviors, such as foraging or rest stops. To evaluate whether changes in daily movements related to a calving event, we used the *bcpa* function in R (Gurarie et al. 2009), which identifies changes in behavior by applying an adjustable time series sweep (a set time period to look for a change in behavior) to trajectory data (Gurarie et al. 2009). We used a moving window size (time series sweep) of 200 data points (200 hours), set the sensitivity to change parameter ‘K’ to 0.3 (smaller values of ‘K’ are less sensitive than larger values), and used the persistence of velocity (rate of change in movement between location) to detect changes in behavior, similar to Nicholson et al. (2019). However, we set the ‘clusterwidth’ (the number of clustered behavior points with similar activity) to 168 points, because we observed elk decreasing their daily movements to lower than their daily mean for seven or more days after a potential calving event (7 days * 24 points/day = 168 points). The BCPA identified 20 changes in behavior for the 14 elk. Four of 14 elk (29%) showed a single behavioral change and the date of change aligned well with daily movement plots

(Figures A6 and A7). Ten of 14 elk (71%) showed two or more changes in behavior. To filter out points that might falsely identify calving events, we compared the BCPA to the daily movement plots and found that the two behavior changes detected before May 11, preceding the calving season, likely were misidentified as a calving event, so we eliminated those detections. For elk that still had multiple behavioral changes, we found that changes at later dates better represented calving events based on observations of where BCPA locations clustered. Earlier changes appeared to be shifts in movements, an increase in daily movements, to reach calving areas, especially for migrant elk that travel from outside of YNP into the interior of the park, so we also removed those points from our calving ground map. We also removed points associated with elk that had a negative pregnancy test (*n* = 2 individuals). When we did not have pregnancy tests to confirm our findings, we assumed that elk in the GYE have high pregnancy rates (Middleton et al. 2013, Proffitt et al. 2014) and relied on both the daily movement data and BCPA results to identify false positive results. After filtering the BCPA data, we had 11 behavior change locations, which we then compared to the buffered calf capture layer and daily movement data in ArcMap (Figure A8). Of the 11 behavior change locations, eight occurred within the clusters of short daily movements and the other three were within 5 km of the clustered points for those elk. Of the 11 behavior changes identified, eight were in the Northern Range and five were found within the borders of the buffered capture location layer. This method suggests that the clustering of short daily movements during the spring months likely were associated with a calving event and further supported the use of the captured calf locations (Barber-Meyer et al. 2008) as a representation of the calving grounds on the Northern Range.

Analysis of full dataset

We applied each of the three methods above to the full data set of 29 elk from 2016 – 2018. We identified 49 calving locations for 27 of the 29 elk based on BCPA. After visually inspecting the results, we found only three locations for 2 individuals incorrectly identified a potential calving event based on the visual inspection of BCPA locations compared to the clustering of short distance daily movement points. The misidentified locations were between 10 and 21 km away from potential calving locations, which were validated by the daily movement data. These two individuals were long-distance migrants that started their travels from areas outside of the YNP to the interior of YNP, which could explain the erroneous detections. Fifteen of the 29 elk had >2 calving events 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 use similar calving areas each year. Of the 49 calving locations, 22 were within the Northern Range and an additional 10 were within 6 km of the Northern Range. In addition, we were able to identify 15 calving locations in the interior of YNP (Figure A9); 6 of these locations coincide with areas where grizzly bears were observed hunting elk calves in the spring during the 1980s and 1990s (French and French 1990, Mattson 1997). To create our final calving grounds layer of the Northern Range, we combined the Barber-Meyer et al. (2008) calf capture locations and the newly-identified BCPA locations and added a 900-m buffer to all locations (Figures A10 and A11).

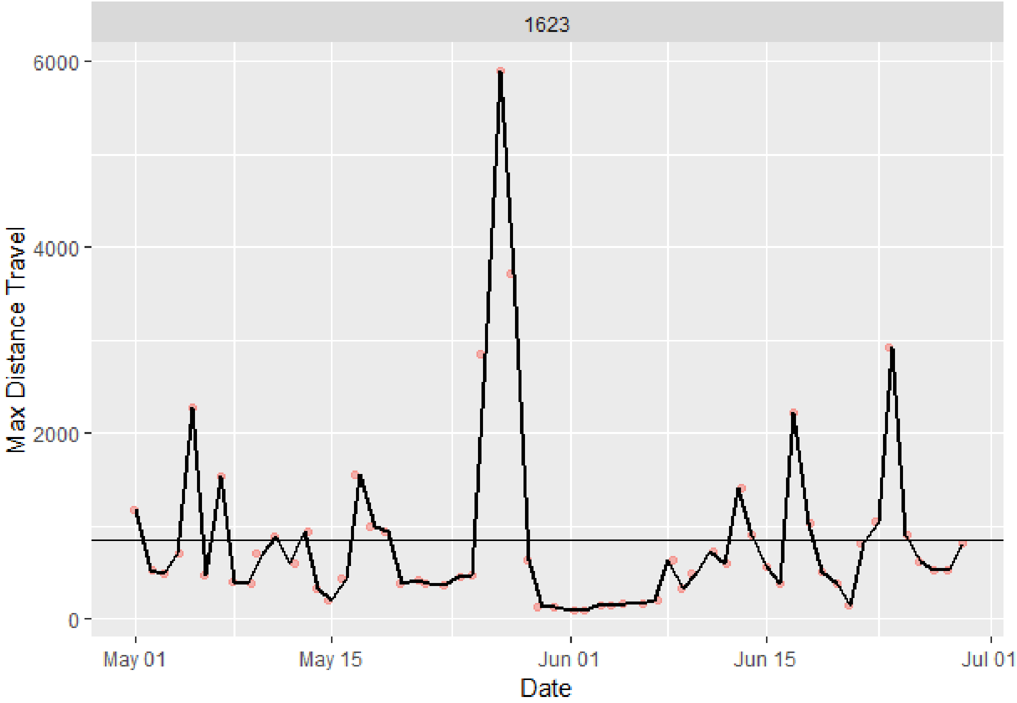


Figure A1. Daily maximum distances traveled by a single elk (#1623) in 2016, demonstrating a change in daily movement distances, which is suggestive of a calving event. The vertical line is the mean daily distance traveled for this individual (852 m/day).

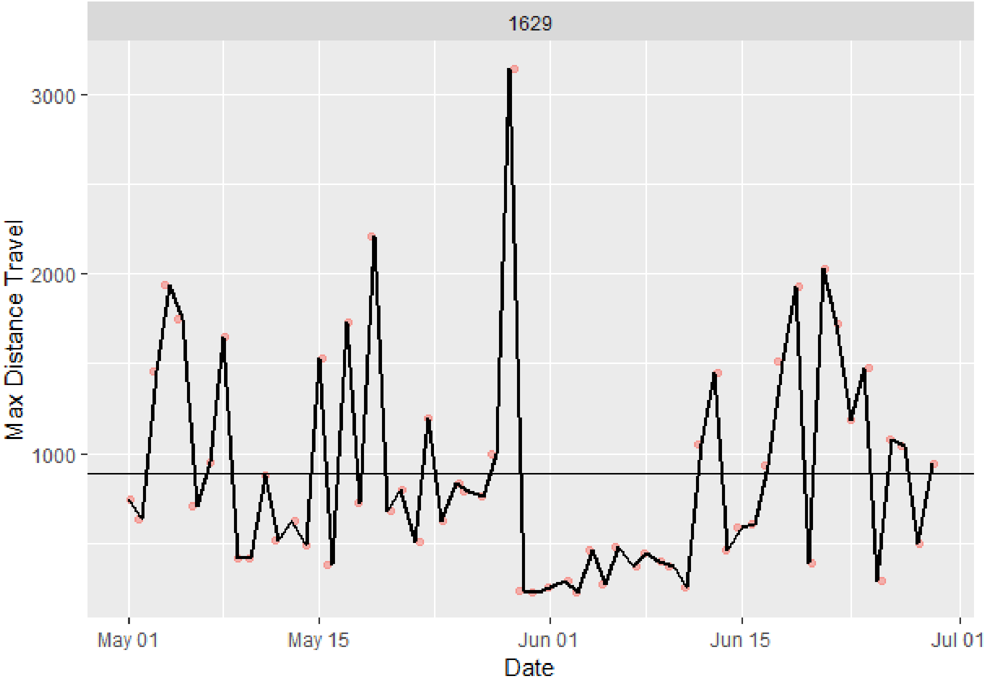


Figure A2. Daily maximum distances traveled by a single elk (#1629) in 2016, demonstrating a change in daily movement distances, which is suggestive of a calving event. The vertical line is the mean daily distance traveled for this elk (891 m/day).

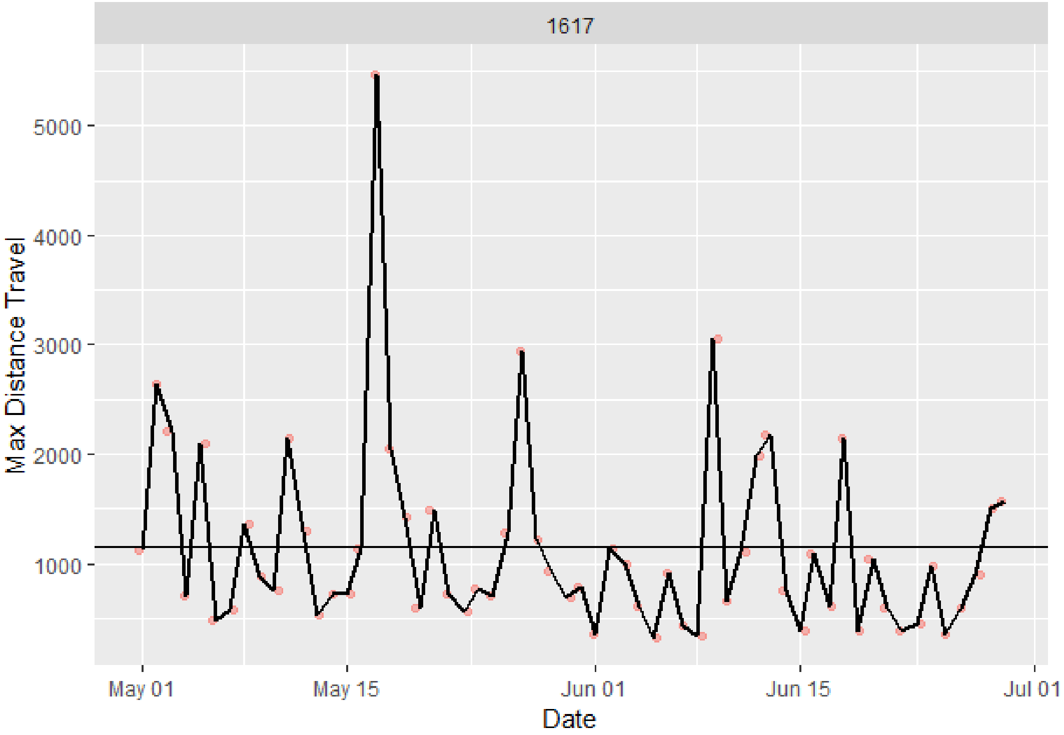


Figure A3. Daily maximum distances traveled by a single elk (#1617) in 2016, demonstrating a lack of a change in daily movement distances, which is suggestive of a calving event. The vertical line is the mean daily distance traveled for this elk (1149 m/day).

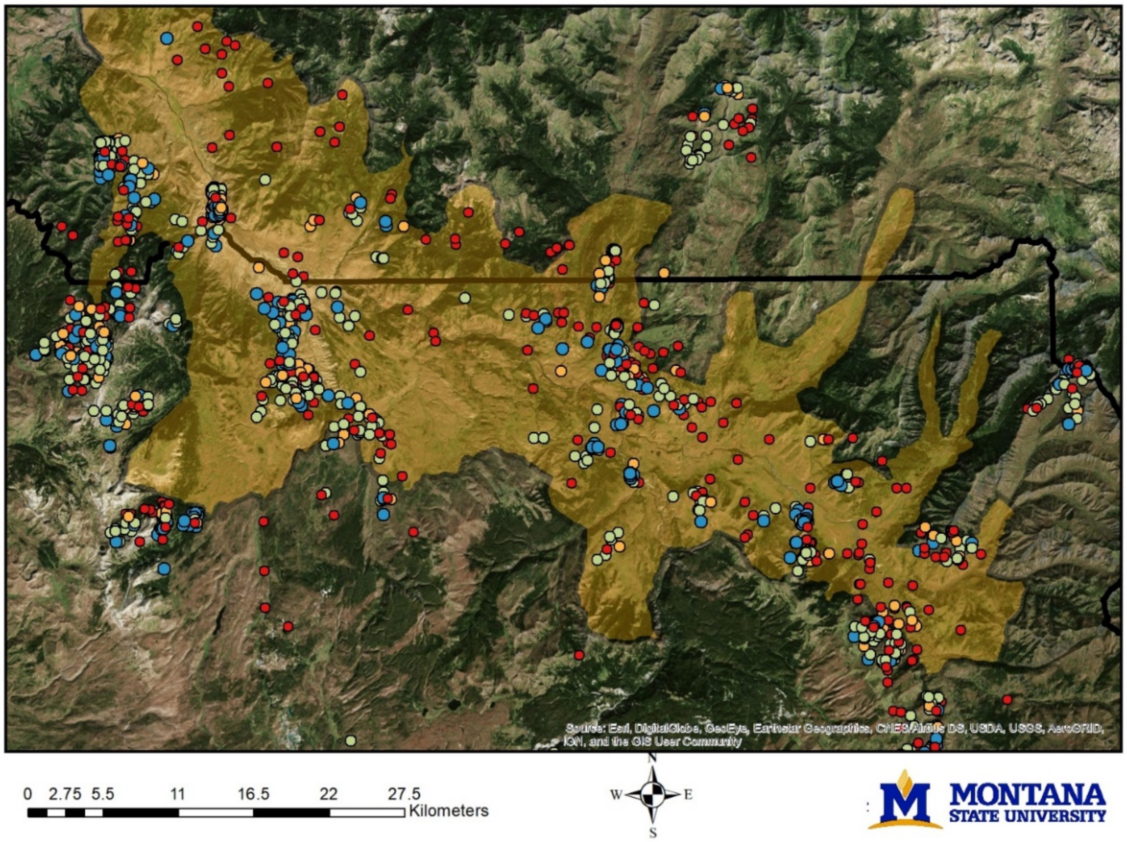


Figure A4. Daily movement points of by GPS-collared elk from 2016, Northern Range (shaded in orange). Daily distances traveled were broken down by quartiles. Blue points indicate the shortest daily distances traveled (i.e., first quartile), green points indicate second shortest distances traveled, orange points represent the second longest distances traveled, whereas red points indicate the longest daily distances.

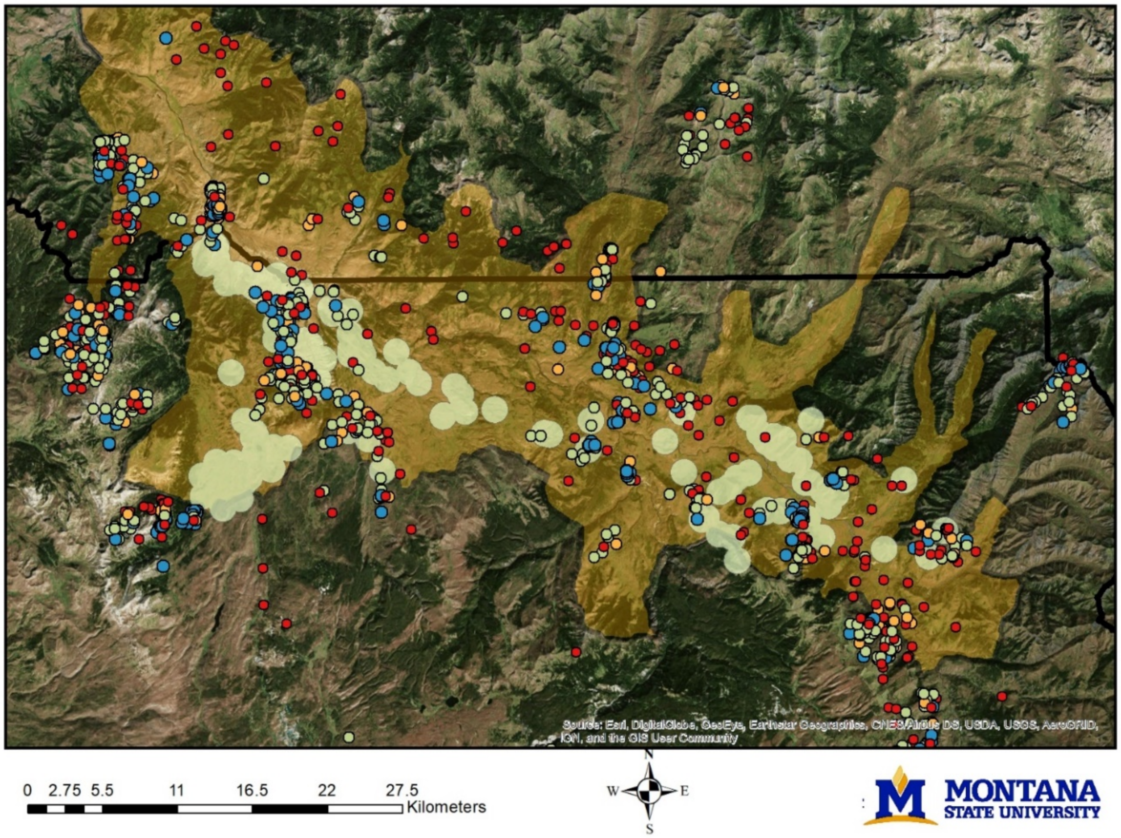


Figure A5. Daily movement points of by GPS-collared elk from 2016 and capture locations (with 900-m buffers in yellow) of elk calves from the early 2000s, Northern Range (shaded in orange). Daily distances traveled were broken down by quartiles. Blue points indicate the shortest daily distances traveled (i.e., first quartile), green points indicate second shortest distances traveled, orange points represent the second longest distances traveled, whereas red points indicate the longest daily distances.

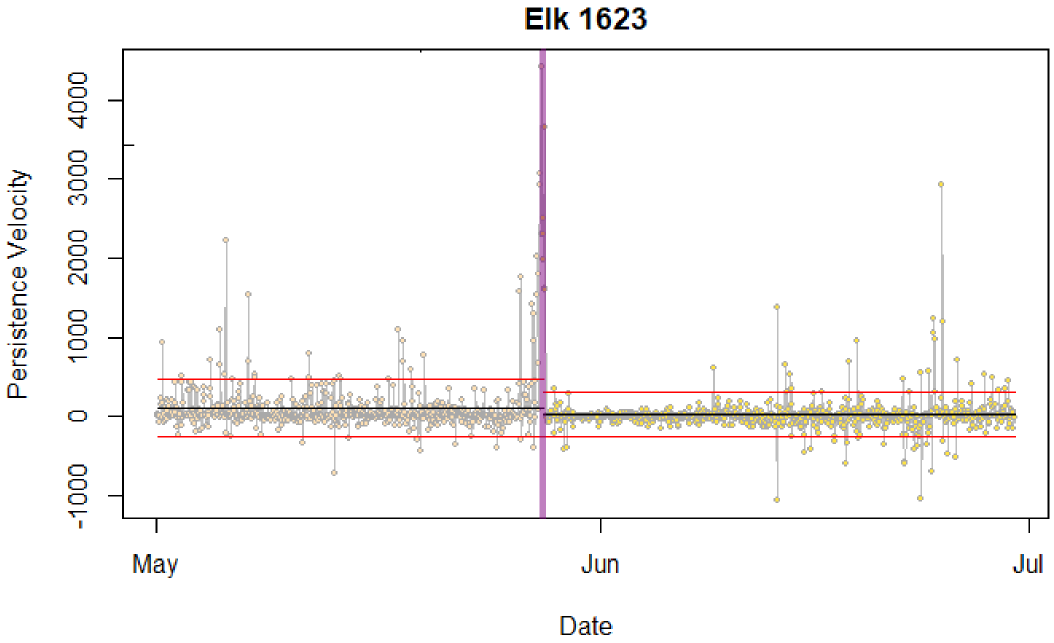


Figure A6. Behavioral point change analysis (BCPA) for elk 1623 in 2016, demonstrating a distinct change in behavior around May 27, 2016, based on the change in frequency of distances traveled before and after a birthing event represented by the purple line. This timing matches well with the change in the daily maximum movement distance (Figure A1) that might indicate a calving event.

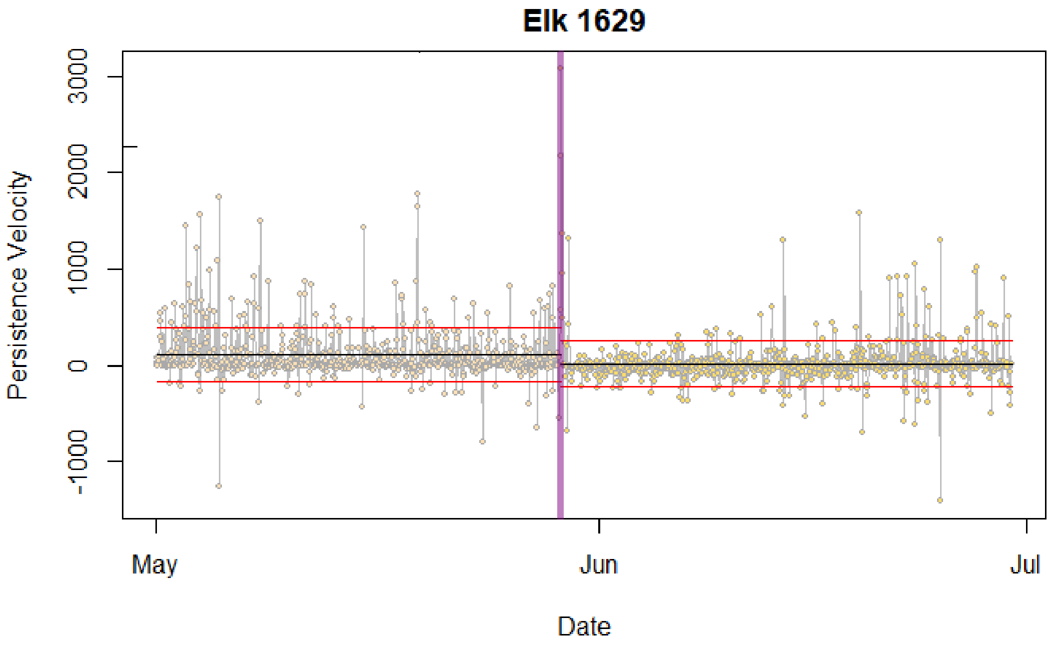


Figure A7. Behavioral point change analysis (BCPA) for elk 1629 in 2016, demonstrating a distinct change in behavior around May 29, 2016, based on the change in frequency of distances traveled before and after a birthing event represented by the purple line.. This timing matches well with the change in the daily maximum movement distance (Figure A2) that might indicate a calving event.

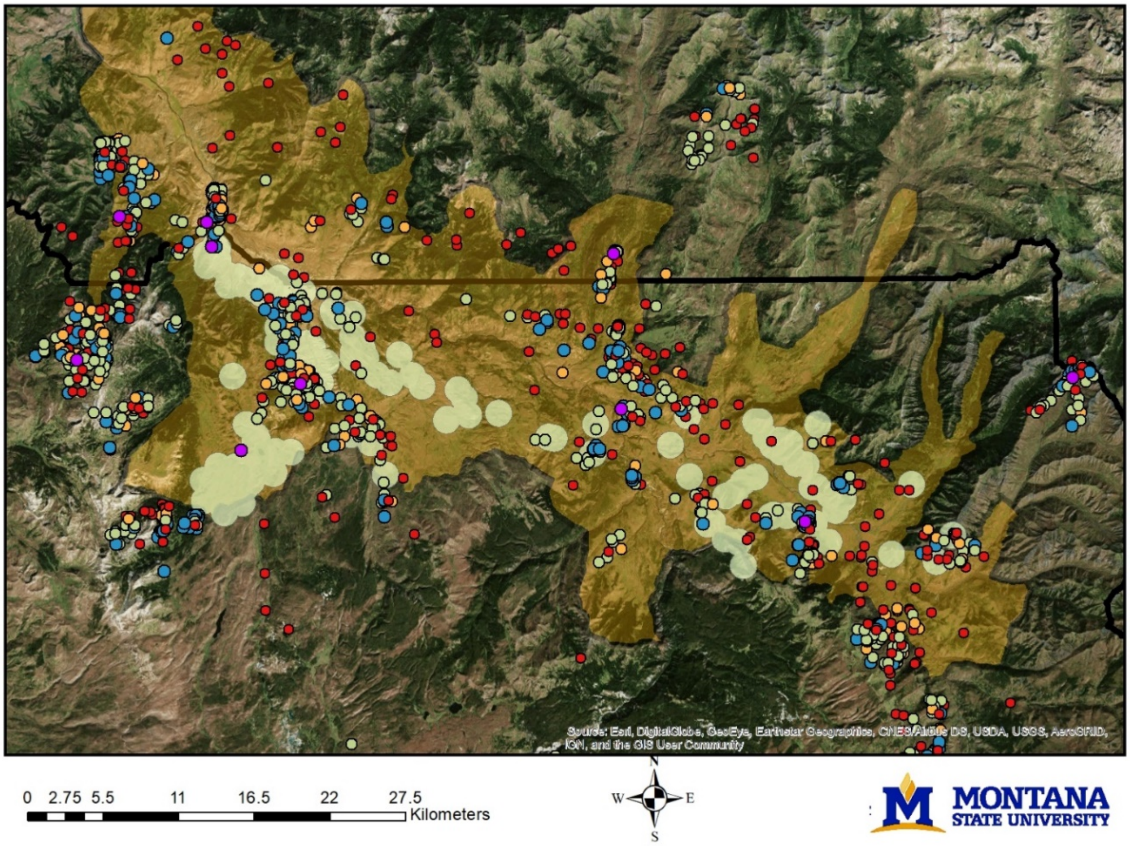
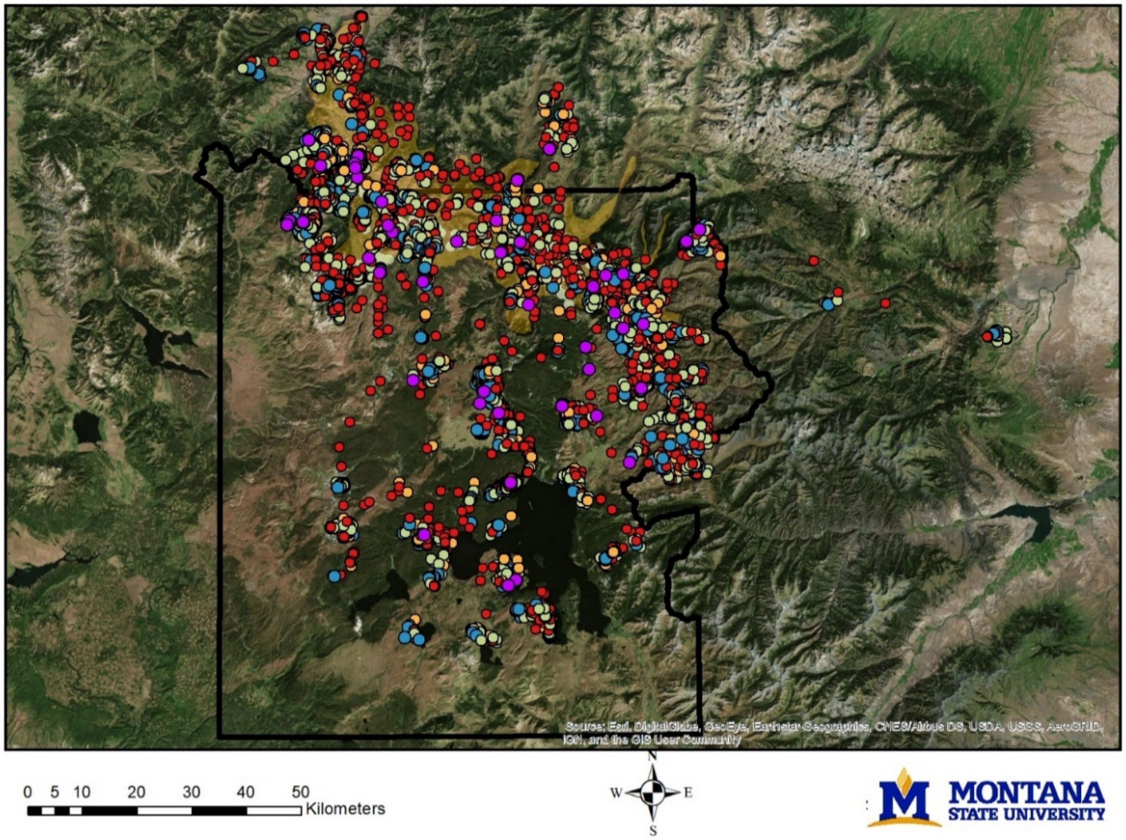
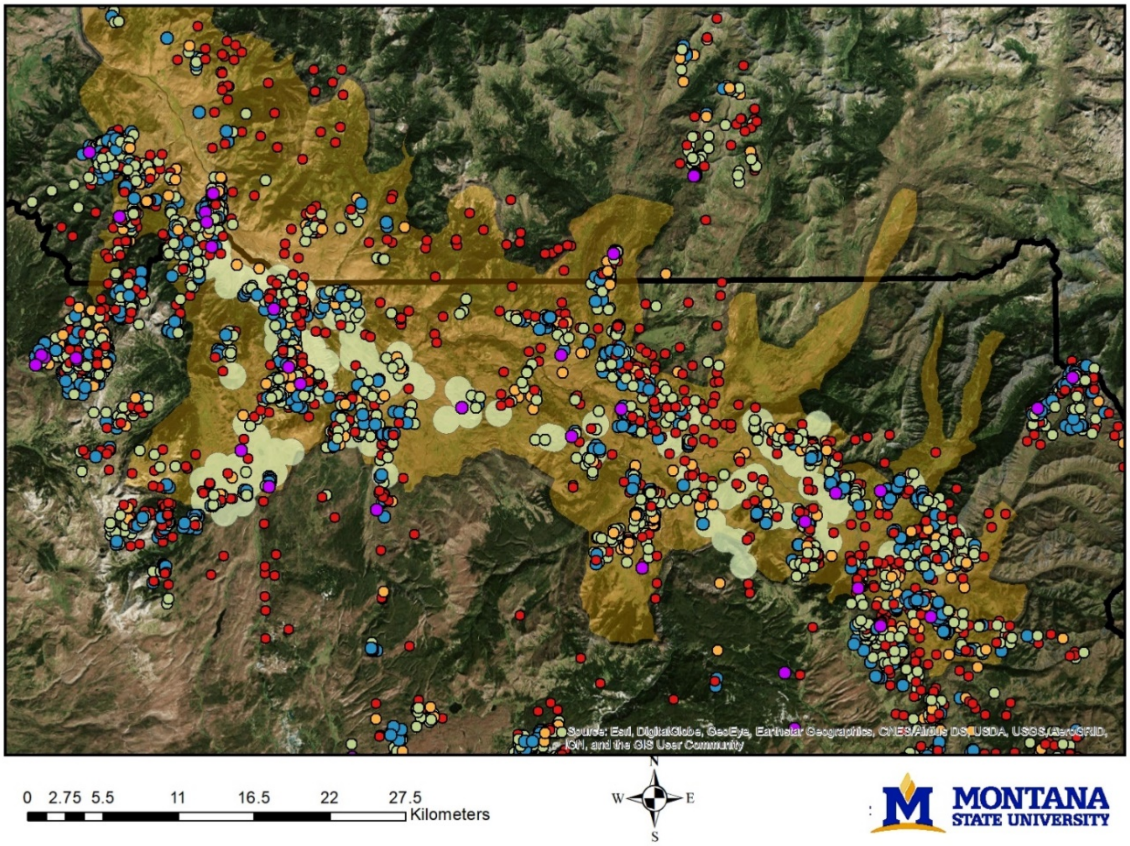


Figure A8. Buffered capture locations for elk calves in the early 2000s (with 900-m buffers in yellow), daily movement points, and behavioral change point analysis (BCPA) points of GPS collared elk, Northern Range (shaded in orange) 2016-2018. Daily distances traveled were broken down by quartiles. Blue points indicate the shortest daily distances traveled (i.e., first quartile), green points indicate second shortest distances traveled, orange points represent the second longest distances traveled, whereas red points indicate the longest daily distances. The BCPA points (purple) were located in close proximity to the shorter daily movement points (blue) and fell within or close to the buffered elk calf capture locations. In some cases, the daily movement points and BCPA suggested calving grounds not previously identified.



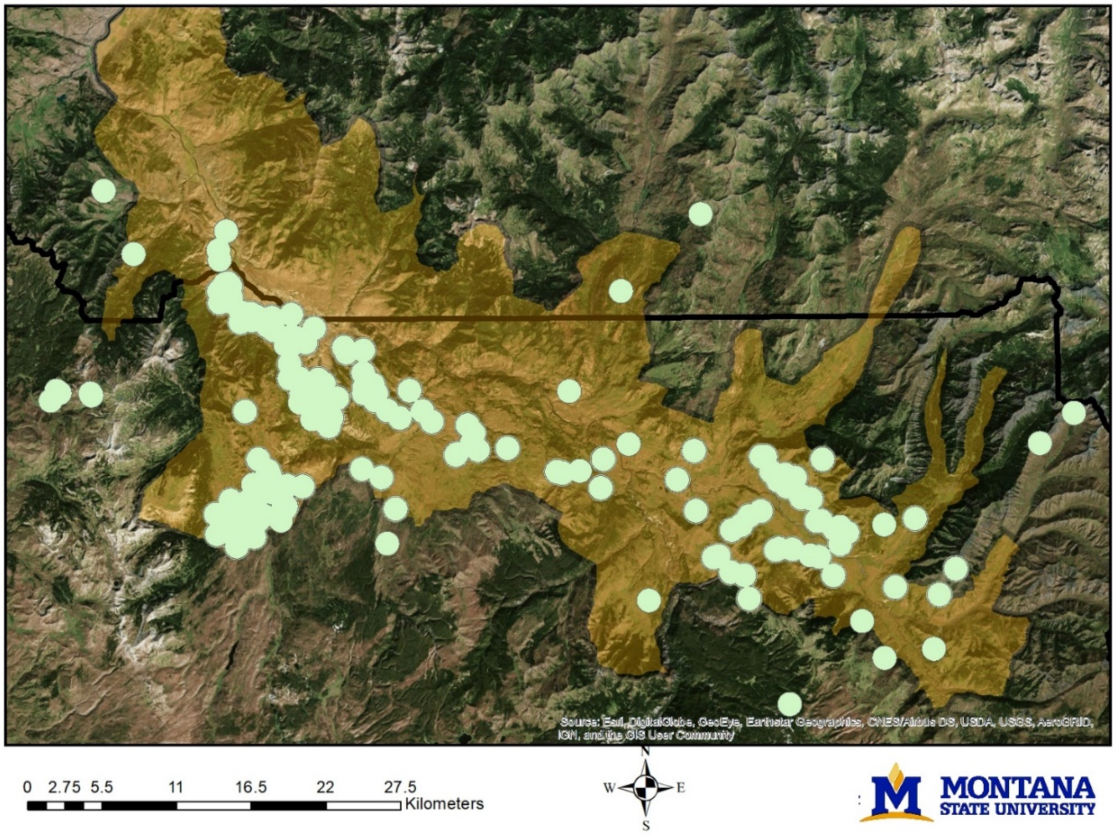
Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure A9. Buffered capture locations for elk calves in the early 2000s (with 900-m buffers in yellow), daily movement points, and behavioral change point analysis (BCPA) points of GPS collared elk, Northern Range (shaded in orange), 2016-2018. Daily distances traveled were broken down by quartiles. Blue points indicate the shortest daily distances traveled (i.e., first quartile), green points indicate second shortest distances traveled, orange points represent the second longest distances traveled, whereas red points indicate the longest daily distances. The BCPA (purple points) were located in close proximity to the shorter daily movement points (blue) and fell within or close to the buffered elk calf capture locations. In some cases, the daily movement points and BCPA located potentially new calving grounds that were not identified previously.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure A10. Buffered capture locations for elk calves in the early 2000s (with 900-m buffers in yellow), daily movement points, and behavioral change point analysis (BCPA) points of GPS collared elk, Northern Range (in orange), 2016-2018. The BCPA (purple) were located in close proximity to the shorter daily movement points (blue) and fell within or close to the buffered elk calf capture locations. In some cases, the daily movement points and BCPA located potentially new calving grounds not previously identified.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure A11. Final calving grounds layer (green circles) built from the elk calf capture locations from the early 2000s and the behavioral change point analysis (BCPA) points of GPS collared elk from 2016-2018 on the Northern Range (shaded in orange).

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APPENDIX B

ASSESSMENT OF GREEN WAVE TRACKING BASED ON VARYING LANDSCAPE FEATURES

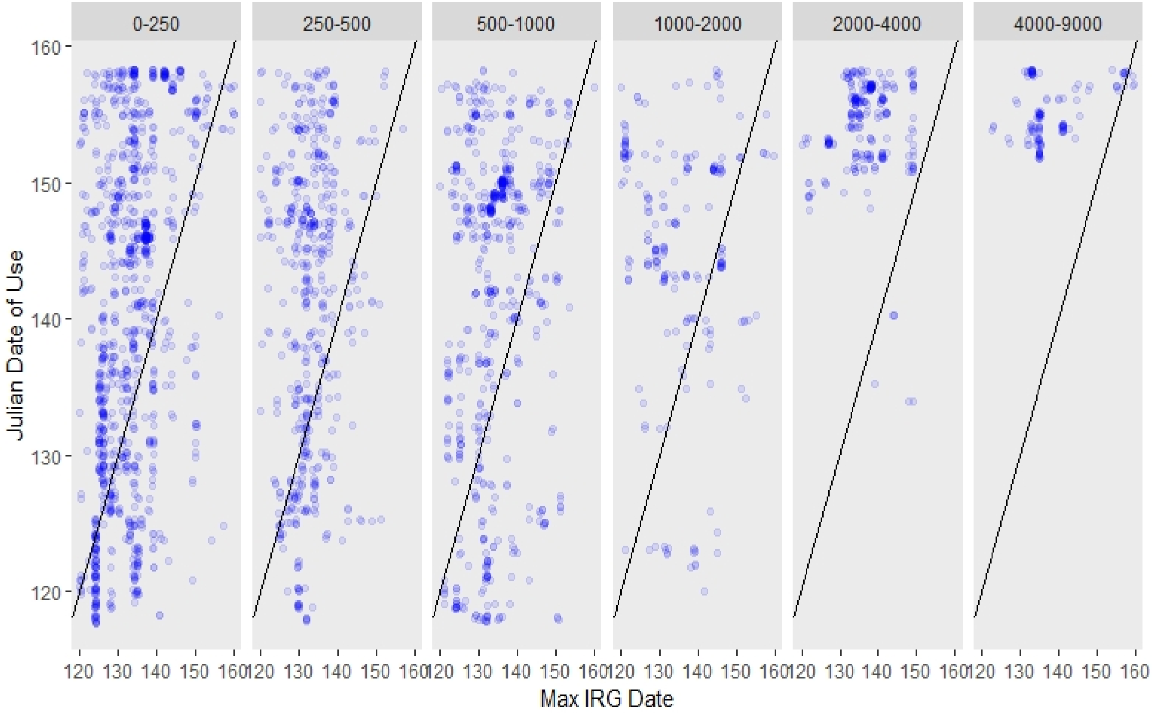

Figure B1. Julian dates when a location on the landscape reached maximum IRG versus Julian dates when that same location was used by a collared bear during the spring green-up period, based on 6 binned distances (m) to roads, Northern Range, Yellowstone National Park, 2017–2018. The black diagonal line represents perfect green wave surfing, if a collared black bear uses a location at maximum IRG. Points falling below the line represent animals following the leading edge of the green wave and points falling above the line represent animals following the trailing edge of the green wave.

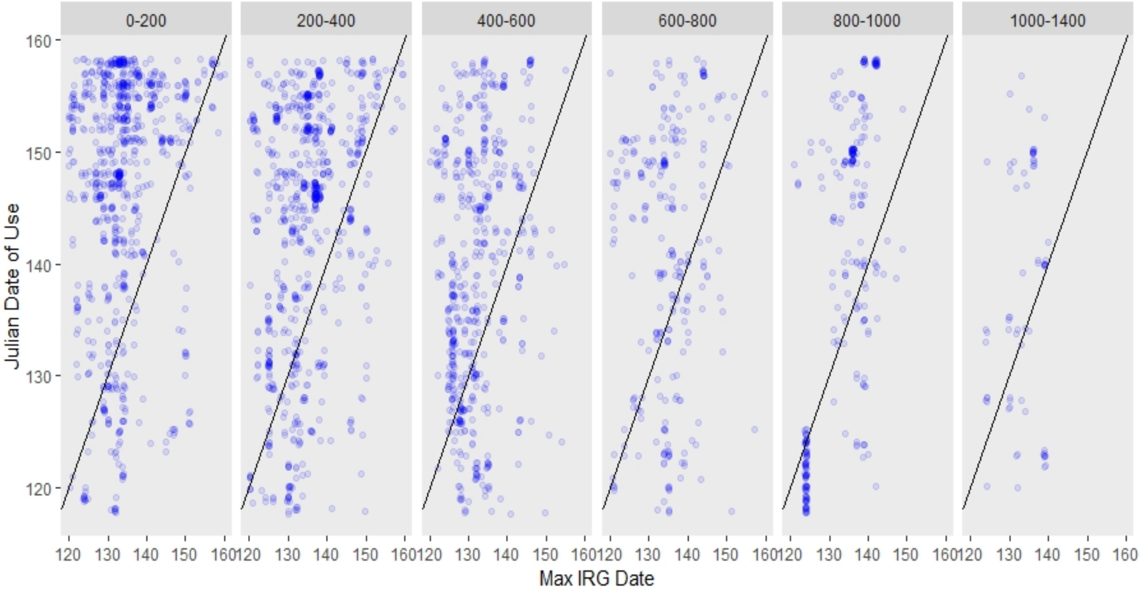

Figure B2. Julian dates when a location on the landscape reached maximum IRG versus Julian dates when that same location was used by a collared bear during the spring green-up period, based on 6 binned distances (m) to streams , Northern Range, Yellowstone National Park, 2017–2018. The black diagonal line represents perfect green wave surfing, if a collared black bear uses a location at maximum IRG. Points falling below the line represent animals following the leading edge of the green wave and points falling above the line represent animals following the trailing edge of the green wave.

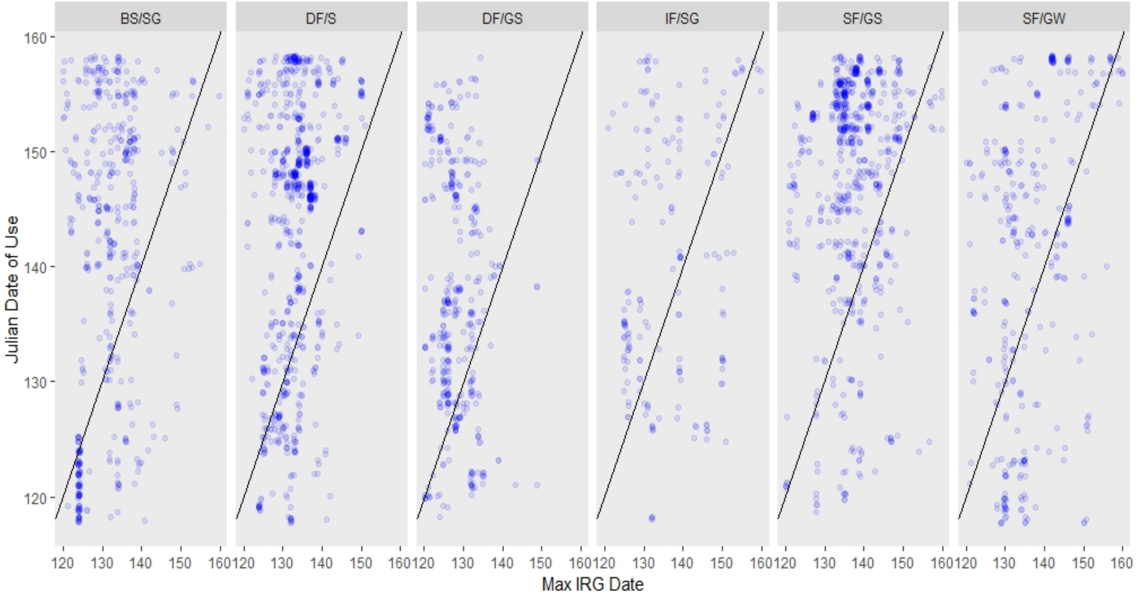

Figure B3. Julian dates when a location on the landscape reached maximum IRG versus Julian dates when that same location was used by a collared bear during the spring green-up period, based on 6 vegetation communities , Northern Range, Yellowstone National Park, 2017–2018. The black diagonal line represents perfect green wave surfing, if a collared black bear uses a location at maximum IRG. Points falling below the line represent animals following the leading edge of the green wave and points falling above the line represent animals following the trailing edge of the green wave. The panel labels are described as follows: Big sagebrush/ sticky geranium = BS/SG, Douglas fir/ snowberry = DF/S, Douglas fir/grass sedge = DF/GS, Idaho fescue/ sticky geranium = IF/SG, Subalpine fir/ grass sedge = SF/GS, Subalpine fir/ grouse whortleberry = SF/GW

APPENDIX C

MODEL SELECTION RESULTS FOR SPATIALLY EXPLICIT CAPTURE-RECAPTURE MODELS FOR BLACK BEARS ON THE NORTHERN RANGE

Table C1. Model selection results (number of parameters, log likelihood values, AICc, and ΔAICc) for all spatially explicit capture-recapture models focused on variables that might influence detection parameters *g0* and *σ* (sigma) while holding density (D) of black bears constant (step 1), Northern Range, Yellowstone National Park, Wyoming and Montana, 2017–2018. Sex was categorized as a group variable (g).

Model	**n par**	**logLik**	**AICc**	**ΔAICc**
g0~1 + g + Method + bk + t + session σ~Method + h2 pmix~h2	18	-2,770.50	5,581.09	0.00
g0~1 + g + bk + t + session σ~Method + h2 pmix~h2	17	-2,772.50	5,582.64	1.55
g0~1 + g + bk + t σ~Method + h2 pmix~h2	16	-2,773.83	5,582.89	1.80
g0~1 + g + Method + bk + t σ~Method + h2 pmix~h2	17	-2,773.07	5,583.79	2.70
g0~1 + Method + bk + t + session σ~Method + h2 pmix~h2	17	-2,776.01	5,589.67	8.58
g0~1 + Method + bk + t σ~Method + h2 pmix~h2	16	-2,779.15	5,593.51	12.42
g0~1 + bk + t + session σ~Method + h2 pmix~h2	16	-2,779.64	5,594.50	13.40
g0~1 + bk + t σ~Method + h2 pmix~h2	15	-2,780.93	5,594.68	13.59
g0~1 + g + bk σ~Method + h2 pmix~h2	8	-2,801.90	5,620.61	39.52
g0~1 + g + Method + bk σ~Method + h2 pmix~h2	9	-2,801.28	5,621.59	40.50
g0~1 + Method + bk σ~Method + h2 pmix~h2	8	-2,807.06	5,630.92	49.83
g0~1 + bk σ~Method + h2 pmix~h2	7	-2,808.61	5,631.85	50.76
g0~1 + Method + bk + t + session σ~h2 pmix~h2	16	-2,803.72	5,642.65	61.56
g0~1 + g + Method + bk + t + session σ~h2 pmix~h2	17	-2,802.58	5,642.81	61.72
g0~1 + Method + bk + t σ~h2 pmix~h2	15	-2,821.10	5,675.01	93.92
g0~1 + g + Method + bk + t σ~h2 pmix~h2	16	-2,820.94	5,677.10	96.01
g0~1 + Method + bk σ~h2 pmix~h2	7	-2,850.40	5,715.43	134.34
g0~1 + g + Method + bk σ~h2 pmix~h2	8	-2,850.34	5,717.49	136.40
g0~1 + g + bk + t σ~Method + g	15	-2,852.57	5,737.97	156.88
g0~1 + g + bk + t + session σ~Method + g	16	-2,853.61	5,742.43	161.34
g0~1 + bk + t σ~Method + g	14	-2,856.26	5,742.97	161.88
g0~1 + bk + t + session σ~Method + g	15	-2,855.81	5,744.44	163.35

Model	**npar**	**logLik**	**AICc**	**ΔAICc**
g0~1 + g + Method + bk + t + session σ~Method + g	17	-2,856.99	5,751.61	170.52
g0~1 + Method + bk + t σ~Method + g	15	-2,861.44	5,755.69	174.60
g0~1 + g + Method + bk + t σ~Method + g	16	-2,860.47	5,756.15	175.06
g0~1 + Method + bk + t + session σ~Method + g	16	-2,863.17	5,761.56	180.47
g0~1 + g + t σ~Method + h2 pmix~h2	15	-2,871.55	5,775.92	194.83
g0~1 + g + Method + bk σ~Method + g	8	-2,879.80	5,776.41	195.31
g0~1 + bk + t σ~Method	13	-2,874.40	5,776.91	195.82
g0~1 + g + t + session σ~Method + h2 pmix~h2	16	-2,871.41	5,778.03	196.94
g0~1 + bk + t + session σ~Method	14	-2,873.86	5,778.17	197.08
g0~1 + Method + bk + t + session σ~Method	15	-2,872.68	5,778.18	197.09
g0~1 + Method + bk + t σ~Method	14	-2,873.88	5,778.21	197.12
g0~1 + g + bk + t σ~Method	14	-2,874.02	5,778.50	197.41
g0~1 + g + Method + bk + t + session σ~Method	16	-2,872.08	5,779.37	198.28
g0~1 + g + Method + bk + t σ~Method	15	-2,873.30	5,779.43	198.33
g0~1 + g + bk + t + session σ~Method	15	-2,873.53	5,779.88	198.79
g0~1 + bk σ~Method + g	6	-2,884.93	5,782.32	201.23
g0~1 + g + Method σ~Method + h2 pmix~h2	8	-2,886.54	5,789.89	208.80
g0~1 + g σ~Method + h2 pmix~h2	7	-2,890.21	5,795.05	213.96
g0~1 + g + session σ~Method + h2 pmix~h2	8	-2,889.86	5,796.54	215.45
g0~1 + t σ~Method + h2 pmix~h2	14	-2,883.11	5,796.68	215.59
g0~1 + t + session σ~Method + h2 pmix~h2	15	-2,883.10	5,799.03	217.94
g0~1 + Method + bk σ~Method + g	7	-2,892.68	5,799.99	218.90
g0~1 + Method σ~Method + h2 pmix~h2	7	-2,894.97	5,804.58	223.49
g0~1 σ~Method + h2 pmix~h2	6	-2,901.42	5,815.31	234.22

Model	npar	logLik	AICc	ΔAICc
g0~1 + bk σ~Method	5	-2,903.26	5,816.85	235.76
g0~1 + session σ~Method + h2 pmix~h2	7	-2,901.41	5,817.45	236.36
g0~1 + g + bk σ~Method	6	-2902.79	5,818.05	236.96
g0~1 + Method + bk σ~Method	6	-2,902.91	5,818.29	237.20
g0~1 + g + Method + bk σ~Method	7	-2,902.26	5,819.14	238.05
g0~1 + Method σ~h2 pmix~h2	6	-2,923.36	5,859.19	278.10
g0~1 + g + Method σ~h2 pmix~h2	7	-2,922.89	5,860.41	279.32
g0~1 + g + Method + bk + t + session σ~1	15	-2,916.77	5,866.37	285.28
g0~1 + Method + bk + t + session σ~1	14	-2,920.40	5,871.25	290.16
g0~1 + g + Method + bk + t σ~g	15	-2,930.15	5,893.12	312.03
g0~1 + g + bk + t + session σ~h2 pmix~h2	16	-2,930.88	5,896.98	315.89
g0~1 + g + Method + bk + t σ~1	14	-2,933.74	5,897.94	316.84
g0~1 + bk + t + session σ~h2 pmix~h2	15	-2,933.62	5,900.07	318.98
g0~1 + Method + bk + t σ~1	13	-2,939.33	5,906.79	325.70
g0~1 + g + bk + t σ~h2 pmix~h2	15	-2,937.48	5,907.79	326.70
g0~1 + bk + t σ~h2 pmix~h2	14	-2,939.02	5,908.50	327.41
g0~1 + g + Method + bk + t + session σ~g	16	-2,938.27	5,911.76	330.67
g0~1 + g + Method + bk σ~g	7	-2,959.26	5,933.15	352.06
g0~1 + Method + bk + t σ~g	14	-2,954.07	5,938.59	357.50
g0~1 + Method + bk σ~g	6	-2,963.42	5,939.31	358.22
g0~1 + g + Method + bk σ~1	6	-2,965.49	5,943.44	362.35
g0~1 + g + bk σ~h2 pmix~h2	7	-2,966.70	5,948.03	366.94
g0~1 + bk σ~h2 pmix~h2	6	-2,967.91	5,948.29	367.20
g0~1 + Method + bk σ~1	5	-2,971.70	5,953.74	372.64
g0~1 + g + t σ~Method + g	14	-3,002.66	6,035.77	454.68
g0~1 + g + t + session σ~Method + g	15	-3,005.95	6,044.72	463.63
g0~1 + t σ~Method + g	13	-3,011.20	6,050.51	469.42

Model	**npar**	**logLik**	**AICc**	**ΔAICc**
g0~1 + g σ~Method + g	6	-3,025.46	6,063.40	482.31
g0~1 + t + session σ~Method + g	14	-3,016.63	6,063.72	482.63
g0~1 + g + Method σ~Method + g	7	-3,025.15	6,064.92	483.83
g0~1 + g + session σ~Method + g	7	-3,025.50	6,065.62	484.53
g0~1 + g σ~Method + g	6	-3,025.46	6,063.40	482.31
g0~1 + t + session σ~Method + g	14	-3,016.63	6,063.72	482.63
g0~1 + g + Method σ~Method + g	7	-3,025.15	6,064.92	483.83
g0~1 + g + session σ~Method + g	7	-3,025.50	6,065.62	484.53
g0~1 + Method + bk + t + session σ~g	15	-3,027.18	6,087.18	506.09
g0~1 + t σ~Method	12	-3,039.36	6,104.53	523.44
g0~1 + g + t σ~Method	13	-3,038.76	6,105.63	524.54
g0~1 + t + session σ~Method	13	-3,039.37	6,106.85	525.76
g0~1 + g + t + session σ~Method	14	-3,038.77	6,107.99	526.90
g0~1 + g + Method σ~Method	6	-3,053.34	6,119.16	538.07
g0~1 + Method σ~Method	5	-3,054.56	6,119.45	538.36
g0~1 σ~Method	4	-3,057.70	6,123.62	542.53
g0~1 + g σ~Method	5	-3,057.06	6,124.45	543.36
g0~1 + session σ~Method	5	-3,057.66	6,125.66	544.57
g0~1 + g + session σ~Method	6	-3,057.01	6,126.48	545.39
g0~1 + g + bk + t + session σ~1	14	-3,048.17	6,126.79	545.70
g0~1 + bk + t + session σ~1	13	-3,049.56	6,127.25	546.15
g0~1 + g + bk + t σ~1	13	-3,055.46	6,139.04	557.95
g0~1 + bk + t σ~1	12	-3,057.49	6,140.79	559.70
g0~1 + g + t + session σ~h2 pmix~h2	15	-3,064.27	6,161.36	580.26
g0~1 + t + session σ~h2 pmix~h2	14	-3,066.61	6,163.67	582.58
g0~1 + bk + t + session σ~g	14	-3,068.31	6,167.09	586.00
g0~1 + g + t σ~h2 pmix~h2	14	-3,070.18	6,170.82	589.73

Model	**npar**	**logLik**	**AICc**	**ΔAICc**
g0~1 + t σ~h2 pmix~h2	13	-3,072.05	6,172.23	591.13
g0~1 + g + session σ~h2 pmix~h2	7	-3,080.12	6,174.88	593.79
g0~1 + g + bk σ~1	5	-3,085.99	6,182.32	601.23
g0~1 + session σ~h2 pmix~h2	6	-3,085.51	6,183.49	602.40
g0~1 + bk σ~1	4	-3,088.58	6,185.38	604.29
g0~1 + g + bk σ~g	6	-3,086.70	6,185.87	604.78
g0~1 + g + Method σ~g	6	-3,088.06	6,188.58	607.49
g0~1 + g σ~h2 pmix~h2	6	-3,089.96	6,192.39	611.30
g0~1 σ~h2 pmix~h2	5	-3,091.63	6,193.59	612.50
g0~1 + bk + t σ~g	13	-3,086.33	6,200.78	619.69
g0~1 + g + Method σ~1	5	-3,102.13	6,214.59	633.49
g0~1 + Method σ~1	4	-3,108.64	6,225.49	644.40
g0~1 + g + bk + t + session σ~g	15	-3,105.94	6,244.71	663.61
g0~1 + Method σ~g	5	-3,117.33	6,245.00	663.91
g0~1 + bk σ~g	5	-3,125.11	6,260.54	679.45
g0~1 + g + bk + t σ~g	14	-3,124.99	6,280.43	699.34
g0~1 + g + t + session σ~g	14	-3,236.90	6,504.26	923.17
g0~1 + t + session σ~g	13	-3,242.67	6,513.45	932.36
g0~1 + t σ~g	12	-3,250.63	6,527.06	945.97
g0~1 + session σ~g	5	-3,261.79	6,533.91	952.82
g0~1 + g + t + session σ~1	13	-3,256.71	6,541.54	960.45
g0~1 + t + session σ~1	12	-3,259.43	6,544.66	963.56
g0~1 + g + t σ~g	13	-3,259.16	6,546.43	965.34
g0~1 + g + session σ~g	6	-3,267.68	6,547.84	966.75
g0~1 + g + t σ~1	12	-3,264.80	6,555.40	974.31
g0~1 + g + session σ~1	5	-3,273.48	6,557.30	976.21
g0~1 + g σ~g	5	-3,275.61	6,561.56	980.47

Model	**npar**	**logLik**	**AICc**	**ΔAICc**
g0~1 + session σ~1	4	-3,277.78	6,563.79	982.70
g0~1 + t σ~1	11	-3,270.96	6,565.45	984.36
g0~1 σ~g	4	-3,283.68	6,575.58	994.49
g0~1 + g σ~1	4	-3,285.14	6,578.49	997.40
g0~1 σ~1	3	-3,292.06	6,590.26	1,009.17

APPENDIX D

HOME RANGE ESTIMATES FOR BLACK BEARS CAPTURED ON YELLOWSTONE'S NORTHERN RANGE FROM 2014 - 2018

Home range estimates for black bears on Yellowstone National Park's Northern Range

Live Capture and Collaring

We captured 10 black bears (2 males, 8 females) 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 jab poles, and handled following approved methods (MSU IACUC protocol 2017-24). We equipped 6 black bears (2 males, 6 females) with Iridium GPS collars and 2 female bears with VHF collars (Telonics, Inc., Mesa, AZ). The VHF active signal was 60 beats per minute (bpm) and the mortality signal was 30 bpm if the collar stopped moving for >8 hours. During April 1–November 30, GPS collars were programmed to record 1 location/hour in 2017 and 1 location/30 min in 2018. Locations were uploaded to the Iridium satellite system every 8 hours. During hibernation (December 1–March 31), we saved battery life by recording only 1 GPS location/month and reducing the VHF signal to 12 bpm. The GPS collars were fitted with a CR-5 collar release system (Telonics, Inc., Mesa, AZ) programmed to release on 15 October 2018, so collars could be retrieved from the field. We used cotton spacers as a secondary drop-off mechanism, which would deteriorate over time causing the collar to drop from the bear if the drop off mechanism failed (Hellgren et al. 1988). VHF collared bears were located, if possible, weekly from the ground and additional locations were obtained from aerial flights on occasion.

In addition, we used the GPS locations collected from 3 male black bears fitted with GPS camera collars as part of a pilot study by NPS from 2014-2016. The camera collars were programmed to record GPS locations every 20 minutes from 0600-2200, and every hour from 2200 to 0600. The camera collars were fitted with remote drop-off mechanism programed to release after 9 weeks, so collars could be retrieved from the field. We again used cotton spacers as a secondary drop-off mechanism.

Home Range Estimates

We generated three different home range estimates for 13 black bears (5 males, 8 females) collared between 2014-2018 (Table D1): Minimum Convex Polygons (MCP), Kernel Density Estimates (KDE), and Local Convex Hull (LoCoH), similar to other studies of black bears in the Greater Yellowstone Area (Borger et al. 2006, Getz et al. 2007). Home ranges were estimated using the *adhabitatHR* package (Calenge 2006) in program R (R Development Core Team 2013) for four different intervals: annual (April 1- October 20), spring (April 1 - June 30), summer (July 1 – August 20), and fall (August 20 – October 20). To be considered for each seasonal interval, bears had to be tracked for at least half of the interval (Tables D2-5).

We calculated 95% MCP and 95% KDE as coarser estimates of home ranges and LoCoH as a finer-scale estimate. Specifically, we used the adaptive or aLoCoH method, which estimates the home range for an animal based on the maximum average distance between '*a*' number of points (Getz et al. 2007). We initially set *a* = 2 and subsequently increased this value in increments of 0.5, until we generated the smallest estimated home range for each individual that contained few to no polygon holes, which we inspected visually in ArcMap (ArcGIS 2011, Bjornlie et al. 2014).

Table D1. Bears that were collared and tracked on the Northern Range, Yellowstone National Park, Wyoming and Montana, 2014–2018.

Bear ID	Sex	Age	Years tracked	Collar type
22517	M	8+	2014	GPS Camera
22519	M	3+	2015	GPS Camera
22521	M	8+	2016	GPS Camera
22522	M	2	2017-2018	GPS
22523	F	2	2017-2018	GPS
22524	F	9	2017-2018	GPS
22526	F	6	2018	GPS
22527	F	14	2018	VHF
22528	F	4	2018	VHF
22529	F	4+	2018	GPS
22530	M	15+	2018	GPS
22531	F	2+	2018	GPS
22532	F	4+	2018	GPS

Table D2. Annual home range estimates (km^2) based on Minimum Convex Polygons (MCP), Kernel Density Estimates (KDE), Local Convex Hull (aLoCoH) methods for 2 male (1 tracked for 2 years) and 8 female black bears collared on the Northern Range, Yellowstone National Park, Wyoming and Montana, 2014-2018. Females were classified as: did not have cubs (No), had cubs of the year (COY), or had yearling cubs (Yrl).

Bear ID	**Sex**	**Age class**	**Cubs**	**Collar type**	**Year**	**Days tracked**	**Number of locations**	**MCP**	**KDE**	**aLoCoH**
22522	M	Sub-Adult	No	GPS	2017	158	2209	51.65	51.93	21.99
22522	M	Sub-Adult	No	GPS	2018	175	2476	480.40	440.11	128.04
22530	M	Adult	No	GPS	2018	130	1837	1331.19	2214.24	403.61
					Average	**154.33**	**2174**	**621.08**	**902.09**	**184.55**
					(SE)			**(376)**	**(665.6)**	**(113.7)**

Bear ID	**Sex**	**Age class**	**Cubs**	**Collar type**	**Year**	**Days tracked**	**Number of locations**	**MCP**	**KDE**	**aLoCoH**
22523	F	Sub-Adult	No	GPS	2017	159	2314	158.45	121.89	55.50
22523	F	Sub-Adult	No	GPS	2018	183	2580	104.64	86.85	27.01
22531	F	Sub-Adult	No	GPS	2018	129	5958	105.56	85.67	34.25
22524	F	Adult	No	GPS	2017	132	1713	213.08	203.97	68.02
22524	F	Adult	COY	GPS	2018	188	2545	166.87	196.30	31.78
22526	F	Adult	Yrl	GPS	2018	183	2489	93.11	87.73	29.66
22529	F	Adult	No	GPS	2018	142	6502	96.25	89.82	36.99
22532	F	Adult	No	GPS	2018	106	4921	235.35	274.25	63.83
22527	F	Adult	Yrl	VHF	2018	193	13	5.65	38.27	10.73
22528	F	Adult	No	VHF	2018	193	12	35.68	334.60	47.14
					Average	**160.80**	**2904.70**	**121.46**	**151.94**	**40.49**
					(SE)			**(22.9)**	**(30.4)**	**(5.7)**

Table D3. Spring home range estimates (km^2) based on Minimum Convex Polygons (MCP), Kernel Density Estimates (KDE), Local Convex Hull (aLoCoH) methods for 4 male (1 tracked for 2 years) and 5 female black bears (2 tracked for 2 years) collared on the Northern Range, Yellowstone National Park, Wyoming and Montana, 2014-2018. Females were classified as: did not have cubs (No), had cubs of the year (COY), or had yearling cubs (Yrl).

Bear ID	**Sex**	**Age class**	**Cubs**	**Collar type**	**Year**	**Days tracked**	**Number of locations**	**MCP**	**KDE**	**aLoCoH**
22519	M	Sub-adult	No	GPS Camera	2015	27	1539	696.98	1214.85	128.25
22522	M	Sub-adult	No	GPS	2017	39	583	26.22	50.11	14.54
22522	M	Sub-adult	No	GPS	2018	71	958	308.11	493.17	131.33
22521	M	Adult	No	GPS Camera	2016	20	2257	99.25	149.35	39.52
22530	M	Adult	No	GPS	2018	27	370	90.76	116.97	44.79
					Average (SE)	**45.67**	**862.50**	**244.26 (122.7)**	**404.89 (216.6)**	**71.68 (24.3)**

Bear ID	**Sex**	**Age class**	**Cubs**	**Collar type**	**Year**	**Days tracked**	**Number of locations**	**MCP**	**KDE**	**aLoCoH**
22523	F	Sub-adult	No	GPS	2017	37	549	22.45	28.81	15.92
22523	F	Sub-adult	No	GPS	2018	77	1089	14.13	17.71	10.72
22531	F	Sub-adult	No	GPS	2018	22	1055	8.98	10.31	5.21
22524	F	Adult	No	GPS	2017	28	421	34.04	40.56	23.58
22524	F	Adult	COY	GPS	2018	84	1058	16.10	27.57	9.07
22526	F	Adult	Yrl	GPS	2018	81	1016	8.45	11.76	6.18
22529	F	Adult	No	GPS	2018	36	1670	38.48	55.69	18.96
					Average (SE)	**52.14**	**979.71**	**20.38 (4.5)**	**27.49 (6.2)**	**12.81 (2.6)**

Table D4. Summer home range estimates (km^2) based on Minimum Convex Polygons (MCP), Kernel Density Estimates (KDE), Local Convex Hull (aLoCoH) methods for 2 male (1 tracked for 2 years) and 6 female black bears (2 tracked for 2 years) collared on the Northern Range, Yellowstone National Park, Wyoming and Montana, 2014-2018. Females were classified as: did not have cubs (No), had cubs of the year (COY), or had yearling cubs (Yrl).

Bear ID	**Sex**	**Age class**	**Cubs**	**Collar type**	**Year**	**Days tracked**	**Number of locations**	**MCP**	**KDE**	**aLoCoH**
22522	M	Sub-adult	No	GPS	2017	50	739	33.65	47.99	17.54
22522	M	Sub-adult	No	GPS	2018	50	744	71.61	89.49	42.47
22530	M	Adult	No	GPS	2018	50	725	978.80	1819.85	326.26
					Average (SE)	**50**	**736**	**361.35 (308.9)**	**652.44 (583.8)**	**128.76 (99)**

Bear ID	**Sex**	**Age class**	**Cubs**	**Collar type**	**Year**	**Days tracked**	**Number of locations**	**MCP**	**KDE**	**aLoCoH**
22523	F	Sub-adult	No	GPS	2017	50	742	115.05	142.77	45.03
22523	F	Sub-adult	No	GPS	2018	50	735	54.91	66.33	19.42
22531	F	Sub-adult	No	GPS	2018	50	2407	89.38	77.05	34.37
22524	F	Adult	No	GPS	2017	50	726	107.70	166.67	71.25
22524	F	Adult	COY	GPS	2018	50	752	142.44	162.07	43.52
22526	F	Adult	Yrl	GPS	2018	50	755	44.75	58.86	29.46
22529	F	Adult	No	GPS	2018	50	2427	61.04	80.78	33.56
22532	F	Adult	No	GPS	2018	50	2328	236.38	216.44	47.32
					Average (SE)	**50**	**1359**	**106.46 (22)**	**121.37 (20.6)**	**40.49 (5.5)**

Table D5. Fall home range estimates (km^2) based on Minimum Convex Polygons (MCP), Kernel Density Estimates (KDE), Local Convex Hull (aLoCoH) methods for 3 male (1 tracked for 2 years) and 6 female black bears (2 tracked for 2 years) collared on the Northern Range, Yellowstone National Park, Wyoming and Montana, 2014-2018. Females were classified as: did not have cubs (No), had cubs of the year (COY), or had yearling cubs (Yrl).

Bear ID	**Sex**	**Age class**	**Cubs**	**Collar type**	**Year**	**Days tracked**	**Number of locations**	**MCP**	**KDE**	**aLoCoH**
22522	M	Sub-adult	No	GPS	2017	67	887	42.13	64.77	12.69
22522	M	Sub-adult	No	GPS	2018	52	774	38.60	45.74	22.69
22517	M	Adult	No	GPS Camera	2014	27	1210	497.48	903.69	91.19
22530	M	Adult	No	GPS	2018	51	742	262.70	566.45	200.07
					Average (SE)	**39.00**	**976.00**	**210.23 (109.2)**	**395.16 (208)**	**81.66 (43.2)**

Bear ID	**Sex**	**Age class**	**Cubs**	**Collar type**	**Year**	**Days tracked**	**Number of locations**	**MCP**	**KDE**	**aLoCoH**
22523	F	Sub-adult	No	GPS	2017	70	1023	106.25	121.40	15.78
22523	F	Sub-adult	No	GPS	2018	54	756	49.60	73.48	10.16
22531	F	Sub-adult	No	GPS	2018	55	2496	69.26	62.67	13.27
22524	F	Adult	No	GPS	2017	52	566	128.62	216.69	22.95
22524	F	Adult	COY	GPS	2018	52	735	79.93	116.76	20.09
22526	F	Adult	Yrl	GPS	2018	50	718	78.67	169.41	45.75
22529	F	Adult	No	GPS	2018	54	2405	87.96	85.80	15.13
22532	F	Adult	No	GPS	2018	54	2575	127.39	221.96	25.38
					Average (SE)	**55.13**	**1409.25**	**90.96 (9.9)**	**133.52 (22.1)**	**21.06 (4)**

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APPENDIX E

DETECTIONS OF BLACK BEARS WITH DIFFERENT SCENT LURES USED AT HAIR SNARE SITES ON YELLOWSTONE’S NORTHERN RANGE

Table E1. Number of detection and unique individual black bears identified at hair snares using one of four scent lures as part of a spatially explicit capture-recapture study, Northern Range, Yellowstone National Park, Wyoming and Montana, 2017–2018. We visited each hair snare once per week from mid-May through mid-July (8 sampling occasions per year) and used one of the four lures during each sampling occasion. The smoky bacon and raspberry doughnut lures were commercial scent lures made by Moultrie Feeders, AL, USA. The blood and fish oil/blood scent lures were composed of rotten cattle blood or a mixture of rotten cow blood and fish oil. We obtained the cattle blood from a local slaughterhouse, and the fish oil was created from ground lake trout (*Salvelinus namaycush*) carcasses supplied by the Yellowstone Lake fish removal program.

Overall	**Lure**	**Detections**	**Individuals**	**Male**	**Female**
	Blood	61	43	14	29
	Fish oil and blood	85	58	22	36
	Raspberry doughnut	31	23	8	15
	Smokey bacon	55	45	19	26

2017	**Lure**	**Detections**	**Individuals**	**Male**	**Female**
	Blood	29	22	10	12
	Fish oil and blood	60	45	17	28
	Raspberry doughnut	20	17	8	9
	Smokey bacon	26	26	10	16

2018	**Lure**	**Detections**	**Individuals**	**Male**	**Female**
	Blood	32	29	8	21
	Fish oil and blood	25	23	7	16
	Raspberry doughnut	11	11	2	9
	Smokey bacon	29	25	12	13